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Context Effects in Temporal Differentiation: Some Data and a Model

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We examined whether temporal context influences how animals produce a time interval. Six pigeons pecked one key to start an interval and then another key to end the interval. Reinforcement followed whenever the interval duration fell within a range of values signaled by the keylight colors. During Phase 1, keylight colors S1 and L1, intermixed across trials, signaled the ranges (0.5-1.5 s) and (1.5- 4.5 s), respectively. During Phase 2, colors S2 and L2 signaled the ranges (1.5-4.5 s) and (4.5-13.5 s), respectively. We asked whether the intervals produced in the presence of L1 and S2, stimuli signalling the same range, varied with their temporal context, short in Phase 1, long in Phase 2. The results showed that a) the intervals produced in the presence of the different keylight colors accorded with the main properties of temporal differentiation, including Weber's law, b) the L1 intervals had slightly higher means than the S2 intervals, a weak contrast effect, c) the L1 intervals also had higher variability than the S2 intervals. An extension of the learning-to-time model to temporal differentiation tasks reproduced some of the major features of the data but left unanswered how context might change the model parameters.

Since the early 1900s, evidence has accumulated that animals can learn to discriminate stimuli based on their durations, and much has been learned about the key properties of such discriminations (for reviews see, e.g., Gallistel, 1990; Richelle & Lejeune, 1980; Church, 2004; Wearden & Lejeune, 2006; Ferster & Skinner, 1957; Skinner, 1938; Stubbs, 1968; Vieira de Castro, Carvalho, Kroger, & Machado, 2013).

A still poorly understood question is whether animals discriminate temporal stimuli based on their absolute or relative durations. To illustrate, in the widely used temporal bisection task, rats readily learn to press a left lever following a 2-s stimulus and a right lever following an 8-s stimulus (e.g., Church & Deluty, 1977). However, we do not know whether they learned the absolute mapping "2 s→left, 8 s→right" or the relative mapping "short→left, long→right" (see Carvalho & Machado, 2012; Carvalho, Machado, & Tonneau, in press; Carvalho, Machado, & Vasconcelos, submitted; Church & Deluty, 1977, Hulse & Kline, 1993; Maia & Machado, 2008; Zentall, Weaver, & Clement, 2004).

Relational responding is a clear instance of a more general phenomenon, the effect of context on timing or, more specifically, of the *temporal context* of a stimulus in the timing of that stimulus. To study context effects, researchers have used mostly stimulus discrimination tasks such as the bisection task described above, the temporal generalization task (e.g., Church & Gibbon, 1982), the fixed-interval reinforcement schedule (e.g., Dews, 1970), and the peak procedure (Catania, 1970; Roberts, 1981). They have used significantly less temporal differentiation tasks, that is, tasks in which the subject has to produce intervals by either maintaining an operandum pressed for a

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given period of time (e.g., differential reinforcement of response duration, Platt, Kuch, & Bitgood, 1973), or by pressing and releasing an operandum to start the interval and later pressing and releasing it again to end the interval (Zeiler, Davis, & DeCasper, 1980). In these tasks, only responses that meet a temporal criterion are reinforced (e.g., Lejeune & Wearden, 2006; Zeiler, Scott, & Hoyert, 1987). Other examples of temporally differentiated tasks include the differential reinforcement of low rate schedule, the differential reinforcement of response latency, the fixed-minimum interval schedule (Mechner & Guevrekian, 1962; Hobson & Newman, 1981) and the differential reinforcement of other behavior (Lejeune & Wearden, 2006; Richelle & Lejeune, 1980).

The present paper explores temporal context effects in a temporal differentiation task. To assess these effects, it is important to review first the three main properties of temporal differentiation because, according to previous research, their presence indicates that the produced intervals stem from a timing process. First, the mean of the produced intervals increases with the criterion specified by the reinforcement schedule, although it remains unclear whether the increase follows a linear (Jasselette, Lejeune, & Wearden, 1990; Lejeune, Cornet, Ferreira, & Wearden, 1998; Lejeune, Huynen, & Ferrara, 2000; Zeiler, 1985; Zeiler & Hoyert, 1989) or a power function (Catania, 1970; Kuch, 1974; Lejeune & Jasselette, 1986; Lejeune & Richelle, 1982; Platt et al., 1973; Zeiler, 1983; Zeiler, Davis, & DeCasper, 1980; Zeiler & Hoyert, 1989). Second, the standard deviation of the produced intervals increases linearly with their mean, another expression of Weber's law for timing. Third, the coefficient of variation of produced intervals remains approximately constant (e.g., Lejeune & Wearden, 2006).

To our knowledge, only one study has examined whether temporal context affects the subjects' reproduction of a time interval. Jazayeri and Shadlen (2010) hypothesized that human subjects perceive the duration of an interval differently under different contexts and, therefore, they should reproduce the interval differently under these contexts. To test the hypothesis, human adults saw several intervals signaled by flashing lights on a computer screen and then reproduced them by pressing a button. Reinforcement occurred when the reproduced interval fell within a temporal window or range centered on the sample. The width of the range was proportional to the sample, and, hence, accommodated Weber's law. Using a range of reinforced values also allowed the reproduced intervals to vary and thereby reveal any potential context effects.

The authors divided the samples into three ranges, *short*, from 494 ms to 847 ms, *intermediate*, from 671 ms to 1023 ms, and *long*, from 847 ms to 1200 ms. The intermediate range shared its shortest samples with the short range and its longest samples with the long range; the 847-ms sample was common to the three ranges. Each range occurred in a different phase and therefore it defined the temporal context of each sample. At issue was whether the participants reproduced the shared intervals differently across contexts.

The results revealed two main features. First, the reproduced intervals increased linearly with the sample intervals, and their coefficients of variation remained roughly constant (≈ 0.1) across contexts. Second, the reproduced intervals were biased towards the average of the current context or range. This assimilation effect was stronger in the long than the short ranges, and, within a range, stronger following the long than the

short samples. It was particularly clear following the common 847-ms sample: The reproduced interval was shorter than 847 ms in the *short context*, not significantly different from 847 ms in the *intermediate context*, and greater than 847 ms in the *long context*.

In the present study, we extended to animals the search for contextual timing in differentiation tasks. To that end, we simplified Jazayeri and Shadlen's (2010) procedure and adapted it to a production task for pigeons. The result was a fixed-minimum interval schedule (Mechner & Guevrekian, 1962; see also Hobson & Newman, 1981; Nevin & Berryman, 1963) with a limited hold. We trained pigeons to peck one key to start an interval and then to peck another key to end the interval. The time between the two pecks defined the produced interval. The color on the two keys signaled the range of the produced intervals that would yield food. We created three ranges, a short range (0.5 to 1.5 s), an intermediate range (1.5 to 4.5 s), and a long range (4.5 to 13.5 s). The ranges, with lower and upper limits geometrically spaced, seemed sufficiently wide to allow the pigeons to express potential context effects.

