



**Universidade do Minho**  
Escola de Psicologia

Marília Pinheiro de Carvalho

## Investigations on relational control of time perception

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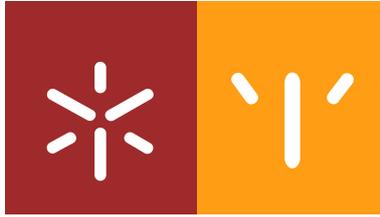
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**Universidade do Minho**

Escola de Psicologia

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**Investigations on relational control  
of time perception**

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Trabalho efetuado sob a orientação do

**Professor Doutor François Tonneau**

e do

**Professor Doutor Armando Machado**

outubro de 2015

## STATEMENT OF INTEGRITY

I hereby declare having conducted my thesis with integrity. I confirm that I have not used plagiarism or any form of falsification of results in the process of the thesis elaboration.

I further declare that I have fully acknowledged the Code of Ethical Conduct of the University of Minho.

University of Minho, October 22<sup>nd</sup>, 2015.

Full name: Marilia Pinheiro de Carvalho

Signature: 



Para os meus pais, a minha irmã e o Pepo



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## Title

Investigations on relational control of time perception

## Abstract

For any given set of stimuli, several relations can be found among its elements based on their physical properties. If we consider two squares, for example, one can focus on their size and conclude that one is larger than the other. Two well-known effects illustrate how the relations in a set of stimuli can affect how subjects respond to a particular set member. In a simple discrimination procedure, subjects may learn to choose a bright gray square (gr+) and to avoid a dark gray square (gr-). Later, given a choice between gr+ and a new, brighter gray square (gr++), subjects surprisingly avoid gr+ and choose gr++. The effect is called *transposition*, because it has been claimed that subjects transpose to the new set of squares a response based on the relation between the members of the previous set (in this case, they would respond ‘choose the brighter of the squares’). In another protocol, a compound stimulus contains a bright gray square (g+) surrounded by a brighter gray square (gr++), and in another compound the same bright gray (gr+) is surrounded by a dark gray square (gr-). When compared, gr+ looks darker in the first than in the second compound. The effect is called *contrast*, because the differences between the elements in the compound are emphasized. Despite their intriguing nature and their relevance to understand how stimulus properties control responding, both transposition and contrast effects research has been circumscribed to stimulus dimensions such as brightness and size. Little is known on how these effects alter responding controlled by stimulus duration. We present here a series of studies in which we tried to reduce this gap and investigate whether and how the relations between a set of time intervals affect responding to these same intervals.

Study 1 followed the tradition on transposition research. Pigeons were presented with two sample intervals (T1 and T2, with  $T1 < T2$ ) and given a choice between two response options (S and L). S was correct following T1 and L was correct following T2. At issue was whether they had learned to choose based on the relative (‘short→S, long→L’), or on the absolute value (‘ $T1 \rightarrow S$ ,  $T2 \rightarrow L$ ’) of the intervals. Later, they learned a new discrimination with the sample intervals T2 and T3 ( $T2 < T3$ ). For half of them, the Relative group, the new discrimination preserved the relative mapping of the task (‘ $T2 \rightarrow S$ ,  $T3 \rightarrow L$ ’; that is, ‘short→S, long→L’). For the other half, the Absolute group, it preserved the absolute mapping (‘ $T2 \rightarrow L$ ,

T3→S'). If in the first discrimination pigeons had learned the relative value of intervals, the Relative group should learn the new discrimination faster than the Absolute group, for the task favored transfer of relational responding. If the pigeons had learned the absolute value of the intervals, the Absolute group should learn the new discrimination faster than the Relative group, for the task favored absolute responding. We also simulated the subjects' performance with the Learning-to-Time (LeT) model and compared the models' predictions against the pigeon data. Study 2 improved Study 1 by introducing generalization tests at the end of training with the first discrimination. We used the generalization data to predict the acquisition curves of the new discrimination. The results of Studies 1 and 2 showed that (a) both groups learned the new discrimination; (b) the generalization gradients from Study 2 predicted the acquisition of the new discrimination for both groups; (c) LeT accounted for the major trends in acquisition (Studies 1 and 2) and generalization curves (Study 2) for both groups. Based on this results, we concluded that there was no evidence of relational responding in this temporal discrimination task.

In Study 3 we used a production task to assess if different temporal contexts affect the judgements pigeons make of interval durations. Under two different contexts, subjects had to produce durations within three ranges, a short [0.5 s – 1.5 s], an intermediate [1.5 s- 4.5 s], and a long [4.5 s – 13.5 s] ranges. The ranges were combined to form two contexts, a 'short context' with the short and intermediate ranges, and a 'long context' with the intermediate and long ranges. We evaluated if the durations produced within the intermediate range, common to both contexts, differed depending on the contexts. The results revealed a small contrast effect whereby the mean of the durations produced within the intermediate range was greater in the 'short context' than in the 'long context'. We simulated the pigeons' performance with the LeT model and found that it accounted for the Gaussian-like shape and for the spread of the distributions of the produced durations.

Together the studies provided unprecedented evidence on the effects of the relations between time intervals on responding. They also successfully extended LeT to few explored empirical problems, and proved for the breadth of the model in accounting for timing.

