

DISRUPTIVE EFFECTS OF STIMULUS INTENSITY ON TWO VARIATIONS OF A TEMPORAL DISCRIMINATION PROCEDURE

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Previous reports using stimulus intensity changes to disrupt temporal discrimination have shown shifts in the psychophysical curve for time, while studies using other disruptors have shown a flattening of the curve. The current study investigated the impact of increases and decreases in stimulus intensity on temporal discrimination in pigeons, to determine if a flattening of the curve could be extended to this disruptor. The brightness of the sample to be timed was manipulated under two procedural variations, in which the response alternatives were differentiated by color or location. Results showed that all subjects in the color procedure, and one in the location procedure, showed a flattening of the psychophysical curve when they experienced increased stimulus intensity in descending order. No subjects exposed to an ascending order of stimulus intensities, and none of the other subjects in the location procedure, showed any impact of changed stimulus intensity. Minimal disruption was found when test sessions presented decreased stimulus intensity levels in a second series. These results, together with those using other types of disruptors, add to the evidence of a flattening of the psychophysical curve when temporal discrimination is disrupted.

Key words: stimulus intensity, temporal discrimination, stimulus control, bisection procedure, pigeon

In attempts to understand the mechanisms underlying timing abilities, disruptors can be applied to the animal's environment to reveal systematic deviations from accurate timing, which can lead to conclusions regarding the causal variables that contribute to this behavior. Various types of disruptors have been used within the timing literature and have produced divergent results, which are still in need of clarification. This study used increased and decreased intensity of the to-be-timed stimulus to determine its disruptive effects on temporal discrimination when presented in an intermittent fashion.

A symbolic Matching to Sample of Durations procedure (MTSD, Church & Deluty, 1977; Stubbs, 1968) is often used to examine temporal discrimination. The task consists of the presentation of stimuli of varying durations followed by two choice alternatives. The subject is trained to classify these durations as

short and *long* by responding on different response alternatives. The response alternatives may be response levers in different locations (e.g., Church & Deluty, 1977; Location variant), or can be response keys illuminated with different colors, with location randomized (e.g., Stubbs, 1968: Color variant). Color and Location procedural variations have been explored in conjunction with *d*-amphetamine to determine their influence on the disruptive effects on timing (McClure, Saulsgiver & Wynne, 2009b, 2009c; Odum & Ward, 2007), but this comparison has never been made with stimulus intensity as a disruptor.

The data from MTSD procedures are presented in the form of a psychophysical curve for time (Blough, 1996; Church & Deluty, 1977; Stubbs, 1968). Typically, the lateral position of the curve (Point of Subjective Equality: PSE), and the slope of the curve are used to assess the effects of disruptive variables, however, other notable effects occur when performance is disrupted. Blough recommended a measure that quantifies the degree of stimulus control using the accuracy of responding at the endpoints of the psychophysical curve. Recent publications examining temporal discrimination have included this measure of stimulus control (McClure, Saulsgiver & Wynne, 2005, 2009a, 2009b, 2009c; Odum & Ward, 2007; Ward, Barrett, Johnson & Odum, 2009; Ward & Odum, 2005, 2006),

We thank the Associate Editor and reviewers for their helpful comments on a previous version of the manuscript. We also thank Eric Beecher for useful comments on the experimental preparation and laboratory assistance. Kathryn A. Saulsgiver is now at the Substance Abuse Treatment Center, University of Vermont, Burlington, VT, USA.

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doi: 10.1901/jeab.2010.94-57

and have noted its decrement due to the presentation of disruptors.

Excluding pharmacological agents as disruptors, there are two major classes of disruptive agents and the literature suggests that they may have different effects on timing. The first, and the one used in the current study, is the manipulation of the to-be-timed stimulus presented to the animal. For example, the intensity (brightness) of the stimulus to be timed has been manipulated in studies using both rats and pigeons (Kraemer, Brown, & Randall, 1995; Kraemer, Randall, & Brown, 1997; Wilkie, 1987). These studies found that increases in stimulus intensity led to more stimuli being responded to as *long*, which was represented as a shift in the lateral positioning of the psychophysical curve to the left (a decrease in PSE). Decreases in stimulus intensity, on the other hand, led to more responses to the *short* response alternative, which was represented as a lateral shift to the right (an increase in PSE).

The second type of disruptor consists of those in which the motivation of the animal is altered by free-food administration during the session, extinction of previously reinforced trials, prefeed before experimental testing, changing rates of reinforcement, etc. A flattening of the psychophysical curve, caused by decreases in accuracy of classifying temporal intervals, is typically observed when these disruptors are used (Bizo & White, 1994; Killeen, Hall, & Bizo, 1999; Morgan, Killeen, & Fetterman, 1993; Ward & Odum, 2006).

The literature reviewed above suggests that different disruptors may have different effects on the psychophysical curve. Specifically, disruptors that affect motivation to respond flatten it whereas those that modify the to-be-timed stimulus shift it. It is possible that increased stimulus intensity is somehow different from other types of disruptors, or it could be that previous reports using stimulus intensity as a disruptor did not use adequate intensity levels or methodologies to reveal a flattening of the curve. The current study used an intermittent presentation methodology to determine whether increasing and decreasing stimulus intensity across a wide range would have the same flattening effect on the psychophysical curve that other disruptors have produced. Both Location and Color procedural variations were used to determine their role,

if any, in modulating disruption of temporal behavior by stimulus intensity.