We then paired the intermediate and short ranges in one experimental phase and the intermediate and long ranges in another experimental phase. Thus, in one phase, the pigeons produced intervals appropriate to the intermediate and short ranges; in another phase, they produced intervals appropriate to the intermediate and long ranges. We reasoned that by producing intervals appropriate to the same range in a short context (intermediate and short) and a long context (intermediate and long) the pigeons might reveal the influence of context on temporal differentiation.

We anticipated two types of contextual effects, each expressed by the mean of the produced intervals appropriate to the intermediate, common range. As in Jazayeri and Shadlen's (2010) study, the mean could shift *towards* the (geometric?; Church & Deluty, 1977) mean of the entire context, an assimilation effect consistent with adaptation level theory (e.g., Thomas, 1993). In this case the mean would be smaller in the short than the long context. Or the mean could shift *away* from the mean of the entire context, a contrast effect. In this case, the mean should be greater in the short than the long context. These two effects do not exhaust the possibilities, for contextual timing may be expressed by differences in parameters other than the mean (e.g., standard deviation), or it may be entirely absent from this temporal differentiation task.

The study of temporal differentiation in general—and of contextual effects on temporal differentiation in particular—is important also for theoretical reasons. How animals space their responses, wait, or, more generally, regulate the temporal properties of their actions, may be as important to adaptation as how they perceive, discriminate or estimate stimulus durations. As Zeiler et al. (1987, p. 192) remarked, "temporal differentiation is particularly interesting, because it involves the coordination of action with time, a feature that would appear to have substantial generality in behavior occurring both outside of and within the laboratory". However, most theories and models of timing, including the scalar expectancy theory (SET; e.g., Gibbon, 1991) and the learning-to-time model (LeT; Machado, 1997; Machado, Malheiro, & Erlhagen, 2009), have dealt significantly more with temporal discrimination than temporal differentiation. Moreover, any evidence of contextual timing effects would be both

intriguing and challenging because most current timing models do not seem capable of predicting them, at least when duration is under the subject's control[1].

Hence, another goal of the present study was to extend the LeT model to temporal differentiation tasks. In the final section of the study, we describe how animals might learn to produce intervals and then compare the model's predictions with the data. The theoretical exercise may pave the way to timing models with greater generality and depth.

To summarize, in the empirical part of this study we ask whether pigeons can learn to produce two time intervals in the same session, each signaled by a different cue, and, in the affirmative, whether temporal context affects their performance. In the theoretical part of the study, we propose a model of how animals might learn to respond according to temporal specifications.

Method

Subjects

Six pigeons participated in the experiment. They had previous training with a similar production task that served as a pilot study to identify reasonable parameter values for the final experiment. The pigeons were maintained at 85-90% of their free-feeding weight, with grit and water continuously available in their home cages. The colony room was under a 13h:11h light-dark cycle, with lights on at 8:00 a.m.

Apparatus

The experiment used three Med Associates® operant chambers for pigeons. Each chamber was enclosed in an outer box equipped with a fan to circulate air and mask extraneous noises. In each chamber, a 7.5-W houselight located in the back panel provided general illumination. In the front panel, a 6 x 5 cm feeder opening, 3.5 cm above the floor and centered horizontally along the wall, provided access to mixed grain. When the feeder was activated, a 7.5-W light illuminated the grain. The front panel also included three keys, each 2.5 cm in diameter, arranged in a row, 9 cm apart, center-to-center, and 18.5 cm above the floor. The left key was not used in the present experiment. The center key could be illuminated with red, green, yellow and blue hues, and the right key could be illuminated with the same hues and with a vertical white bar on a dark background. A personal computer programmed in Visual Basic 2008 and running the Whisker software (Cardinal & Aitken, 2010) controlled the events and recorded the data with a resolution of approximately 1 ms.

Procedure

Throughout the experiment, the pigeons learned to produce interval durations that fell within one of three ranges, 0.5 to 1.5 s (short), 1.5 to 4.5 s (intermediate), and 4.5 to 13.5 s (long). Each trial started with the houselight turned on and the right key illuminated with the vertical bar. A peck at the right key turned off the keylight, illuminated the right and center keys with the same keylight color, and started the interval. The keylight color signaled the operative range during the trial, that is, the range of reinforceable intervals.

[1] In temporal discrimination tasks, LeT but not SET predicts at least some forms of contextual timing in double bisection tasks (e.g., Arantes & Machado, 2008; Machado & Arantes, 2006; Machado & Keen, 1999; Machado & Oliveira, 2009; Machado & Pata, 2005; Oliveira & Machado, 2008, 2009; Vieira de Castro & Machado, 2012; Vieira de Castro, Machado, & Tomanari, 2013). In simple bisection tasks, the evidence for relational effects remains controversial (see Church & Deluty, 1977; Carvalho & Machado, 2012; Carvalho et al., 2015; Maia & Machado, 2008; Zentall et al., 2004). For a generalization-gradient based account of simple and double bisection tasks, see Carvalho et al. (submitted).

To illustrate, in the presence of red, the produced interval would be reinforced provided it was longer than 0.5 s and shorter than 1.5 s. During the interval, the pigeon could, but did not have to, peck the right key. These pecks produced no scheduled consequences. A peck at the center key turned all lights off and ended the interval. If the interval was within the operative range, the pigeon gained access to grain. To minimize extra-session feeding, we adjusted the duration of reinforcement for each pigeon during the first training sessions; final values ranged from 2 to 6 s. After reinforcement, a 10-s intertrial interval (ITI), with all lights off, followed. If the produced interval was outside the operative range, either too short or too long, the ITI followed immediately.

We paired the three ranges to form two temporal contexts. The short context included the short (0.5-1.5 s) and intermediate (1.5-4.5 s) ranges; the long context included the long (4.5-13.5 s) and intermediate (1.5-4.5 s) ranges. Critically, the intermediate range, common to both contexts, was relatively long in the short context, but relatively short in the long context. Hence, to distinguish the ranges, and in particular to distinguish the intermediate range in the short context from the intermediate range in the long context, henceforth we refer to them as S1-L1 for the short context, and S2-L2 for the long context, with S1 < L1 = S2 < L2.

The four keylight colors signaled the four ranges as follows (see Table 1). For half of the pigeons, the mapping was S1 = Green, L1 = Red (short context), and S2 = Yellow, L2 = Blue (long context); for the other pigeons, the mapping was S1 = Blue, L1 = Yellow (short context), and S2 = Red, L2 = Green (long context). Thus, Red and Yellow always signaled the two equal ranges, L1 and S2.