## Título

Investigações sobre o controlo relacional na percepção temporal

## Resumo

Num conjunto de estímulos, podemos identificar relações entre seus elementos com base em suas propriedades físicas. Se consideramos dois quadrados, por exemplo, podemos focar em seus tamanhos e concluir que um é maior do que o outro. Dois famosos efeitos ilustram como as relações inerentes a um conjunto de estímulos podem afetar a maneira como os sujeitos respondem aos elementos do conjunto. Numa procedimento de discriminação simples, os sujeitos podem aprender a escolher um quadrado cinzento claro (gr+) e a evitar um quadrado cinzento escuro (gr-). Posteriormente, dada a escolha entre gr+ e um novo quadrado cinzento mais claro (gr++), os sujeitos surpreendentemente evitam gr+ e escolhem gr++. O efeito é chamado de *transposição* por que se alega que os sujeitos transpuseram para o novo conjunto de quadrados uma resposta baseada na relação entre os elementos do primeiro conjunto (neste caso, eles aprendem a ‘escolher o mais claro dos quadrados’). Num outro protocolo, um estímulo composto contém um quadrado cinzento claro (gr+) rodeado por um quadrado cinzento mais claro (gr++), ao passo que num outro estímulo composto gr+ está rodeado por um quadrado cinzento escuro (gr-). Quando comparados, gr+ parece mais escuro no primeiro do que no segundo estímulo composto. O efeito é chamado de *contraste*, por que as diferenças entre os elementos do composto estão enfatizadas. Apesar de sua natureza intrigante e de sua relevância para compreendermos como as propriedades dos estímulos controlam o responder, as investigações sobre transposição e contraste têm estado circunscritas a dimensões de estímulo como o brilho e o tamanho. Pouco se sabe sobre como estes efeitos alteram o responder controlado pela duração dos estímulos. Nós apresentamos aqui uma série de estudos em que tentamos preencher esta lacuna e investigamos se e como as relações entre um conjunto de intervalos temporais afetam o responder a estes mesmos intervalos.

O Estudo 1 seguiu a tradição da investigação em transposição. Dois intervalos de tempo ( $T_1$  e  $T_2$ ,  $T_1 < T_2$ ) eram apresentados, e pombos deviam escolher entre duas opções de resposta (S e L). S era correta após  $T_1$  e L após  $T_2$ . Estava em causa se os sujeitos aprenderam a responder com base no valor relativo (‘curto  $\rightarrow$  S, longo  $\rightarrow$  L’) ou no valor absoluto (‘ $T_1 \rightarrow$  S,  $T_2 \rightarrow$  L’) dos intervalos. Posteriormente, os sujeitos aprenderam uma nova

discriminação com os intervalos T2 e T3 ( $T2 < T3$ ). Para metade deles, o grupo Relativo, manteve-se o mapeamento relativo da tarefa ( $T2 \rightarrow S, T3 \rightarrow L$ , isto é, ‘curto  $\rightarrow S$ , longo  $\rightarrow L$ ’). Para a outra metade, manteve-se o mapeamento absoluto ( $T2 \rightarrow L$ ). Se na primeira discriminação os pombos aprenderam o valor relativo dos intervalos, o grupo Relativo deveria aprender a nova discriminação mais rapidamente do que o grupo Absoluto, por que a nova tarefa daquele grupo favorecia a transferência do responder relacional. Se aprenderam o valor absoluto, o grupo Absoluto deveria aprender mais rapidamente, por que a tarefa deles favorecia a transferência do responder absoluto. Também comparamos o desempenho dos sujeitos com simulações que fizemos com o modelo Learning-to-Time (LeT). O Estudo 2 replicou o Estudo 1 e introduziu testes de generalização ao fim da primeira discriminação. Nós usamos os dados de generalização para prever as curvas de aquisição da nova discriminação. Os resultados de ambos os estudos revelaram que (a) ambos os grupos aprenderam as discriminações; (b) os gradientes de generalização previram a aquisição da nova discriminação; (c) o LeT previu as principais características das curvas de aquisição e generalização de ambos os grupos. Concluímos que não houve evidência de responder relacional nesta tarefa de discriminação temporal.

O Estudo 3 usou uma tarefa de produção para avaliar se diferentes contextos temporais afetam os julgamentos que pombos fazem de intervalos de tempo. Sob dois diferentes contextos, os sujeitos produziram durações pertinentes a três *ranges*, um curto [0.5 s – 1.5 s], um intermédio [1.5 s- 4.5 s] e um longo [4.5 s – 13.5 s]. Combinamos os *ranges* curto e intermédio para formar um ‘contexto curto’, e os *ranges* intermédio e longo para formar um ‘contexto longo’. Avaliamos se as durações produzidas dentro do *range* intermédio, comum a ambos os contextos, diferiram a depender dos contextos. Os resultados revelaram um pequeno efeito de contraste, por que a média das durações produzidas para o *range* intermédio foi maior no ‘contexto curto’ do que no ‘contexto longo’. Simulações do desempenho dos pombos com o modelo LeT reproduziram as principais características das distribuições das durações produzidas.

Tomados em conjunto, os estudos produziram evidências inéditas sobre o efeito da relação entre intervalos de tempo no controlo do responder. Eles também estenderam o LeT para questões empíricas pouco exploradas e confirmaram a polivalência do modelo.

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## **Abbreviations, acronyms and symbols**