METHOD

Subjects

Ten White Carneau pigeons (*Columba livia*) served as subjects. All had previous experimental histories with temporal discrimination and fixed ratio procedures. Half of the subjects had previous experience with *d*-amphetamine administration. At least 12 weeks had elapsed since they last received *d*-amphetamine. They were separated randomly regardless of drug and behavioral history into two procedural groups: Location and Color. The birds were individually housed in a humidity- and temperature-controlled colony room with a 16:8 hr light–dark cycle. Water and grit were continually available in the home cages. Postsession feedings were given when necessary to maintain body weights at 83% of free-feeding levels.

Apparatus

Two standard operant test chambers (Med Associates Inc., St. Albans, VT, USA, Model ENV-007) served in this experiment. The chambers had internal dimensions of $30.5 \times 24.1 \times 29.2$ cm. The doors and opposite side panels consisted of clear polycarbonate. The intelligence panels and back walls were constructed from aluminum. The intelligence panel contained three 2.5-cm diameter circular response keys (Model ENV-123AM) that could be transilluminated with red, green or white light. The three keys were 6.5 cm from the top of the chamber. Each side key was located 2.25 cm from the side walls and the center response key was 6 cm from each side key. The force required to depress a response key was between 0.12 and 0.15 N. Grain could be accessed from a hopper (Model ENV-205M) through a 5.5×6.5 cm rectangular opening that was positioned 13 cm below the center response key and 8.5 cm from both sides of the chamber. A light in the hopper activated whenever grain was available, while all other lights in the chamber were extinguished. On the opposite aluminum wall a 28-V houselight (Model ENV-215M) was placed 1 cm from the top of the chamber and 11.5 cm from the sides. The equipment was contained

in a sound-attenuating chamber (Model ENV-018M) and controlled with Med-PC IV software.

Varying light intensities were presented from a ceiling-mounted lighting frame that held four lights within the sound-attenuating chamber but outside the experimental chamber, which had a ceiling of clear Plexiglas. The lighting frame was located above the back wall of the operant chamber, opposite the intelligence panel, and contained two pairs of lights that faced towards one another at a distance of 3 cm. All lights were covered by translucent plastic diffusers. There were four light intensities. The lowest light intensity ("Dim") was a 28-V 3-W houselight (2 lux at 12 cm). The next intensity "Med-low", was one 28-V 25-W light (689 lux). "Med-bright" consisted of two 28-V 25-W lights (1938 lux). "Bright", the highest intensity, consisted of three 28-V 25-W lights (3875 lux).

Behavioral Training

No key peck training was required and temporal discrimination training began immediately. Five subjects were randomly distributed into each procedural group (Location and Color). Sessions started with a 5-min blackout for both groups. Each trial began with white illumination of the center key; a single response to this key initiated the trial. This initiating response terminated the center-key illumination and was followed immediately by houselight illumination for one of the two training durations: either 2 or 8 s. The durations were chosen randomly on each trial, with the limitations that a duration could not appear more than twice in succession, and that both were presented equally often in a session. Directly following the termination of the houselight, two side response keys were illuminated simultaneously. For the Color group, one alternative was red, the other green. Location of the colors was randomized with the constraint that no color could appear on the same side more than twice in succession. The location of the reinforced response choice was also randomized across sides, with the constraint that the location could not be the same for more than two trials. A single peck on the *short* key was reinforced with 2-s access to grain following a 2-s duration stimulus; a response on the *long* key was reinforced in the same way after an 8-s duration stimulus. The *short* key was red for 3

subjects, and green for the others. For the Location group, both choice alternatives were illuminated red. For 3 subjects in the Location group, the left key was always the *short* key, and so a response on the left key after a 2-s duration was followed by reinforcement. A response on the right key after an 8-s duration was reinforced. For the other 2 subjects, the left and right keys were counterbalanced for short and long. Reinforcement was followed by an intertrial interval (ITI) with an average duration of 10 s, and a range of 1 to 20 s. Incorrect responses led directly to the ITI. Sessions consisted of 96 trials or 50 min, whichever came first.

Once a subject's accuracy in discriminating the training durations was over 80% for five consecutive sessions, intermediate stimulus durations were introduced, along with the training values, in order to generate psychophysical curves. The values of the intermediate duration stimuli were selected to create four equal logarithmic steps between 2 and 8 s (2.6, 3.48, 4.6, and 6.1 s). Sessions consisted of 96 trials or 70 min, whichever came first. Training durations (2 and 8 s) were presented for 48 of the 96 trials, and the four intermediate durations were presented 12 times each. Durations could not appear more than twice in succession in each block of 24 trials. For both procedural groups, correct responses to training durations were reinforced at all times and responses to intermediate durations were never reinforced. The Dim stimulus intensity level was used during training and the introduction of the intermediate stimulus durations for all subjects. Training data were not included in the results, but provided confirmation that performance was stable over 10 sessions before testing began.

Two test series were run. The first followed the training described above and involved temporal discrimination sessions using brighter houselights (Dim baseline test series) interspersed with control sessions, in which the Dim houselight was used. Then, after retraining temporal discrimination using the Bright houselight intensity, a second test series was run in which Bright was the control stimulus and lower intensities were tested (Bright baseline test series). In all test sessions, the full range of houselight durations were used so psychophysical curves could be constructed.