Training in the two contexts proceeded separately along two phases, with half of the pigeons learning the short context in Phase 1 and the long context in Phase 2, and the other half learning them in the opposite order. Training with each context proceeded across three conditions (see Table 1). In the first, all trials (N = 60) involved the intermediate range of 1.5-4.5 s (L1 or S2). In the second, all trials (N = 60) involved the other range of the same context (S1 if L1, L2 if S2). Finally, in the third, a randomly chosen half of the trials (N = 60) involved the intermediate range and the other half of the trials (N = 60) involved the other range. Training continued for a minimum of five (Conditions 1 and 2) or 10 (Condition 3) sessions and until the median and the relative frequency distribution of produced intervals seemed stable by visual inspection.

Performance on each trial consisted of a three-link chain, “peck the right key with a vertical bar”, “wait in the presence of the colored lights”, and “peck the center key”. To maintain the initial link of the chain, on a few trials of each session, reinforcement followed immediately the peck at the right key with a vertical bar. Each session began with one of these immediate-reinforcement trials. In each of the first two sessions with a new range (first and second conditions in Table 1) there were four additional immediate-reinforcement trials randomly intermixed with the regular trials.

If during training with a new range most produced intervals fell outside the operative range for several consecutive sessions, we relaxed the range limits appropriately. For example, during training with the short range of 0.5-1.5 s, if most produced intervals were longer than 1.5 s, we increased the upper limit of the range for a few sessions and then gradually brought it back to 1.5 s across successive sessions. In addition, when most trials ended in extinction, we attempted to maintain the initial link of the chain by increasing the number of immediate-reinforcement trials. These adjustments occurred only during the first two conditions of each phase. When the range limits returned to their standard values, training continued until the pigeon met the stability criterion and completed the minimum number of sessions mentioned above.

Table 1
Sequence of Training. Red, Green, Yellow and Blue stand for the keylight colors that signaled the operative, reinforced range (in seconds).

	Pigeons	
	P463, P536, P748	P501, P665, P948
Phase 1		
Condition 1	Red: 1.5-4.5	Red: 1.5-4.5

	Green: 0.5-1.5	Green: 4.5-13.5
Condition 2	Red: 1.5-4.5 and Green: 0.5-1.5	Red: 1.5-4.5 and Green: 4.5-13.5
Condition 3		
Phase 2		
Condition 1	Yellow: 1.5-4.5	Yellow: 1.5-4.5
Condition 2	Blue: 4.5-13.5	Blue: 0.5-1.5
Condition 3	Yellow: 1.5-4.5 and Blue: 4.5-13.5	Yellow: 1.5-4.5 and Blue: 0.5-1.5

Results

We focus the analysis on the last three sessions of each phase, when two ranges occurred in the same session. During these sessions, each pigeon produced 180 intervals for each range. A preliminary analysis of these intervals revealed a few extreme long values, which strongly affected statistics such as the standard deviation. Hence, for each range, we removed the largest eight intervals (< 5%) and based all subsequent analysis on the remaining 172 trials.

To determine whether the intervals produced in the presence of each discriminative stimulus accorded with the key properties of temporal differentiation, Figure 1 shows three statistics of these intervals, the means (μ), standard deviations (σ), and coefficients of variation (γ = σ/μ). The top panel plots the means against the lower limit of each range. For all pigeons, the mean interval increased linearly with the range (all $r^2 \geq 0.99$), and the least-squares regression line had a slope close to 1 (M = 1.1, range: 0.98-1.25). For four pigeons, the slope did not differ significantly from 1 (P463: $p = 0.11$; P536: $p = 0.16$; P748: $p = 0.79$; P665: $p = 0.98$ based on t-test); for the other two pigeons, the slope (1.13 and 1.25) was significantly greater than 1 (P501: $p < 0.01$; P948: $p = 0.02$). The intercepts were slightly greater than 0 (M = 0.33 s, range: 0.02-0.76).

The middle panel in Figure 1 shows that the standard deviations increased linearly with the mean ($r^2 \geq 0.91$). The regression lines had slopes ranging from 0.15 to 0.27 (M = 0.19) and intercepts ranging from -0.05 to 0.12 (M = 0.09 s). All slopes differed significantly from 0 (P463: $p = 0.04$; P536: $p < 0.01$; P748: $p = 0.04$; P501: $p < 0.01$; P665: $p < 0.01$; P948: $p < 0.01$).

The bottom panel in Figure 1 shows that the coefficients of variation remained roughly constant across the three ranges. The regression lines had slopes close to 0 (M = -0.01, range: -0.02-0.01, P463: $p = 0.41$; P536: $p = 0.90$; P748: $p = 0.75$; P501: $p = 0.29$; P665: $p = 0.83$; P948: $p = 0.63$). The intercepts ranged from 0.17 to 0.30 (M = 0.22).

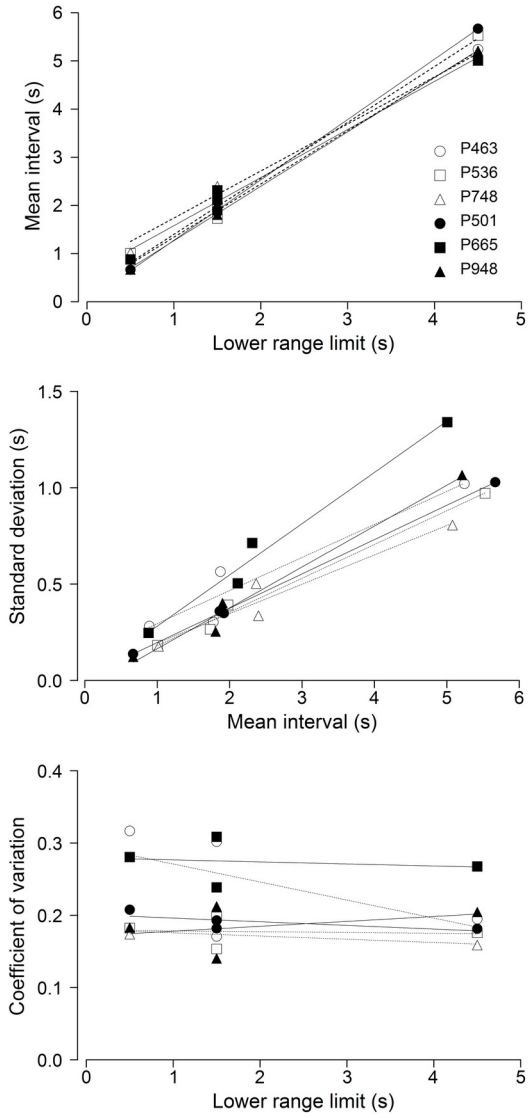

Figure 1. The symbols show the mean of the produced intervals for each range as a function of the lower limit of the range (top), the standard deviation of the produced intervals as a function of the mean (middle), and the coefficient of variation of the produced intervals for each range as a function of the lower limit of the range (bottom). The lines show the best-fitting regression lines.