**ANOVA** – Analysis of Variance

**ABA** – Experimental design

**ABA'B'** – Experimental design

**AL** – Adaptation Level

**BEM** – Behavioral Economic Model

**BeT** – Behavioral Theory of Time

**CI** – Confidence Interval

**d** – Cohen's d

**FI** – Fixed Interval schedule

**FOPP** – Free Operant Psychophysical Procedure

**GM** – Geometric Mean

**gr+** - Bright gray stimulus

**gr++** - New, brighter gray stimulus

**gr-** - Dark gray stimulus

**ITI** – Inter Trial Interval

**k** – Gaussian random variable

**L** – 'left' response

**L1** – 'long' time interval in a 'short context'

**L2** – 'long' time interval in a 'long context'

**LeT** – Learning-to-Time

**n** – Behavioral state n

**n\*** - Behavioral state active at reinforcement

**PSE** – Point of Subjective Equality

**R** – 'right' response

® - Registered trade mark

**S<sub>n</sub>** – Stimulus indexed by a number

**S** – Stimulus

**S<sub>1</sub>** – Choice key, or a time interval

**S<sub>2</sub>** – Choice key, or a time interval

**S+** - Positive stimulus

**S-** - Negative stimulus

**SEM** – Standard Error of the Mean

**SET** – Scalar Expectancy Theory

**R** – Response

**R(t)** – Response rate at moment t

**R<sub>1</sub>** – a “type” of response

**R<sub>2</sub>** – a “type” of response

**T (or t)** – Time interval or reinforcement moment

**TS** – Time interval

**TL** – Time interval

**T1** – Time interval

**T2** – Time interval

**T3** – Time interval

**VI** – Variable Interval schedule

**W(n)** – Coupling strength between behavioral state n and an operant response

**W<sub>E</sub>** – Coupling strength of the emitted response

**W<sub>Left(n)</sub>** – Coupling strength between behavioral state n and the ‘left’ response

**W<sub>NE</sub>** – Coupling strength of the non-emitted response

**W<sub>Right(n)</sub>** – Coupling strength between behavioral state n and the ‘right’ response

**W<sub>0</sub>** – Initial value of coupling strength

**X<sub>Acc</sub>** – Number of pulses in the accumulator

**X<sub>Left</sub>** – Sample extracted from the memory for ‘left’

**X<sub>Right</sub>** – Sample extracted from the memory for ‘right’

$\bar{x}$  – Average

$\alpha$  – Extinction parameter

$\beta$  – Reinforcement parameter

$\Delta W$  – Amount of increase or decrease in the coupling strength

$\lambda$  – Rate of the pacemaker in SET and Speed of activation of successive behavioral states in

LeT

$\mu$  – Mean of the speed of activation of behavioral states

$\omega^2$  – Variance accounted for

$\sigma$  – Standard deviation of the speed of activation of behavioral states

$\Theta$  – Threshold parameter

$\tau$  – Residence time in behavioral states

$\gamma$  – Coefficient of variation

## Figures

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Figure 24. Panel a: A three sample Temporal Generalization trial. Responses are extinguished after the shortest TS and the longest TL samples, and reinforced after the intermediate T samples. Panel b: Hypothetical excitatory gradient for the task. Panel c: Profile of link strengths predicted by LeT. Compare with Figure 23.

Figure 25. Generalization gradient obtained by Leak and Gibbon (1995) with a group of pigeons exposed to a Mixed FI 10s-FI 120s schedule. The gradient is bimodal (one mode at 10 s and another at 120 s) and shows the scalar property. The minimum response rate occurs close to 35 s, the geometric mean of 10 and 120.

Figure 26. Panel a: A Mixed FI-FI trial with its contingencies. Panel b: Three excitatory gradients, a Gaussian gradient from a peak procedure with reinforcement at  $T_1$ , a half Gaussian gradient from a FI  $T_2$  schedule, and the sum of the two gradients. Panel c: Profile of link strengths predicted by LeT. Two states have the strongest links with the response, the modal states at  $T_1$  and  $T_2$ .

Figure 27. Panel a: A trial of a Free-Operant Psychophysical Procedure (FOPP) and its contingencies. 'Left' responses are reinforced during the first half of the trial and extinguished during the second half. 'Right' responses have the opposite contingencies. Panel b: Hypothetical excitatory gradients for 'left' and 'right' responses. Panel c: Profile of link strengths predicted by LeT. Each state is linked to both responses. 'Initial' states are linked strongly with 'left' and weakly with 'right'; 'late' states are linked strongly with 'right' and weakly with 'left'. When the VI's are equal, 'intermediate' states are linked equally to both responses.

Figure 28. Panel a: A Simple Bisection trial and its contingencies. Responses on 'red' and 'green' keys are reinforced after the short and long samples, respectively. Panel b: Hypothetical excitatory gradients for 'red' and 'green' responses. Panel c: Profile of link strengths predicted by LeT. 'Initial' states are linked strongly with 'red' and weakly with 'green'; 'late' states are linked strongly with 'green' and weakly with 'red'. Subsequent states retain their initial link strength.

Figure 29. Temporal generalization gradients obtained by Church and Deluty (1977) with rats in two simple bisection tasks, one with 1 s vs. 4 s samples, and the other with 4 s vs. 16 s samples. The gradients follow an ogive curve, cross indifference at the geometric mean of the training samples, and overlap when plotted in a common scale.

Figure 30. Panel a: A Double Bisection procedure and its contingencies. The subject learns two simple bisection tasks. In one (left), 'red' and 'green' responses are reinforced after 1-s and 4-s samples, respectively. In the other (right), 'blue' and 'yellow' responses are reinforced after 4-s and 16-s samples, respectively. Panel b: Hypothetical excitatory gradients for 'red' and 'green' responses (left) and for 'blue' and 'yellow' responses (right). Panel c: Profile of link strengths predicted by LeT.

Figure 31. The context effect obtained by Machado and Keen (1999) after training pigeons in a double bisection task. Given a choice between 'green' and 'blue', the keys associated with the 4-s sample but in different sample contexts, preference for 'green' increases with sample duration.

Figure 32. Panel a: Generalization gradients obtained by Vieira de Castro et al. (2013) after training pigeons in a double bisection tasks with 2 s vs. 6 s samples in one task, and 6 s vs. 18 s samples in the other. 'Green' and 'blue' were reinforced after the 6-s sample, but 'green' was extinguished after the 2-s sample and 'blue' after the 18-s sample. Panel b: Obtained gradient for 'green' over 'blue' (the context effect), and the gradient predicted from the two gradients in Panel a.