Table 1
Session number and stimulus intensity level presented in each test series.

Session #	Intensity level (Dim baseline test series)		Intensity level (Bright baseline test series)	
	Descending group	Ascending group	Descending group	Ascending group
1, 2	Dim (Control)	Dim (Control)	Bright (Control)	Bright (Control)
3	Bright	Med-Low	Med-Bright	Dim
4, 5	Dim (Control)	Dim (Control)	Bright (Control)	Bright (Control)
6	Med-Bright	Med-Bright	Med-Low	Med-Low
7, 8	Dim (Control)	Dim (Control)	Bright (Control)	Bright (Control)
9	Med-Low	Bright	Dim	Med-Bright

Note. The order of stimulus intensity presentations is shown for both Descending and Ascending groups during both the Dim baseline test series and Bright baseline test series. This table represents one complete cycle of all stimulus intensity presentations. A total of three were given.

Testing

Dim baseline test series. After training with the Dim intensity, three higher stimulus intensities were tested, each presented separately for an entire session. Every third day was a test day in which a different intensity level was presented (Med-low, Med-bright, or Bright), and the Dim stimulus intensity was used in the intervening control sessions. Three out of five birds in each procedural group were exposed to the Bright test value first and each subsequent intensity level was dimmer (Descending group). The remaining birds were exposed to the Med-low intensity first, and subsequent levels were more intense (Ascending group). The sequence in Table 1 represents one cycle of stimulus intensity presentations. All subjects experienced a total of three such cycles. Only data from the nine test sessions, and the immediately preceding control sessions (18 sessions in all) were analyzed.

Bright baseline test series. Immediately following the Dim baseline test series, training began with the highest houselight intensity (Bright). Training continued for 10–13 consecutive sessions for all subjects. This was adequate for subjects to reach stability and habituate to the Bright stimulus intensity level. Subjects were then tested on three lower stimulus intensity levels (Dim, Med-low, Med-bright) with the Bright stimulus intensity serving as control. Stimulus intensity levels were again presented in descending or ascending order. The sequence of intensities is given in Table 1 and as before, only data from the test sessions and immediately preceding control sessions were analyzed.

Data Analysis

The data analyzed came from each test session and the preceding control session for

both test series. For each session the proportion of responses to the long response alternative was plotted as a function of stimulus duration. The resultant psychophysical curves were analyzed by fitting a cumulative Gaussian function with four free parameters, following Blough (1996). The equation fit was the integral of:

$$f(t) = a + \frac{b}{\sqrt{2\pi}\sigma} e^{-\left(\frac{(t-\mu)^2}{2\sigma^2}\right)} \tag{1}$$

where $f(t)$ is the proportion of long responses at a given duration t of a stimulus, a is the minimum of the function, b is the range, μ is the mean (Point of Subjective Equality, PSE), and σ is the standard deviation (slope). All curve fitting was performed using Microsoft Excel® (see McClure et al., 2005).

Mixed model ANOVAs with repeated measures were carried out on all parameters derived from Equation 1. Within-subjects factors were Intensity level (Dim, Med-low, Med-bright, and Bright) and Session (three sessions/intensity level), and the between-subject factors were Group (Color, Location) and Order (Ascending, Descending). Analyses for the two test series were run separately. Dependent on significant main effects, post hoc Scheffé tests were run to determine which intensity levels were different from baseline. An alpha level of .05 was adopted for all statistical analyses.

RESULTS

The psychophysical curves for the Color group are shown in Figure 1. Results from Dim and Bright baseline test series are shown within the same panels. For the Dim and