We conclude that pigeons learned to produce different intervals each signaled by a different stimulus. Moreover, the statistical properties of these intervals accorded with the key properties of temporal differentiation.

The statistics for the intermediate range displayed in Figure 1 suggest that any effect of context, if present at all, was small. To appreciate it better, Figure 2 shows the frequency distributions of the intervals produced in the presence of each discriminative stimulus. The x-axis is logarithmic to spread the curves apart and facilitate their analysis. The three ranges yielded differently located distributions, with S1 producing the shortest, L2 the longest, and L1 and S2 intermediate intervals. Consider the two middle curves of each panel, L1 and S2, corresponding to the intermediate, common

range in the short and long contexts, respectively. Two effects seem to be present: Most L1 curves seem to be slightly to the right and have a greater spread than the S2 curves. Statistical analyses corroborated these impressions. First, the means for L1 (short context, M = 2.06 s) tended to be slightly greater than the means for S2 (long context, M = 1.95 s): paired t-test $t(5) = 2.72$, $p = 0.04$. Although the effect size was large (Cohen's $d = 1.11$), its 95% CI [0.04, 2.12] suggests that the true effect size could range from the very small to the very large. Second, the standard deviations for L1 (short context, M = 0.49 s) tended to be larger than for S2 (long context, M = 0.34 s), paired t-test $t(5) = 3.99$,

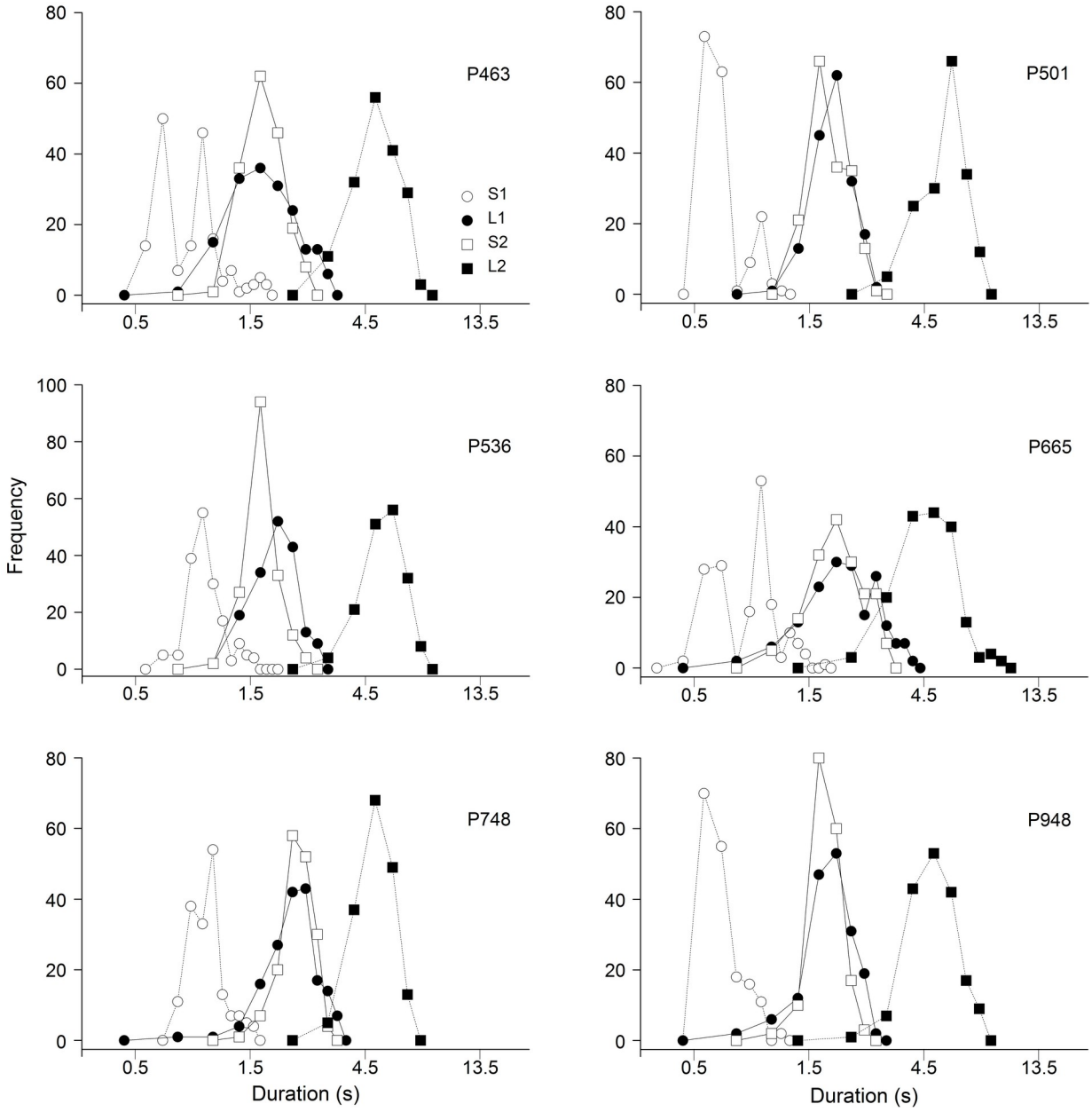

Figure 2. Frequency distributions of the intervals produced in the presence of the four discriminative stimuli. S1 and L1 define the short context, and S2 and L2 define the long context. The stimuli signal the following reinforced ranges: S1: 0.5-1.5, L1 and S2: 1.5-4.5, and L2: 4.5-13.5

p = 0.01, d = 1.63, 95% CI [0.34, 2.86]. Third, the coefficients of variation for L1 (short context, M = 0.24 s) tended to be larger than for S2 (long context, M = 0.17 s): paired t-test $t(5)$ = 3.33, p = 0.02, d = 1.36, 95% CI [0.19, 2.48]. As for the mean, the large confidence intervals for the effect sizes of the standard deviation and coefficient of variation suggest that the true effect sizes could range from the small to the large. In any case, timing of the intermediate range seemed to be relatively more precise in the long context than the short context.

The frequency distributions for the intermediate and long ranges adopted the expected Gaussian-like shape. In contrast, the distributions for the short range were either Gaussian-like (P536 and P748), or mixtures of Gaussians, with multiple modes (P463, P501, and P665) or right tails (P948).