Figure 33. Panel a: Generalization gradients obtained by Vieira de Castro and Machado (2012) in a double bisection, go/no-go task, with 1 s vs. 4 s samples in the first task, and 4 s vs. 16 s samples in the second task. 'Green' and 'blue' were reinforced after the 4-s sample, but 'green' was extinguished after the 1-s sample and 'blue' after the 16-s sample. Panel b: Obtained gradient for 'green' over 'blue' (the context effect), and the gradient predicted from the two gradients in Panel a.

Figure 34. Panel a: The two types of bisection trials used in some studies about relational temporal control. In the first bisection task (left), ‘left’ and ‘right’ responses are reinforced after 1-s and 4-s samples, respectively. In the second bisection task, for the Relative group (middle) ‘left’ and ‘right’ responses are reinforced after 4-s and 16-s samples, respectively; for the Absolute group (right) ‘left’ and ‘right’ responses are reinforced after 16-s and 4-s samples, respectively. Panel b: Hypothetical excitatory gradients for each response in each task. Panel c: Profile of link strengths predicted by LeT. In the second task, the Relative group reverses the link strengths from the modal state at 4 s (cf. middle circle in middle panel).

Figure 35. Acquisition curves for the Relative (full circles) and Absolute (empty circles) groups in the second bisection task. Panel a: Results obtained by Church and Deluty (1977) with rats. Panel b: Results obtained by Hulse and Kline (1993) with starlings.

Figure 36. Pigeons learned two bisection tasks, one with a ‘2s→red, 8s→green’ mapping, and the other with a ‘4s→horizontal, 16s→vertical’ mapping. Next they were exposed to new test samples but with the same comparisons. Zentall et al.’s (2004) data show the preference for ‘red’ over ‘green’ following the 4-s sample (filled squares), and the preference for ‘horizontal’ over ‘vertical’ following the 8-s sample. Maia and Machado’s (2009) data show how the preference for ‘red’ (filled circles) or ‘horizontal’ (empty circles) varied with sample duration.

Figure 37. Generalization gradients produced by pigeon P751 (symbols) in Carvalho et al.’s (2015) study and the curves fitted by the LeT model. The pigeon learned the following bisection tasks (in each phase of the ABA’B’ design): ‘2s→red, 6s→green’ (A and A’), and ‘18s→red, 6s→green’ (B and B’).

Figure 38. 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.

Figure 39. 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 = [1.5-4.5] = S2, and L2 = [4.5-13.5].

Figure 40. 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 = [1.5-4.5] = S2, and L2 = [4.5-13.5]. Logarithmic x-axis.

Figure 41. 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 proportion predicted from the Gaussian fits.

Figure 42. 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.

Figure 43. 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 = [1.5-4.5] = S2, and L2 = [4.5-13.5].

Figure 44. 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 = [1.5-4.5] = S2, and L2 = [4.5-13.5]. Logarithmic x-axis.

Figure 45. 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 proportion predicted from the Gaussian fits.

Figure 46. 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.

Figure 47. Simulation results of the LeT model. 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:  $\mu_\tau = 0.5$  s,  $\sigma_\tau = 0.075$  s,  $\beta = 0.02$ , and  $\alpha = 0.16$ . Right:  $\mu_\tau = 0.3$  s,  $\sigma_\tau = 0.03$  s,  $\beta = 0.04$ , and  $\alpha = 0.2$ .

Figure 48. 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 ( $\mu_\tau$ ,  $\sigma_\tau$ ,  $\alpha$ ,  $\beta$ ): Left, S1 = (0.5, 0.05, .1, .04), L1 = (0.5, 0.1, .1, .08), S2 = (0.5, 0.05, .1, .08), and L2 = (0.5, 0.075, .2, .05). Right: S1 = (0.475, 0.0475, .2, .04), L1 = (0.4, 0.048, .2, .04), S2 = (0.4, 0.032, .053, .04), and L2 = (0.45, 0.0675, .22, .02).



## Tables

Table 1. Experimental design. Four groups (Relative Upshift, Absolute Upshift, Relative Downshift, and Absolute Downshift) were exposed to an ABA design. In the three rightmost columns, each cell shows the two sample durations. The left sample was assigned to the 'left' key and the right sample to the 'right' key.

Table 2. Experimental groups and the bisection tasks to which they were exposed across phases.

Table 3. Sequence of training. 'red', 'green', 'yellow' and 'blue' stand for the keylight colors that signaled the operative, reinforced range (in seconds).



**CHAPTER I - GENERAL INTRODUCTION**



## 1. Responding to relations between stimuli

Gestalt psychologist Wolfgang Köhler proposed that animals can respond to relations between stimuli. In one of his studies, Köhler (1918/1938) simultaneously presented to chickens a bright gray (gr+) and a dark gray (gr-) rectangle, and reinforced choices of the bright gray, gr+. Afterwards, he presented a new pair of rectangles, the familiar and reinforced bright gray (gr+) and a new, brighter gray (gr++), and found that the birds chose mainly the new brighter gray, gr++. Köhler suggested that the subjects transposed to test a response based on the relative brightness of the squares, a response that was acquired during training. Since the relative value of a stimulus emerges from a qualitative or a quantitative relation between two stimuli, *transposition* instantiated a transfer of responding based on the relation among stimuli, rather than on their absolute value. Transposition expressed a topic dear to Gestalt Psychologists, the perception of stimulus relations (Reese, 1968).

Köhler's results would be less surprising had he explicitly trained his subjects to respond to the relation between the stimuli – for example, by using multiple pairs of stimuli differing in brightness and reinforcing choice of the brighter member of the pair. The fact that he obtained evidence of relational learning using only one pair of training stimuli suggested to him that relations may be the most salient aspect of the stimulus configuration to which the subject responds.