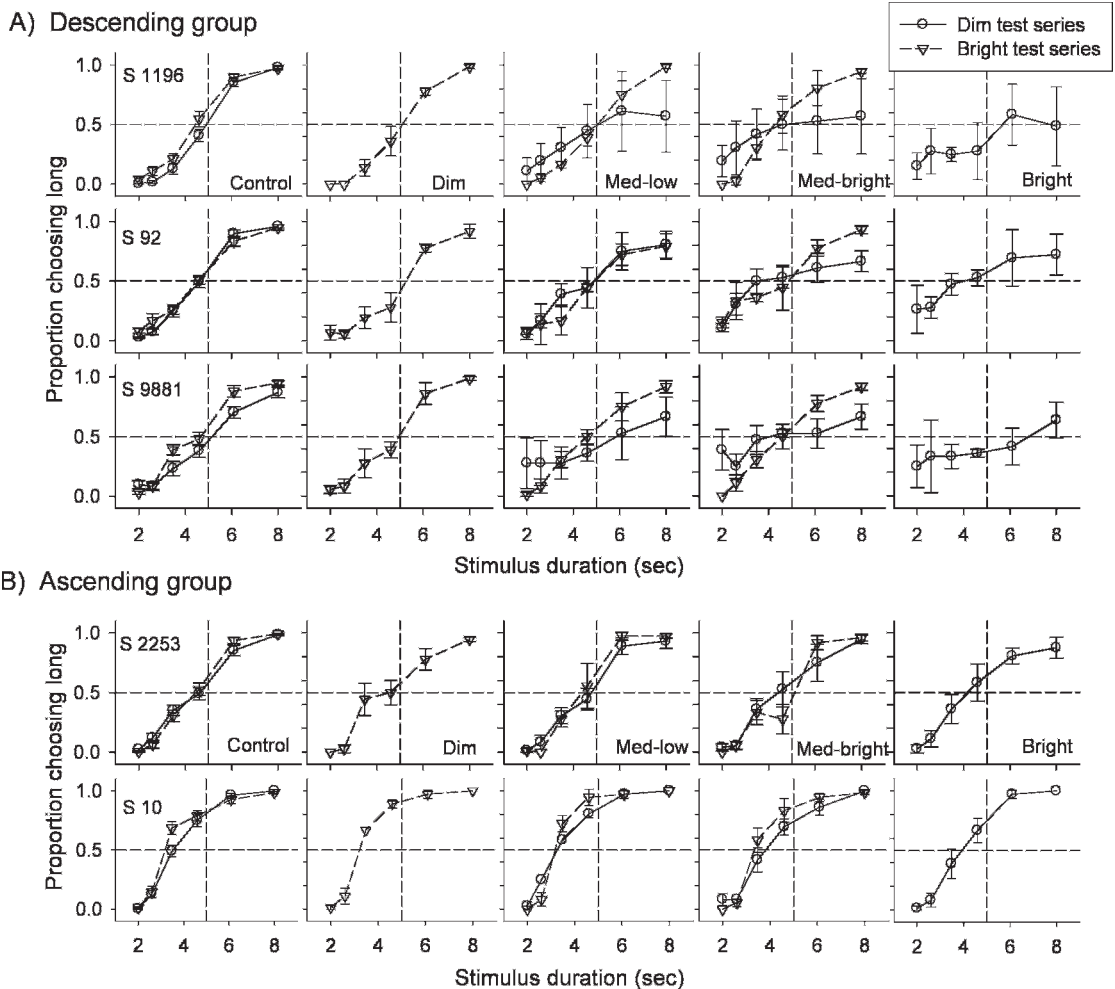


Fig. 1. Proportion of choices of the long response alternative as a function of stimulus duration for the Color group. A) Subjects in the Descending order group, and B) subjects in the Ascending order group. The leftmost column shows control data for both Dim and Bright baseline test series. The next four columns are the psychophysical curves for each of the stimulus intensity presentations. Data paths are averages of three intensity presentations. Circles represent data from Dim baseline test series. The triangles represent data from the Bright baseline test series. Control days were those sessions immediately preceding testing sessions. Error bars represent standard error.

Bright intensities, only one curve is shown because the control intensity level was not presented in a test session. The order of presentation of the test stimuli for the Descending group goes from right to left in the figure (Bright, Med-Bright, and Med-Low), and for the Ascending group, the order goes from left to right (Med-Low, Med-Bright, and Bright). Changes in brightness disrupted temporal discrimination for subjects in the Descending order group during the Dim baseline series (Figure 1A), in that the psychophysical curves were flattened at nearly all

intensity levels (Med-low, Med-bright, and Bright). Subjects in the Ascending order group showed no disruption (Figure 1B). During the Bright baseline test series, presentation of lower stimulus intensities (Dim, Med-low, Med-bright) produced seemingly no disruption in temporal discrimination for either the Ascending or Descending groups, except for slight decreases in accuracy at the extremes for Subject 92 in the Color, Descending group.

The psychophysical curves for the Location group are shown in Figure 2. Less disruption