Figure 3 shows how well the Gaussian density function fit the data. We divided each set of absolute frequency values displayed in Figure 2 by the total number of trials, 172, to change them into proportions and then divided the proportions by the bin size (0.1 for S1, 0.3 for L1 and S2, or 0.9 for L2) to obtain density functions. Then, for each pigeon and data set (e.g., L1), we computed the mean and standard deviation parameters that minimized the mean square error between predicted and obtained values. Finally, to facilitate the visual inspection of the results, the densities for the intermediate (L1 and S2) and long (L2) ranges were scaled up, the former multiplied by 3 and the latter by 9 so that, if the means and standard deviations remained proportional, the three sets of curves would be equally spread apart and have similar heights and widths.

The curves fit well the two data sets from the intermediate range, with ω^2 averaging 0.95 for L1 (short context) and 0.96 for S2 (long context). Consistent with the former analyses of means and standard deviations, the densities for L1 tended to be slightly to the right of the densities for S2 (except for P748), and have larger spreads (except P501). That is, for both location and spread, five pigeons showed the same effect, but one pigeon did not. The statistical analyses of the best-fitting means and standard deviations yielded similar results: The difference in means (L1 = 2.02 s vs. S2 = 1.90 s) was almost significant, $t(5) = 2.39$, $p = 0.06$, and the difference in standard deviations (L1 = 0.48 s vs. S2 = 0.32 s) was significant, $t(5) = 3.79$, $p = 0.01$, $d = 1.55$, 95% CI [0.29, 2.75]. We conclude that the context manipulation produced a weak contrast effect, with the mean of L1 about 7% larger than the mean of S2. It also affected the precision of the produced intervals, with the standard deviation of L1 about 45% larger than that of S2.

The Gaussian functions also fit the long-range data well, with ω^2 averaging 0.98. In contrast, they did not fit well all data sets from the short range (average $\omega^2 = 0.73$). We return to this finding below.

The pigeons were relatively efficient at collecting the available reinforcers, but their efficiency varied with the range. Figure 4 (left panel) shows the proportion of reinforced trials for each range. Obtained reinforcers decreased with the range, from $M = 0.98$ at S1, 0.87 at L1, 0.89 at S2, and 0.75 at L2. A paired t-test for the intermediate, common range was not significant, $t(5) = 0.64$, $p = 0.55$, 95% CI for the mean difference [-0.06, 0.04]. However, the overall proportion of reinforced trials in the short context (L1 and S1, $M = 0.93$) was greater than in the long context (S2 and L2, $M = 0.82$), $t(5) = 6.36$, $p < 0.01$, $d = 2.60$, 95% CI [0.83, 4.33]. We conclude that the pigeons were more efficient in the short than the long context, not because their efficiency varied between the two instances of the intermediate range, but because they were more efficient in the short (S1) than the long (L2) range.

The right panel of Figure 4 further compares the obtained proportions of reinforced trials with the corresponding values computed from the best-fitting Gaussian functions (i.e., area under the curve and between the range limits). Although reasonably close, the predicted values underestimated slightly the obtained values; the pigeons were more efficient than predicted by the Gaussian fits.

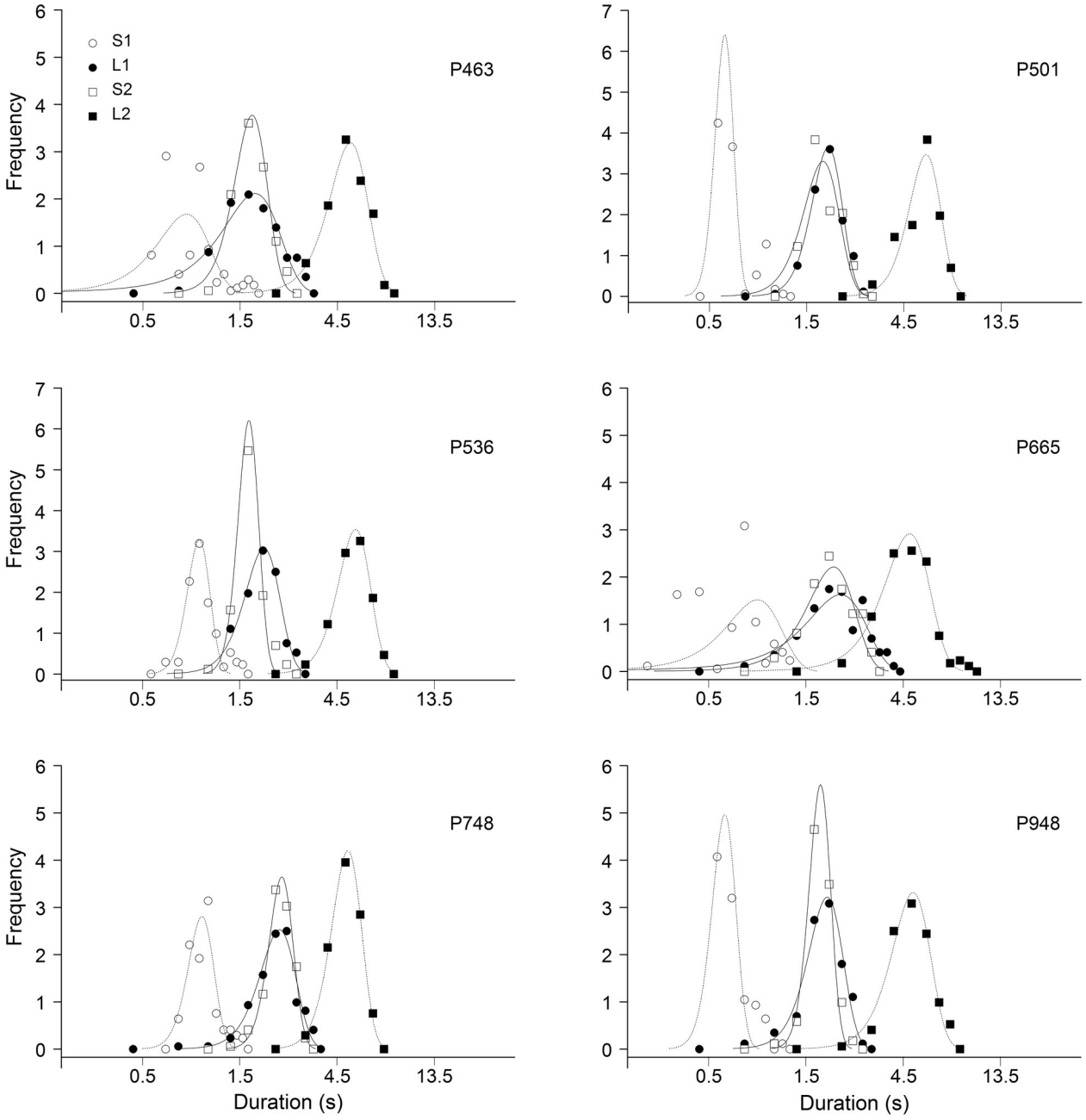

Figure 3. Obtained densities (symbols) and best-fitting Gaussian functions (lines) of the intervals produced in the presence of the four discriminative stimuli. S1 and L1 define the short context, and S2 and L2 define the long context. The stimuli signal the following reinforced ranges: S1: 0.5-1.5, L1 and S2: 1.5-4.5, and L2: 4.5-13.5. Logarithmic x-axis.