Reese (1968) highlighted that the question of relational responding is central to the understanding of the stimulus control of behavior, and argued in favor of a research program that identified instances of relational learning across different species, and determined the conditions under which relational learning takes place. According to him,

“the problem is therefore not only to determine whether organisms of a given species or age level can respond to relations, but also to determine under what conditions they do or do not respond to relations. The two problems are obviously related, but presenting them separately provides an opportunity to point out that there is no logical reason to expect that organisms of all species at all age levels will respond to relations. [...] It is one thing to determine whether or not a given animal is *capable* at all of responding to relations; it is another thing to find out whether or not animals *tends* or prefers to respond to relations rather than to absolute properties” (Reese, 1968; p. 7).

Returning to Köhler, he did not deny that animals could learn to choose also on the basis of the absolute properties of stimuli, or generalize along stimulus dimensions. But he believed that relational learning could not be derived from absolute learning and stimulus generalization, because the new gray stimulus, gr++, was presumed sufficiently different from gr+ that it would fall outside the basin of the generalization gradient of the latter. He concluded: “structural function [as he called relational learning] arises from the elementary properties of the nervous system (or living substance in general) just as readily and just as soon as do the most simple absolute sensations” (Köhler, 1918/1938, p. 223).

Despite Köhler claim that relational responding is a process just as basic as responding controlled by the absolute properties of stimuli, Spence (1937) proposed an alternative, elegant account of transposition. He hypothesized that two gradients formed during discrimination training: An excitatory gradient centered at the S+ and manifest in a tendency to respond to that stimulus and adjacent stimuli, and an inhibitory gradient centered at the S- and manifest in a tendency to refrain from responding to that stimulus and adjacent stimuli. In the excitatory gradient, the tendency to respond decreases as stimuli successively depart from the S+, and in the inhibitory gradient, the tendency to avoid responding decreases as stimuli depart from the S-. The curves in Figure 1 illustrate the hypothetical gradients. Spence conceived of the “net” tendency to respond to a stimulus as the result of subtracting the inhibitory gradient from the excitatory gradient. The solid vertical lines between the two gradients illustrate the “net” tendency to respond and show that the net gradient is greater at gr++ than at gr+, yielding the transposition effect.

Spence’s account is elegant because it is parsimonious. By arguing in favor of combination of simpler and well described processes, such as reinforcement, extinction and generalization decrement to derive complex behavior, Spence made it unnecessary to appeal to a relational, more complex account. More importantly, his account can deal with the perception of relations without relying on sensory organs that would be sensitive to non-physical abstractions.

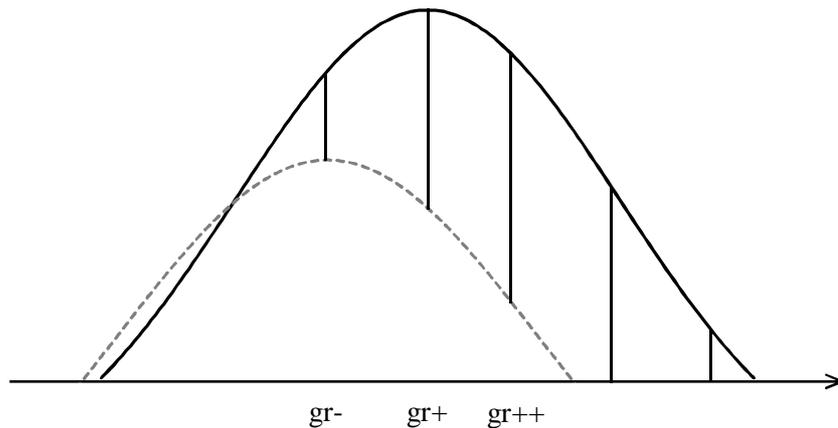


Figure 1. Spence's excitatory (solid curve) and inhibitory gradients (dashed curve) hypothesized to explain Köhler's classical transposition study with a dark gray (gr-), a bright gray (gr+) and a new, brighter gray (gr++) squares. The vertical lines between the two gradients show the "net" tendency to respond to each stimuli.

Since Spence's seminal work, many other studies have shown that relational responding to different stimulus dimensions, including brightness, size, orientation, shape, and frequency, could be derived from generalization gradients and their combination (for revisions, see Lazareva, 2002; Mackintosh, 1974). The success of the generalization account of the transposition effect, however, does not negate the heuristic value of Köhler's work. From our point of view, another important aspect of his findings was to show that the functional value of a stimulus (S) depends not only on its corresponding reinforcement schedule, but also on the stimulus arrangement or configuration (Gestalt) in which it occurred or of which it was part. To further develop our argument, we assume here that a set of stimuli that share a common dimension (e.g., brightness) define a context with respect to this dimension. Köhler showed that, with respect to brightness, the bright gray  $g+$  was a *positive* stimulus in the context where the dark gray  $g-$  was present, but was a *negative* stimulus in the context with the new, brighter gray  $g++$ . Hence, a stimulus that preserves its value along a physical dimension across contexts may occasion different responses induced by the difference in contexts. Conversely, stimuli that differ quantitatively along a dimension may occasion similar responding provided the contexts in which they occur remain similar.

The literature on perception provides a classical example of such context-dependent effects. In the contrast effect, the sensation of a stimulus dimension enhances or diminishes depending on the stimulus being presented along another stimulus with a smaller or a greater value on the dimension, respectively. In Figure 2, the same gray-hue square is presented within two other gray squares, a brighter, and a darker one. The inner squares are equal, but we see them as different depending on their surroundings<sup>1</sup>: the bright surrounding makes the square look darker, and the dark surrounding makes it look brighter (Robinson, 1972). Another way to describe contrast is to say that it exaggerates the perception of differences in a stimulus dimension.