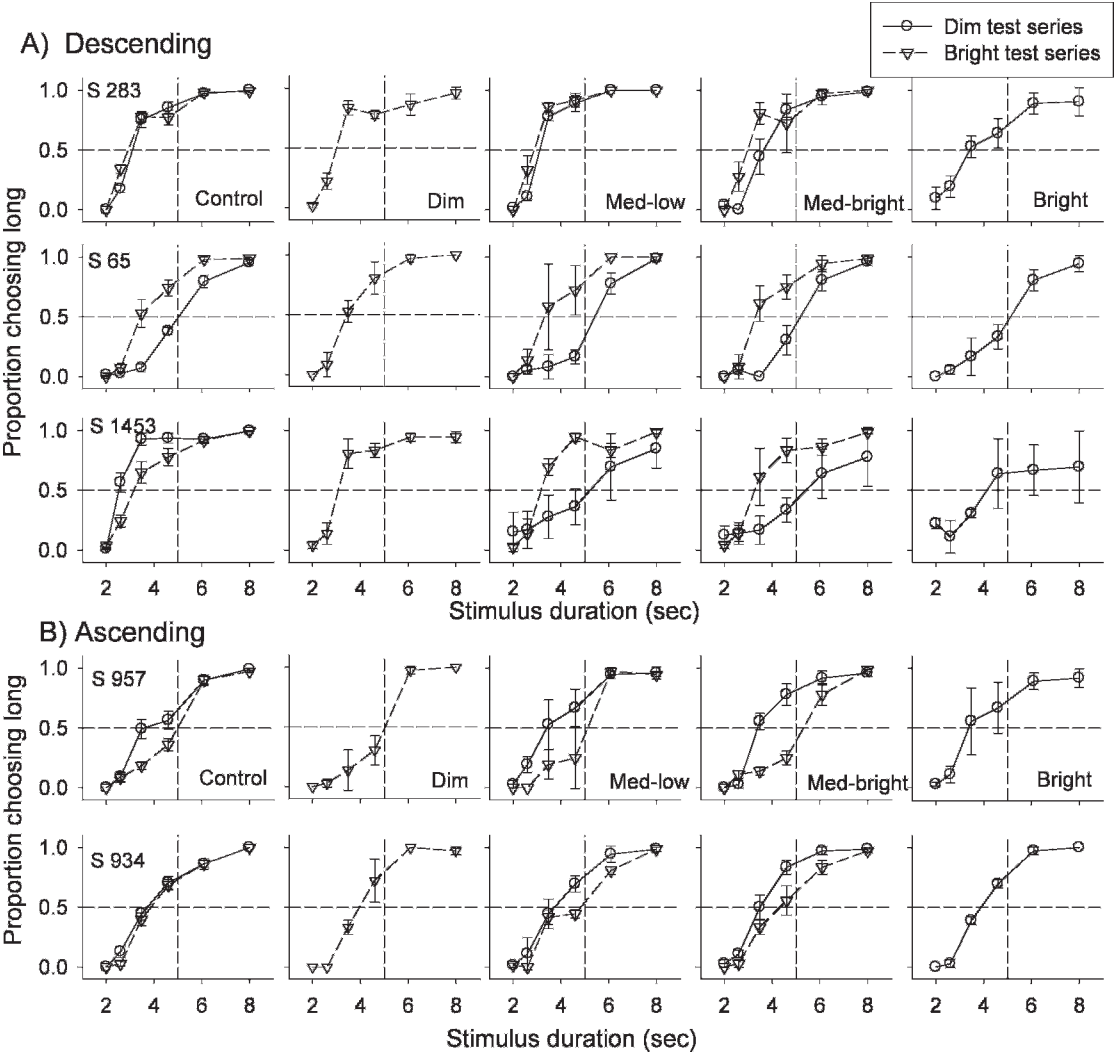


Fig. 2. Proportion of choices of the long response alternative as a function of stimulus duration for the Location group for A) Subjects in the Descending order group, and B) Ascending order group. Other details similar to Figure 1.

was seen in this group as compared to the Color group shown in Figure 1. During the Dim baseline test series, 1 of 3 subjects in the Descending group (Subject 1453) showed a flattening of the psychophysical curve, much like that seen in the Color, Descending group. No other changes in the psychophysical curves were evident, and no disruption during the Bright baseline test series was found.

Psychophysical curves were fitted using Equation 1, yielding parameters Range, PSE, Sd, and Min (see also McClure *et al.*, 2005; 2009a; 2009b; 2009c). Range served as a measure of stimulus control and accuracy of

classifying intervals. Range values for Color and Location groups are shown in Figure 3 as a function of Intensity condition. For the Color group, Range values appeared to decrease for all 3 subjects in the Descending order group (Figure 3A), which was evident in the psychophysical curves shown in Figure 1A. This was confirmed by statistical tests, which showed that during the Dim baseline test series, a main effect of Intensity was found for Range, with differences occurring between Dim (control) and Med-Low and Bright stimulus intensity levels during testing sessions. Range values did not appear to change

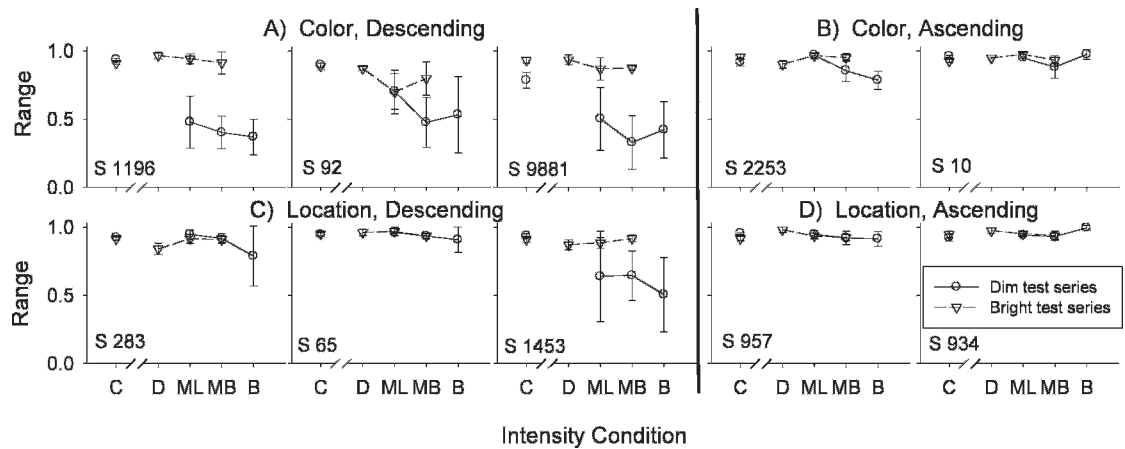


Fig. 3. Fitted values of the Range parameter as a function of intensity condition for A) Color, Descending group, B) Color, Ascending group, C) Location, Descending group, and D) Location, Ascending group. Circles show results from the Dim baseline test series and triangles show results from the Bright baseline test series. Control data points represent averages of the nine sessions that preceded stimulus intensity test sessions. Data points for each stimulus intensity level represent averages of three presentations of each intensity level. Error bars are standard errors of the means. Color groups subjects are shown in the top row, while Location subjects are shown in the bottom row.