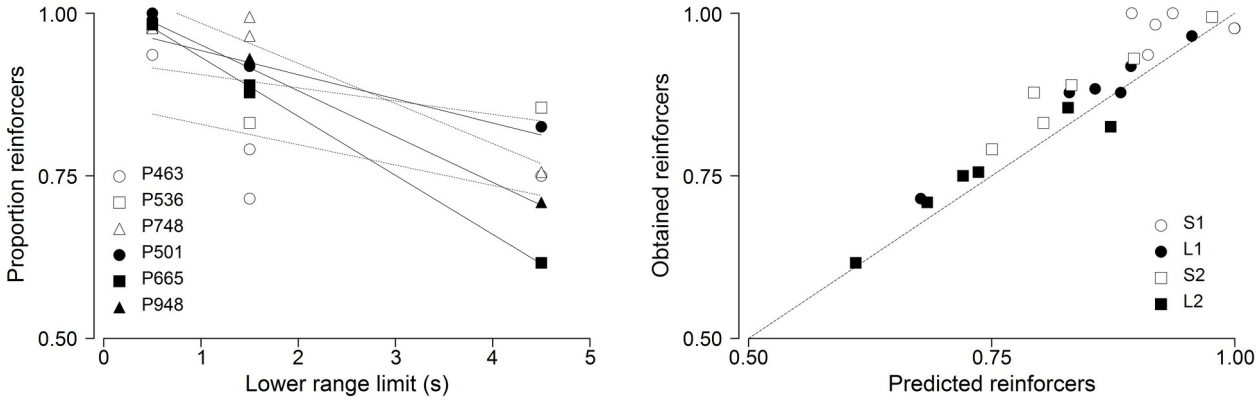

Figure 4. Left: Proportion of obtained reinforcers as a function of the lower limit of each range and best-fitting regression lines. Right: Proportion of obtained reinforcers as a function of the

Discussion

Pigeons received food for producing different intervals of time in the presence of two pairs of distinctive stimuli, (S1, L1) and (S2, L2). One member of each pair (L1 and S2) signaled a common range of reinforced intervals, from 1.5 to 4.5 s. The other member of each pair signaled a shorter range (S1, from 0.5 to 1.5 s) or a longer range (L2, from 4.5 to 13.5 s). We asked whether the pigeons could learn the task and whether the different temporal contexts of L1 and S2 would affect the duration of the intervals produced in their presence. In what follows, we answer these questions and then describe how the LeT model may account for temporal differentiation.

Across two experimental phases, the pigeons effectively learned to produce the pairs of intervals signaled by the discriminative stimuli, intervals following S1 shorter than following L1, and intervals following S2 shorter than following L2. These intervals accorded globally with the key properties of temporal differentiation, for their means increased linearly with the lower limit of the ranges, their standard deviations increased linearly with their means, and their coefficient of variation remained approximately constant. These results are consistent with previous studies on temporal differentiation procedures (Hobson & Newman, 1981; Jasselette et al., 1990; Lejeune et al., 1990; Lejeune et al., 2000; Lejeune & Jasselette, 1986; Platt, 1979; Zeiler, 1985; Zeiler & Hoyert, 1989). Our study adds to previous findings on temporal differentiation the fact that pigeons can learn two temporal differentiations simultaneously.

The distribution of the intervals produced in the presence of L1 and S2 differed slightly in location and more appreciably in spread. Specifically, they were longer and more variable in the short context than the long context. The difference in the means is consistent with a contrast effect, but we must be cautious in interpreting it, for the difference was small, was obtained with only six pigeons, and the confidence interval for the effect size was wide, revealing substantial uncertainty about the true magnitude of the context manipulation. The difference in standard deviations, though, was larger, and

it suggests that temporal differentiation was less variable in the long than the short context.

What factors might explain these effects? One factor may be the difference in the proportion of reinforced trials or, more generally, the difference in reinforcement rates between the two contexts. The reinforcement proportions in the presence of L1 and S2 did not differ, but in the presence of S1 and L1 combined (short context) were higher than in the presence of S2 and L2 combined (long context). According to some timing models and studies (e.g., Killeen and Fetterman's behavioral theory of timing, 1988), higher overall reinforcement rates correlate with higher speeds and higher accuracies of the internal clock. However, this effect is the opposite of the effect obtained in the present experiment, for the context with lower reinforcement rate yielded the smaller variability in temporal differentiation.

If the difference in reinforcement rates cannot explain the differences in the standard deviation, it may help to explain the small difference in the mean of the L1 and S2 intervals. Lower overall reinforcement rates may weaken the first links of the chain "peck the right key, wait, and peck the center key" and thereby shorten the waiting period. Machado, Costa and Maia (2009) observed a similar effect with a numeric analog of the current schedule. In their study, pigeons had to peck one key at least N times before a peck on another key yielded food. The produced number of pecks on the first key—the run length—corresponds to the produced interval in the present study. In extinction, the pigeons emitted the same distribution of run lengths as during reinforcement, but some pigeons also produced a large number of runs of length zero (i.e., they pecked the second key immediately). If runs of length 0 are functionally analogous to shorter waiting periods, then both would increase when reinforcement rate decreases. In the present study, shorter waiting periods in the 'long context' would reduce the mean of the produced intervals in S2.

Alternatively, lower overall reinforcement rates may increase resistance to extinction, an effect akin to the partial-reinforcement-extinction effect (see Capaldi, 1966, 1967). In this case, early responses could remain stronger in S2 than in L1 and account for the lower mean of produced intervals during S2. We return to this hypothesis below.