Figure 2. The contrast effect. The inner rectangles are colored with the same gray hue; but the left one looks darker than the right one.

## 2. The research on relational responding and context effects on timing

Time is a pervasive attribute of physical stimuli, and is embedded in all of the interactions of the organisms with the environment. As Titchener (1915) put it:

“the attribute of duration [...] is the bare going on, going forward, keeping like itself, that may be observed in any every sensation; you recognize it most easily, perhaps, if you listen to a tone, or attend to the kinesthetic complex as you slowly extend your arm from the elbow. It is *the elementary time-factor in all our perceptions of time* – in the perceptions of period, of interval, of rate, or rhythm, and so on [...]” (Titchener, 1915, pp. 122-123).

In the last century, we have witnessed the blossoming of the investigations on timing, that is, the investigations on how organisms regulate their behavior according to time intervals. Today, the key properties of animal timing are robust and well described. We know that animals can discriminate one interval from another, that they can anticipate the moment a reinforcer is delivered, or that they can emit responses that accord with a specific time

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<sup>1</sup> If Köhler's chickens could talk, probably they would say that gr+ was brighter when it was by the side of gr- than when it was by the side of gr++. They would also tell us that they chose gr++ during test because what they learned in training to be a gr+ brightness was not present during test.

requirement. We also know that Weber's law applies to timing, that the coefficient of variation of time judgements remains constant across time intervals, and that the experimental protocol may affect the shape of the temporal generalization gradients (for a review, see Richelle & Lejeune, 1980). Elaborate and powerful quantitative models on how animals respond to time have also been put forward, even though none of them are yet able to account for the full set of experimental findings (for more on this consideration, see Machado, Malheiro, & Erlhagen, 2009).

Despite the prolific experimental program on timing, only a few studies investigated relational responding with temporal stimuli. They all used the same procedure, the *bisection task*. One of two time intervals is presented and, say, a rat has to choose between two options conditionally on the interval. One option (S) is correct following one interval, and the other option (L) is correct following the other interval. If the animals learn that one interval is 'short' and the other interval is 'long', and also learn that S goes with 'short' and L goes with 'long', later they can transpose such relational-based responding to a similar, new task that uses other intervals but maintains S and L as the choice options, yielding faster acquisition of the new task. Not surprisingly, the design rationale resembles that of Köhler's study. The results from rats (Chuch & Deluty, 1977) and starlings (Hulse & Kline, 1993) suggested that these species learn to respond relationally. A study with pigeons, with a slightly different bisection task, also suggested relational learning (Zentall, Weaver, & Clement, 2004), but results from our lab did not corroborate their findings (Maia & Machado, 2009). We return to these studies in the next chapters.

Belke (1992) reported indirect evidence on relational timing. He trained pigeons on two separate Concurrent Variable Interval schedules. In one schedule, a white key signaled a 20-s VI for food, and a red key signaled a 40-s VI. In the other schedule, a green key signaled a 40-s VI, and a yellow key signaled an 80-s VI. In the first schedule, the 40-s VI was relatively "poor" for its rate of reinforcement was half that of the 20-s VI, whereas in the second schedule, the 40-s VI was relatively "rich" because the rate of reinforcement was twice that of the 80-s VI. Later, Belke gave pigeons a choice between the red and the green keys, those associated with the 40-s VI and found that they preferred the green key, despite both of them delivering food at the same rate on average. The results, thus, were at odds with the matching law (Herrnstein, 1970) that predicted equal distribution of the choices between the two keys, and suggested that the relative value of the keys, defined by the *relative time*

between reinforcement deliveries, determined the subjects' choices, since they preferred the key that previously signaled relatively smaller delays between reinforcements.

These few studies exhaust the list of investigations on relational responding and context effects in animal timing. They all have used the bisection task and adopted the rationale described above. Protocols to study the effects of different contexts on the responses to a stimulus duration have not been used so far.

### **3. The present thesis**

Here we report three studies that investigated relational responding and context effects on timing. The studies had two main goals. First, to assess if pigeons can respond relationally to interval durations, and if their temporally-controlled responses are subject to context effects. Second, assuming that temporal tasks are occasions for the occurrence of relational responding and context effects, to apply a Spencean approach to timing. The Spencean approach assumes control by the absolute properties of stimuli and derives performance on the task from the induced generalization gradients. Hence, when feasible, we obtained empirical gradients and used them to predict performance. Along similar lines, since one of the most prominent timing models, the Learning-to-Time model (LeT: Machado et al., 2009; Machado, 1997), formalizes the Spencean approach by presupposing exclusively absolute responding and generalization gradients induced by reinforcement and extinction to derive temporally regulated behavior, we used LeT to simulate performance in our tasks and later contrasted the models' predictions with the pigeons' data. In the following chapters, along with our presentation of the results, we describe the structure of the model and how it applies to each task. While we analyze the appropriateness of LeT's account of our data, we also draw considerations concerning the influential Scalar Expectancy Theory of timing (SET; e.g., Gibbon, 1991; Gibbon, Church, & Meck, 1984).

Chapter II describes a study that replicated with pigeons Church and Deluty's (1977) bisection procedure for assessing relational responding. Chapter III describes a study with an improved bisection procedure, in which we introduced generalization tests and, in doing so, were able to directly measure how well the gradients obtained in one discrimination explained the acquisition of another discrimination. In both studies, our reasoning resembled Köhler's in that we tried to assess transposition of relational responding to other stimuli. In Chapter IV we put our Spencean approach to test by proposing that performance in a variety

of well-known timing tasks can be synthesized from generalization gradients and their combination. LeT served as our formal Spencean-like model and we analyzed whether more complex timing findings are derivable from how the model conceives of generalization gradients. Chapter V describes our attempts to investigate for the first time context-effects in the production of temporal intervals by pigeons. In two experiments, we tried to determine whether pigeons produce differently time intervals and whether their production of a given interval depended on context. We used a variation of Mechner and Guevrekian's (1962) Fixed Minimum Interval task and adapted to pigeons the rationale first proposed by Jazayeri and Shadlen (2010) to study context-effects in temporal reproduction tasks with humans. Chapters II to V present the studies in their publication form. The structure of the argument in each article was therefore kept intact; also, we wanted each chapter to be readable independently of the others. Accordingly, some redundancies may be found from chapter to chapter, particularly in the description of the LeT model and of previous studies that inspired ours. Finally, Chapter VI summarizes our main findings and their implications for the understanding of temporal stimulus control in general and for the timing models in particular.