in the Color, Ascending group (Figure 3B). For the Location group, no change in Range was found for 4 of the 5 subjects (Figure 3C and D), while Subject 1453 showed a decrease in Range at all stimulus intensity levels. Overall, 3 out of 5 subjects in the Color group (Figure 3A and B) showed decreased Range values due to increased stimulus intensity as compared to 1 of 5 subjects in the Location group (Figure 3C and D), which was confirmed by a significant main effect of Group. Differences were also found in Range between Descending and Ascending groups. Four out of six subjects in the Descending group

(Figure 3A and C) showed disruption at all stimulus intensity levels during the Dim baseline test series compared to 0 out of 4 subjects in the Ascending order group (Figure 3B and D). This result is confirmed by a significant interaction of Intensity by Order, as well as a significant effect of Order. All significant main effects and interactions for all derived parameters are given for the Dim baseline testing series in Table 2.

Visual inspection of Range values during the Bright baseline test series showed that decreased stimulus intensity levels during testing produced very subtle changes, if any at all, in

Table 2

F values of mixed model ANOVAs with repeated measures during Dim baseline test series for parameters Range, Sd, Min, and PSE.

Parameter	Intensity (df = 3, 18)	Intensity by Order (df = 3, 18)	Group (df = 1, 6)	Order (df = 1, 6)	Scheffe's test (df = 18)
Range	7.6 (0.56)**	4.2 (0.41)*	6.4 (0.52)*	13.6 (0.70)**	4.7* (D – MB) 4.9 * (D – B)
Sd	-	-	-	-	-
Min	-	-	-	7.8 (0.57)*	-
PSE	-	-	-	-	-

Note. Degrees of freedom (df) are shown in parentheses following the main effects or interactions. Only statistically significant effects are shown. Intensity level and Session were within-subject factors, while Group and Order were between-subject factors. Numbers in parentheses following F values are partial eta-squared values indicating effect size. A post hoc Scheffé's test was run if significance was found for a main effect. T values are shown for Scheffé's test followed by the conditions that were different from one another (Dim (D), Med-low (ML), Med-bright (MB), and Bright (B)).

* p < .05
** p < .01

Table 3

F values of mixed model ANOVAs with repeated measures during Bright baseline test series for parameters Range, Sd, Min, and PSE.

Parameter	Intensity (df = 3, 18)	Intensity by Group by Order (df = 3, 18)	Intensity by Session (df = 2, 12)	Intensity by Ses by Ord by Group (df = 1, 6)	Group (df = 1, 6)	Group by Order (df = 1, 6)
Range	-	3.2 (0.35)*	-	-	-	-
Sd	-	-	-	-	-	-
Min	-	-	-	-	-	-
PSE	-	-	2.8 (0.32)*	2.7 (0.31)*	-	21.7 (0.78)**

Note. All details are similar to Table 2. No differences were found using Scheffé’s test for main effects.

* $p < .05$

** $p < .01$

temporal discrimination. A significant Intensity by Group by Order interaction was found during the Bright baseline test series and was due to Subject 92 in the Color, Descending group (Figure 3A), which showed disruption by decreased intensity levels. Significant main effects and interactions for all parameters for the Bright baseline test series can be found in Table 3.

PSE values derived from Equation 1 for Color and Location groups are shown in Figure 4 as a function of stimulus intensity level. During the Dim baseline test series, changes in PSE were typically accompanied by decreases in the Range parameter, as was seen for all subjects in the Color, Descending group (Figure 3A). Effects of stimulus intensity on PSE were not consistent across subjects. For the Color, Descending group (Figure 4A), Subject 1196 showed an increase of PSE, while Subject 92 showed a decrease. Subjects in the Color, Ascending (Figure 4B), Location, Descending (Figure 4C) and Location, Ascending (Figure 4D) groups showed very little change in PSE values, and larger changes were marked by high variability. Statistical analyses identified no significant main effects or interactions during the Dim baseline test series for PSE (largest $F = 2.4$) as seen in Table 2.

During the Bright baseline test series for PSE, differences were found between sessions at the Med-low and Med-bright stimulus intensity levels, which were confirmed by an Intensity by Session interaction. Differences were also found between sessions at the Intensity levels Med-low and Med-bright for the Color, Descending group, which was represented by an Intensity by Session by Order by Group interaction. Averaged PSE values during the Bright baseline test series

across groups and orders were also found to be different (Color, Descending = 4.8 s; Color, Ascending = 3.9 s; Location, Descending = 3.2 s; and Location, Ascending = 4.7 s), as evidenced by a Group by Order interaction.

Of the two remaining derived parameters (Minimum and Standard deviation), which were not shown here, only Minimum showed a significant effect of Order during the Dim baseline test series. Four out of six subjects in the Descending order group showed slight increases in Min, as compared to zero out of four subjects in the Ascending order group, which is visible in Figures 1 and 2.