The Gaussian density function described the shape of the intermediate- and long-range distributions, and of half of the short-range distributions. The remaining short-range distributions had multiple modes that suggest mixtures of distributions. These mixtures do not seem to be due to some kind of interaction between the S1 and L1 performances because they occurred also during training with the short range exclusively (i.e., before we combined the short and intermediate ranges in the same session; see Table 1). In addition, they do not seem to be due to failures of stimulus discrimination. If in the presence of S1 a pigeon occasionally produced an interval appropriate to L1, the resulting distribution would be bimodal, but the second mode would fall within the range of intervals produced in the presence of L1. However, as Figure 2 shows, the second mode did not fall inside the L1 distribution. Perhaps different topographies of moving from the right to the center key, or even of pecking the center key, each with a different speed, could underlie the mixture. We suggest yet another hypothesis below, a hypothesis suggested by the LeT model.

The Learning-to-Time (LeT) Model

As Figure 5 shows, LeT assumes that three processes underlie the temporal regulation of behavior, the serial activation of a set of behavioral states, the modification, through reinforcement and extinction, of a set of links connecting the states to the operant response, and the decision rule regarding the emission of the operant response itself. To extend the model, we assume that the peck on the right key (the time marker) activates the first state in the series. This state remains active for a random interval, τ, at the end of which the animal pecks the center key (ending the interval) with a probability equal to the strength of the link connecting the state with the operant response. If we designate by W(1) the strength of the link from state 1 to the response, then the decision rule states that the subject responds with probability p_1 = W(1). If the response is reinforced, W(1) increases by the amount $\Delta W(1) = \beta[1 - W(1)]$, with $0 < \beta < 1$ a reinforcement parameter; if the response is not reinforced W(1) decreases by the amount $\Delta W(1) = -\alpha W(1)$, with $0 < \alpha < 1$ an extinction parameter. If the waiting period does not end, state $n = 2$ becomes active (and state $n = 1$ becomes inactive), and the process described above repeats. That is, after τ more seconds, with probability p_2 = W(2) the waiting period ends and W(2) changes according to the linear rules mentioned above; with probability 1 - p_2, the waiting period continues with the activation of the third state for another τ seconds.

The model assumes that the residence time in each state, τ, is a Gaussian random variable (mean μ_τ and standard deviation σ_τ) sampled at trial onset. Thus, the residence time of each state remains the same within trials but varies randomly between trials. Note that in the LeT model for temporal discrimination tasks, the Gaussian random variable is not the residence time τ but its reciprocal, the speed of activation of the behavioral states, usually denoted by λ (Machado et al., 2009). We changed the random variable because initial simulations with λ showed that the model generated distributions of produced intervals that were asymmetric, with right tails, similar to inverse-Gaussian or lognormal distributions, in contrast with the Gaussian-like data displayed in Figure 3 or reported in previous temporal differentiation studies (e.g., Figure 15, Mechner & Latranyi, 1963; Figure 2, Nevin & Berryman, 1963). Hence, temporal differentiation and discrimination tasks entail different random variables for the state dynamics, state residence time and speed of activation, respectively.

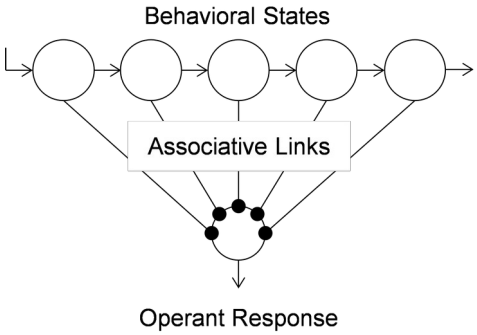

Figure 5. Structure of the learning-to-time (LeT) model. The response that initiates the interval activates a set of behavioral states serially. Each state is linked with the operant response that ends the interval, and the strength of the link equals the probability of emitting that response while the corresponding state is active. When a response is emitted, the link from the active state changes with the outcome, reinforcement or extinction.

To understand the model's predictions–in particular, how the links change across trials–consider the short range with limits t_0 = 0.5 s and t_1 = 1.5 s. During training, the states that are active mostly before t_0 see their links decrease because the responses they occasion are extinguished. The first state that is active at t_0 with a relatively high probability sees its link strengthened because the responses it occasions are reinforced. When the link of a state reaches a high value, say 0.8, that state, when active, occasions a response with that same (high) probability, and that response, by ending the trial, prevents the activation of subsequent states and any changes in their links. At the end of training, the very first states have links close to 0, and one or two states have links so strong that a response is almost certain to occur when one of them is active. According to the model, then, temporal differentiation is mostly about learning to suppress early responses via extinction of the links from the early states. Other authors have conceived of temporal differentiation in similar ways (e.g., Richelle & Lejeune, 1980).

To obtain the model's predictions for the present experiment, we initialized the link strengths W(n) with random numbers between 0 and 1 and then, using the same set of parameters, simulated 800 trials for each of the three ranges. On each trial, the model produced an interval within or without the operative range, and then updated the links according to the trial outcome, reinforcement or extinction. Next, we analyzed the data from the last 180 trials in the same way as we analyzed the pigeon data. Finally, to obtain more stable estimates, we averaged the results from 100 simulations.

Figure 6 shows two sets of results, each obtained with a slightly different set of parameters. With μ_τ = 0.5 s, σ_τ = 0.075 s, $\beta = 0.02$, and α = 0.16 (left panel), the model produced Gaussian-like functions for the intermediate and long ranges, with means closer to the lower than the upper range limit, and a bimodal distribution for the shortest range, with the lower mode at the left. The average proportion of reinforced trials decreased with the range (0.95, 0.91, and 0.78). With μ_τ = 0.3 s, σ_τ = 0.03 s, $\beta = 0.04$, and α = 0.20 (right panel), the model produced similar results but for the shortest range the lower mode was at the right. Again, the proportion of reinforced trials decreased with the range (0.96, 0.88, and 0.71).