**CHAPTER II<sup>2</sup> – STUDY 1: RELATIVE VERSUS ABSOLUTE STIMULUS  
CONTROL IN THE TEMPORAL BISECTION TASK**

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<sup>2</sup> This Chapter reproduces the publication

Carvalho, M. P., & Machado, A. (2012). Relative versus absolute stimulus control in the temporal bisection task. *Journal of the Experimental Analysis of Behavior*, 98, 23-44. Changes were made to the formatting style, but not to the content presented in the original paper.



**Abstract**

When subjects learn to associate two sample durations with two comparison keys, do they learn to associate the keys with the short and long samples (relational hypothesis), or with the specific sample durations (absolute hypothesis)? We exposed 16 pigeons to an ABA design in which Phases A and B corresponded to tasks using samples of 1 s and 4 s, or 4 s and 16 s. Across phases, we varied the mapping between the samples and the keys. For the Relative group, short and long samples always associated with the same keys (e.g., Phase A: '1s→left, 4s→right'; Phase B: '4s→left, 16s→right'); for the Absolute group, the 4-s sample associated always with the same key (e.g., Phase A: '1s→left, 4s→right'; Phase B: '16s→left, 4s→right'). If temporal control is relational, the Relative group should learn the new task faster than the Absolute group, but if temporal control is absolute, the opposite should occur. We compared the results with the predictions of the Learning-to-Time (LeT) model, which accounts for temporal discrimination in terms of absolute stimulus control and stimulus generalization. The acquisition curves of the two groups were generally consistent with LeT and therefore more consistent with the absolute than the relative hypothesis.

*Key words:* relative versus absolute, LeT model, stimulus control, timing, pigeon



## 1. Introduction

In the present study, we examine the issue of absolute versus relative stimulus control in the time domain. Can temporal control be relational, and, in the affirmative, under what circumstances and through what processes? To elaborate the issue, consider a prototypical temporal discrimination task, the bisection task. On each trial, a rat is presented with one of two sample stimuli, for example, a houselight illuminated for 1 s or 4 s. Following the sample, the rat is given a choice between two comparison stimuli, a ‘left’ lever and a ‘right’ lever. Choices of the ‘left’ lever are reinforced following the 1-s sample, and choices of the ‘right’ lever are reinforced following the 4-s sample. We represent these reinforcement contingencies by the mapping ‘1s→left, 4s→right’. After a dozen sessions or so, the rat responds correctly on more than 90% of the trials. What did the rat learn?

The Absolute Hypothesis states that the rat learned an absolute discrimination, to choose one or the other lever based on one or the other absolute duration of the sample. Moreover, the choice of one lever is not restricted to a specific duration but generalizes to adjacent durations (stimulus generalization). In contrast, the Relational Hypothesis states that the rat learned the relation between the stimulus durations, in particular, that the ‘left’ choice is reinforced following the shorter stimulus, and the ‘right’ choice is reinforced following the longer stimulus. A third hybrid hypothesis is also possible – the rat may have learned to choose the levers on the basis of both the absolute and the relative stimulus durations –, but for clarity we will continue to stress the two pure hypotheses.

Two studies have claimed evidence for relational control in bisection tasks. Zentall, Weaver and Clement (2004) exposed pigeons to the following mappings ‘2s→red, 8s→green’ (first bisection task with red and green keylights as comparisons) and ‘4s→vertical, 16s→horizontal’ (second bisection task with a vertical or a horizontal white bar projected on a dark key as comparisons). Critically, in the first task, the long duration of 8 s equaled the geometric mean of the durations used in the second task (i.e.,  $8 = \sqrt{4 \times 16}$ ) and, conversely, in the second task, the short duration of 4 s equaled the geometric mean of the durations used in the first task ( $4 = \sqrt{2 \times 8}$ ). The reason to choose these specific values relies on a robust empirical finding obtained in timing studies, namely, that the point of subjective equality of two durations is their geometric mean (Catania, 1970; Church & Deluty, 1977; Gibbon, 1981, 1991; Gibbon, Church, & Meck, 1984; Killeen & Fetterman, 1988; Platt & Davis, 1983; Stubbs, 1968). After learning the two bisection tasks, the pigeons received two types of test trials. On one type, they chose between the ‘red’ and ‘green’ comparisons

following 4-s test sample; on the other type, they chose between the ‘vertical’ and ‘horizontal’ comparisons following 8-s test sample. According to Zentall et al. (2004), the Absolute Hypothesis predicted indifference on both test trials because the sample duration equaled the geometric mean of the training durations associated with the comparison stimuli. However, the Relational Hypothesis predicted a preference for ‘red’ over ‘green’ on the first type of test trial and a preference for ‘horizontal’ over ‘vertical’ on the second type of test trial. The predictions follow because, according to the Relational Hypothesis, the pigeons learned during the second task that the 4-s sample was the short sample, and, during the first task, that after the short sample choice of ‘red’ was reinforced; hence the preference for ‘red’ after the 4-s test sample. Similarly, the pigeons learned during the first task that the 8-s sample was the long sample, and, during the second task, that after the long sample choice of ‘horizontal’ was reinforced; hence the preference for ‘horizontal’ following the 8-s test sample. The results were consistent with the Relational Hypothesis – the pigeons preferred the ‘red’ key after 4-s sample and the ‘horizontal’ key after the 8-s sample, although only the former effect was statistically significant.