DISCUSSION

In the current study, disruption of temporal discrimination in the Color, Descending group was shown in the form of a decrease in Range values during the Dim baseline test series, while only 1 out of 3 subjects in the Location, Descending group showed similar disruption of temporal behavior. Descending order was always required for disruption to occur. During the Bright baseline test series, decreased stimulus intensity levels still led to some disruption in behavior, specifically changes in Range and PSE values, though to a much smaller degree than in the Dim baseline test series. These results showed that disruption by decreased stimulus intensity was minimal compared to increased stimulus intensity. Disruption was always in the form of a flattening of the psychophysical curve.

Previous reports have demonstrated a shift of the psychophysical curve to the left when increased stimulus intensity was presented in nonhuman animals, and a shift of the curve to the right during decreased stimulus intensity

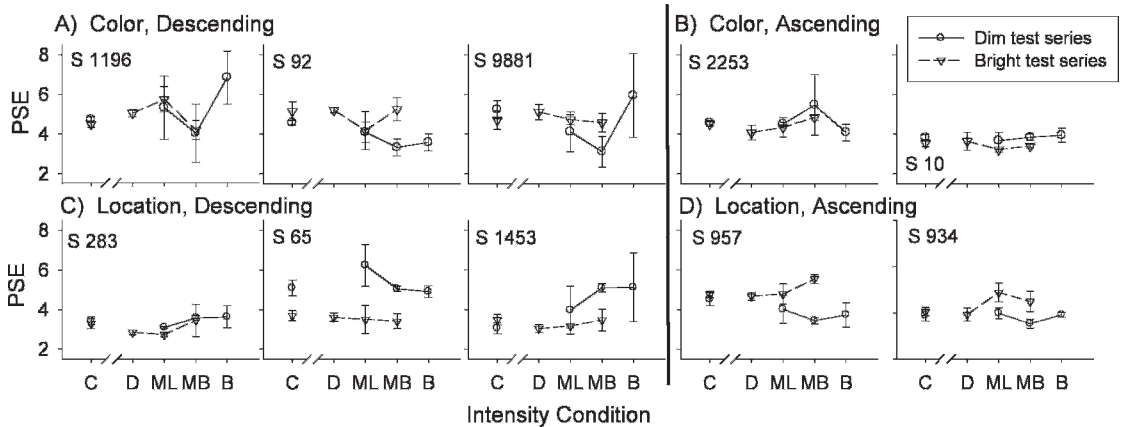


Fig. 4. Fitted values of the PSE parameter as a function of intensity condition for A) Color, Descending group, B) Color, Ascending group, C) Location, Descending group, and D) Location, Ascending group. Other details similar to Figure 3.

presentation (Kraemer et al., 1995; Kraemer et al., 1997; Wilkie, 1987). Leftward and rightward shifts have also been observed after administration of dopaminergic agonists and antagonists respectively (Bizot, 1997; Cevik, 2003, Exp. 2; Chiang, Al-Ruwaitea, Mobini, Ho, Bradshaw, & Szabadi, 2000, Exp. 1; Maricq & Church, 1983; Maricq, Roberts & Church, 1981; Meck, 1983, 1986).

Our results, however, did not reveal lateral shifts of the curve, but rather, a flattening of the psychophysical curve and decrease in accuracy of temporal discrimination. This effect has been shown in previous reports that used disruptors influencing the motivation to respond, such as pre-session feeding or extinction of previously reinforced trials (Bizo & White, 1994; Killeen et al., 1999; Morgan et al., 1993; Ward & Odum, 2006). Our results also agree with a number of other studies that have shown a similar result due to the administration of pharmacological agents (Cevik, 2003, Exp. 1; Chiang et al., 2000, Exp. 2; Harper, Bizo & Peters, 2006, Exp. 2; McClure et al., 2005, 2009b, 2009c; Odum, Lieving & Schaal, 2002; Odum & Ward, 2007; Sanchez-Castillo, Chavez, Miranda & Velazquez-Martinez, 2007; Santi, Coppa & Ross, 2001; Stanford & Santi, 1998; Stubbs & Thomas, 1974; Ward et al., 2009; Ward & Odum, 2005). These studies, in conjunction with the current data set, reveal that a diverse array of agents produce disruption of temporal accuracy and stimulus control. This result is robust in the literature,

whereas a specific effect on timing abilities in the form of shifts in PSE are not so consistently demonstrated.

The differences between our results and those of Wilkie (1987), Kraemer et al. (1995), and Kraemer et al. (1997) could be due to a number of procedural variations. For example, Kraemer et al. (1995) and Kraemer et al. (1997) first trained their subjects on the brightest intensity, and all testing was done with dimmer stimuli. Initially, we used only the Dim stimulus for training in all subjects, and testing sessions consisted of more intense lights to which the animals had never been exposed. By the time our subjects were exposed to a condition similar to that described in Kraemer et al. (1995) and Kraemer et al. (1997), which occurred during the Bright baseline test series, they had already experienced all stimulus intensity levels with relatively high frequency. Wilkie (1987) gave pigeons training on both bright and dim stimuli before testing, although order of presentation was not stated in the report. Bright and dim lights were tested within the same sessions, while the current study tested effects of stimulus intensity levels across sessions. Another relevant factor is that Wilkie and Kraemer et al. (1995) and Kraemer et al. (1997) used a narrower range of intensities than in the present study, which suggests that a larger range of intensity levels is required for the decrease in temporal accuracy shown in the present results. Finally, it should be noted

that in those studies, there is evidence of slight to moderate decreases in accuracy during increased or decreased stimulus intensity presentation, though none of those studies analyzed changes in Range values, and were mainly concerned with changes in the lateral position of the curve (PSE).