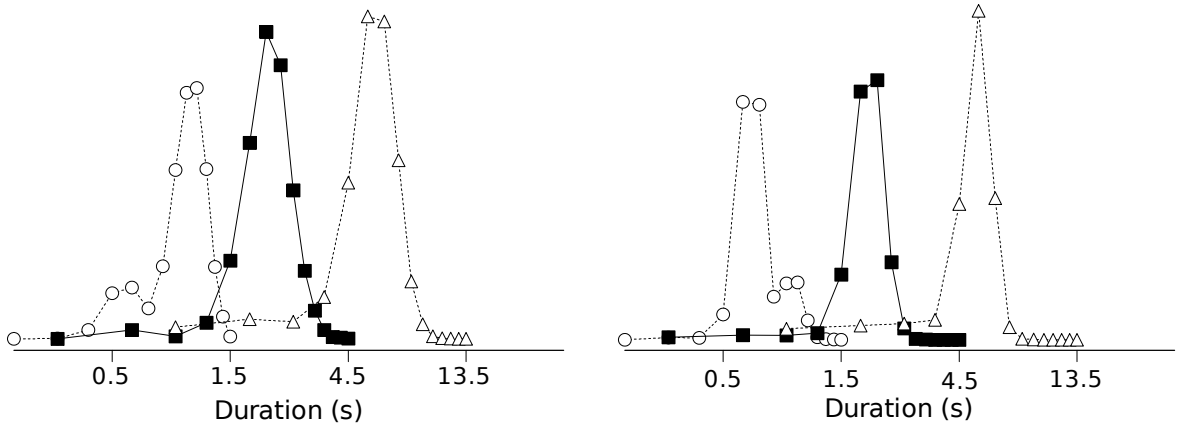

Figure 6. Simulation results of the LeT model. In in each panel, the left, middle, and right curves show the density function of the intervals produced when the reinforced ranges were 0.5-1.5, 1.5-4.5, and 4.5-13.5, respectively. Left: μ_τ = 0.5 s, σ_τ = 0.075 s, $\beta = 0.02$, and α = 0.16. Right: μ_τ = 0.3 s, σ_τ = 0.03 s, $\beta = 0.04$, and α = 0.20.

These two sets of results reproduce some of the key features of the pigeons' behavior, namely, Gaussian-like curves for the two longest ranges, with their center closer to the lower than the upper range limit, multimodal curves for the short range, and a decreasing proportion of reinforced trials across the three ranges.

Two-mode distributions occur when the mean residence time (e.g., μ_τ = 0.5 s or μ_τ = 0.3 s) is close to the range's lower limit and a significant fraction of the range (e.g., 1/3). Because responses occur at the end of the residence time in a state, the responses occasioned by two successive states will occur on the average μ_τ-s apart; hence the two distinct modes. For the intermediate and longest ranges, μ_τ is significantly lower than the ranges' lower limits.

The model assumes no interaction between the two discriminations of each context. Hence, without parameter changes, it predicts the same average results for the intermediate range. However, if the parameters are allowed to change, the model can produce results similar to the pigeons' data provided the long context has a higher relative effect of extinction over reinforcement (α/β) and a lower coefficient of variation of residence times (σ_τ/μ_τ) than the short context. In this case, the curves for S2 will be to the left of, and have smaller spreads than, the curves for L1, the observed contrast effect.

Figure 7 illustrates these effects with model fits to two data sets. We chose the data from pigeons P463 and P536 to illustrate both the main effects of context on the distributions of the intermediate range, and the different types of distributions for the short range, multi- and single-mode. Because the study is exploratory, we settled for parameters that yielded reasonable (by visual inspection) rather than the best statistical fits.

The two panels show that with smaller coefficients of variation (see figure caption for the parameter values) the model produces S2 distributions narrower than L1 distributions. Because the moments a state becomes active vary less with smaller coefficients of variation (σ_τ/μ_τ), the response occasioned by any state or set of states also will vary less with smaller coefficients of variation. Although the model provides a mechanism to explain how a smaller coefficient of variation of residence times narrows the distributions of produced intervals, it does not explain why the coefficients of variation should be smaller in the long than the short context.

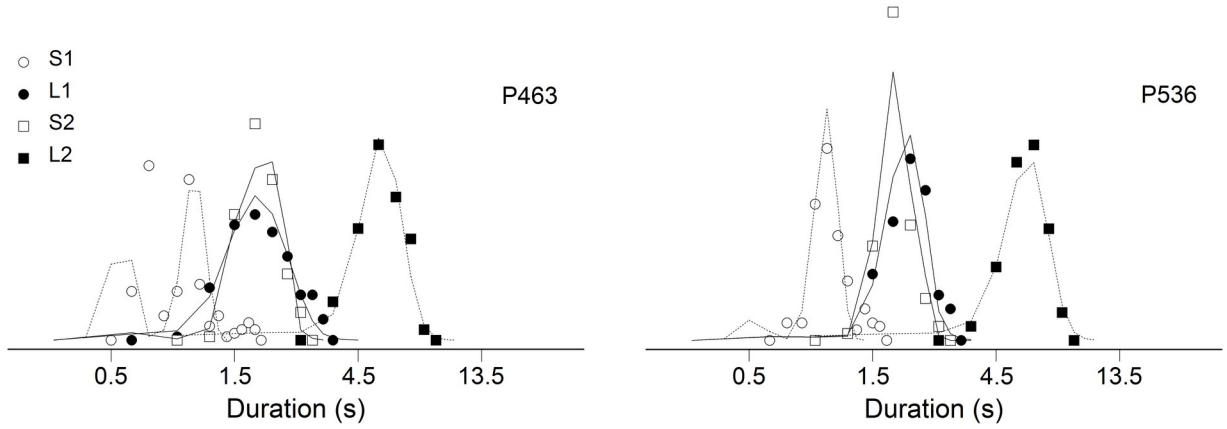

Figure 7. The symbols show the relative frequencies of the produced intervals for two pigeons, and the curves show the simulation results of the LeT model with the following parameter values (μ_τ, σ_τ, α, β): Left, S1 = (0.5, 0.05, 0.10, 0.04), L1 = (0.5, 0.1, 0.10, 0.08), S2 = (0.5, 0.05, 0.10, 0.08), and L2 = (0.5, 0.075, 0.20, 0.05). Right: S1 = (0.475, 0.0475, 0.20, 0.04), L1 = (0.4, 0.048, 0.20, 0.04), S2 = (0.4, 0.032, 0.053, 0.04), and L2 = (0.45, 0.0675, 0.22, 0.02).

On the other hand, the right panel shows that a smaller ratio of α/β produces S2 distributions to the left of L1 distributions. The reason for the effect is that, all else being equal, the ratio α/β determines the final link strength of a state–lower ratios entail stronger links and therefore higher response probabilities. Hence, according to the model, contexts with lower overall reinforcement rates may engender greater resistance to extinction, which in turn may produce contrast effects (left-shifted distributions).

The curves in Figure 7 also show that the model can reproduce the location and spread of the L1 and S2 distributions; it can reproduce S1 distributions with one or two modes, although it cannot reproduce distributions with two modes with similar heights (as the data of P463 demanded). Finally, with respect to the proportion of reinforced trials, the model's predictions were always within 5% of the pigeon data.

In conclusion, the results from the present experiment show that pigeons can learn to produce two temporal intervals simultaneously, and that these intervals accord with Weber's law. They also show that the mean and variability of a produced interval are slightly higher when it is paired with a shorter than with a longer interval, a weak context effect. An extension of the LeT model accounts for some of the main experimental properties of temporal differentiation. It accounts for contrast effects via

parameter changes, but it does not explain in a principled way why or how the parameters change with context.

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