We also found differences in the extent of disruption across several conditions in the present study, which are most likely the result of habituation effects. Only when brightness increased abruptly (i.e., Dim baseline test series and Descending order) was disruption of temporal discrimination observed reliably. Disruption was not reliably found when brightness was increased progressively (Ascending series), arguably promoting habituation. Similarly, very little disruption was observed in the Bright baseline test series, which was the second condition to be conducted for all subjects. Prior exposure to the first condition meant that all subjects already had extensive experience with the full range of brightness levels used in the experiment. Habituation effects are further indicated in a comparison of disruptive effects across successive test sessions with a given intensity level. These comparisons confirmed that when disruption did occur reliably, it was significantly less in the subjects' second and third exposures to a given brightness than in their first exposure.

Color and Location Variants

Color and Location variations had never been tested with the use of stimulus intensity as a disruptor of temporal discrimination, and procedure proved to be important in the modulation of disruptive effects. The Location version of this task has been shown to be more quickly acquired than the Color version (Chatlosh & Wasserman, 1987; McClure *et al.*, 2009b; Odum & Ward, 2007), which was confirmed in the present report, as subjects in the Location group reached stability almost three times as fast as those in the Color group (Color: 90–130 sessions; Location: 33–98 sessions). It was also found that average Range values during control sessions were significantly higher in the Location group as compared to the Color group during the Dim baseline testing series, $t(88) = -2.22$, $p < .05$, indicating greater stimulus control for the Location group.

The reason for differences in acquisition and accuracy is unknown. Some have suggested that the Location version of the task may be less complicated and hence easier to learn than the Color version because the animal develops mediating behavior, which aids in accurate timing. In the Location variant, animals can use their own behavior to indicate which alternative is correct based on the duration of the sample stimulus (Fetterman, Killeen & Hall, 1998; Machado & Keen, 2003). The Color variation has not been shown to lead to mediating behavior occurring during the sample presentation (Fetterman *et al.*, 1998). The location cues, which are available for the Location version of this task, may make acquisition occur more quickly and could provide a way in which disruptive effects are minimized. Mediating behavior may also explain why the Location group exhibited higher accuracy, which is indicative of superior stimulus control, and may have contributed to the resistance to disruption in that group. It has been shown previously that greater stimulus control on a procedure leads to less disruption by pharmacological agents (Katz, 1982; Laties, 1972, 1975; Laties, Wood & Rees, 1981; Odum *et al.*, 2002; Odum & Ward, 2007; Saulsgiver, McClure & Wynne, 2007; Ward & Odum, 2005). More studies should be conducted to determine the role of mediating behavior in temporal discrimination and its development when these procedural variations are used.

Assessing Temporal Disruption

The explanation of the different results for the Color and Location versions of the task proposed above raises questions about how changes in the psychophysical curve under disruption should be interpreted. It is commonly assumed that temporal discrimination is being selectively altered, however, there are a number of possible processes being affected by disruptors, such as motivation to respond, motoric activity, color discrimination, latency to respond to choice alternatives, attention to the sample, etc. Any of these variables could be affected but would be interpreted as an effect on timing mechanisms. Some reports have even argued that disruptors affect stimulus control more generally in this procedure by altering nontiming processes, rather than specific temporal effects (McClure *et al.*,

2005; 2009b; 2009c; Odum et al., 2002; Odum & Ward, 2007; Rapp & Robbins, 1976; Santi et al., 2001; Stanford & Santi, 1998; Ward and Odum, 2005).

The possibility that nontiming processes are disrupted applies to the current study as we only showed clear disruption in the Color group, but generally not in the Location group. A potential explanation is that increased stimulus intensity could have disrupted color discrimination, thus causing a differential result between procedural groups. Another possibility is that the Location procedure is not as sensitive to disruptors based on the evidence discussed above regarding mediating behavior and superior stimulus control. Until proper tests have separated these aspects of the procedure, we cannot say with confidence that this is an effect of temporal abilities.

Conclusions

The current results and previous literature show that a wide range of disruptors have the same effect on temporal discrimination in the form of a flattening of the psychophysical curve and decrease in Range values. Therefore, different types of disruptors do not appear to lead to different forms of disruption of temporal discrimination. We have also shown that different outcomes found with Color and Location response alternatives reveal how slight variations in procedure on a temporal discrimination task may modulate the effect of a manipulation, which has also been demonstrated with *d*-amphetamine as a disruptor (McClure et al., 2009c).

There is a mounting body of literature that fails to support lateral shifts of the psychophysical curve when temporal discrimination is disrupted. This demands further empirical inquiry to determine why these differential results exist and the conditions under which disruptive agents lead to a decrease in Range values as opposed to a change in the lateral position of the curve. Also, conceptualizations and theories of timing must account for a number of diverse disruptors, since the evidence shows that many agents serve a similar disruptive function. Future research should work to characterize and explain the disruptive effects of agents on temporal discrimination, taking into consideration procedural variations used and their potentially modulating

effects. It should also address the relationship between temporal and nontemporal behavior to determine if the controlling mechanisms are the same.

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Received: March 4, 2009

Final Acceptance: April 12, 2010