Maia and Machado (2009) reproduced Zentall et al.’s (2004) study but used more sample durations during the test trials so that full psychometric functions relating preference for ‘red’ and ‘horizontal’ to sample duration could be plotted. Their results were inconsistent with the Relational Hypothesis but consistent with the Absolute Hypothesis, because preference for ‘red’ after 4-s sample did not differ significantly from preference for ‘horizontal’ after 8-s sample. Similarly, when Russell and Kirkpatrick (2007) tested the absolute versus relational account of bisection with a more complex procedure – rats learned to associate three stimulus durations with two or three responses –, they obtained results more consistent with the Absolute than the Relative Hypothesis.

The other study that addressed the Relative versus Absolute issue in the bisection task followed a different approach. Church and Deluty (1977) trained one group of four rats in the bisection task ‘1s→left, 4s→right’. Next, they divided the rats into a Relative group and an Absolute group, and each group learned a second bisection task involving sample durations of 4 s and 16 s. The Relative group learned the mapping ‘4s→left, 16s→right’, which retains the relational structure of the first task because the ‘left’ and ‘right’ levers remain the correct choices after the short and long samples, respectively. The Absolute group learned the reverse mapping ‘4s→right, 16s→left’, which retains (part of) the absolute structure of the first task because the ‘right’ lever remains the correct choice after the common, 4-s sample.

To summarize, the experiment involved training the rats in two bisection tasks, the second of which preserved either the relative or the absolute mapping of the first. At issue was which group would learn the second task faster.

The results showed that the proportion of correct choices following the 4-s sample, increased faster in the Relative group than in the Absolute group. In fact, somewhat surprisingly, accuracy in the Absolute group remained below 75% even after 15 training sessions. Church and Deluty's results suggested that preserving the relative mapping 'short → left, long → right' enhanced learning, which is more consistent with the Relational Hypothesis (see Church & Deluty, 1977, for more experimental details and data interpretation).

Important as it was for our understanding of temporal discrimination in general and temporal bisection in particular, Church and Deluty's (1977) study has a few shortcomings. First, no data were reported concerning performance on trials in which 16-s and 1-s sample stimuli were presented. If the Relative and Absolute groups differed also in the speed of acquisition of the 16-s or 1-s discriminations, then we may need to revise our conclusions concerning the Absolute versus Relative issue.

Second, before the experiment described above, all eight rats had been exposed to another temporal discrimination task ('2s → left, 8s → right') and this fact may contribute to explain the differences between the two groups. On the one hand, when we consider the three mappings learned by each group – one with 2-s and 8-s samples, one with 1-s and 4-s samples, and one with 4-s and 16-s samples – we realize that whereas for the Relative group the second and third mappings preserved the relational structure of the previous mapping, for the Absolute group the second mapping preserved the relational structure of the first mapping, but the third mapping preserved the absolute structure of the second mapping. That is, the Relative group had a consistent history, but the Absolute group did not. On the other hand, the results could reflect also the differential effects of the generalization gradients induced by the 2 s vs. 8 s training on the acquisition of the third discrimination. In either case, the 2 s vs. 8 s previous task confounds the interpretation of the data. Finally, it is also the case that Church and Deluty's (1977) study has never been replicated with either the same or a different species. Hence, the robustness and generality of their findings remain uncertain.

The first goal of the present study was to improve Church and Deluty's study and extend it to another species. We exposed 16 pigeons to an ABA design in which Phases A and B corresponded to bisection tasks with different pairs of sample durations (1 s and 4 s, or

4 s and 16 s) and different stimulus-response mappings (e.g., '1s→left, 4s→right'). For half of the birds, the task learned in Phase B and the second Phase A (henceforth, A') preserved the relational mapping of the task learned in Phase A (Relative group); for the other half, the task learned in Phases B and A' preserved part of the absolute mapping of the task learned in Phase A (Absolute group). In addition, within each group, half of the birds learned first the task with the 1-s and 4-s samples and next the task with the 4-s and 16-s samples (Upshift group), and the other half learned the two tasks in reverse order (Downshift group). By comparing the acquisition curves for the common (4-s) sample and the other (1-s or 16-s) samples in the Relative and Absolute groups during Phases B and A', we expected to gain a deeper understanding of the Relational versus Absolute form of stimulus control in the temporal bisection task.

The Absolute versus Relational issue is also important to test theoretical models of timing. Hence, the second goal of the present study was to test one of these models, the Learning-to-Time (LeT) model (Machado, 1997; Machado, Malheiro, & Erlhagen, 2009). We focus on LeT because, in contrast with other models such as Scalar Expectancy Theory (SET, e.g., Gibbon et al., 1984), the Behavioral Theory of Timing (BeT, e.g., Killeen & Fetterman, 1988), or the Behavioral Economic Model (BEM, e.g., Josefowicz, Staddon, & Cerutti, 2009), LeT makes specific predictions concerning acquisition and phase transitions. In addition, as we explain below, the LeT model is a clear instantiation of the Absolute Hypothesis.

### ***1.1. The LeT model – general overview***

Developed from earlier work by Killeen and Fetterman (1988), LeT assumes that temporal discrimination depends on three processes (see Figure 3 top), the activation of a set of behavioral states, the learning of associations between the states and the operant responses, and the selection of the choice response. We describe briefly how the model applies to temporal bisection and refer the reader to Machado et al. (2009) for quantitative details and applications to other temporal tasks.

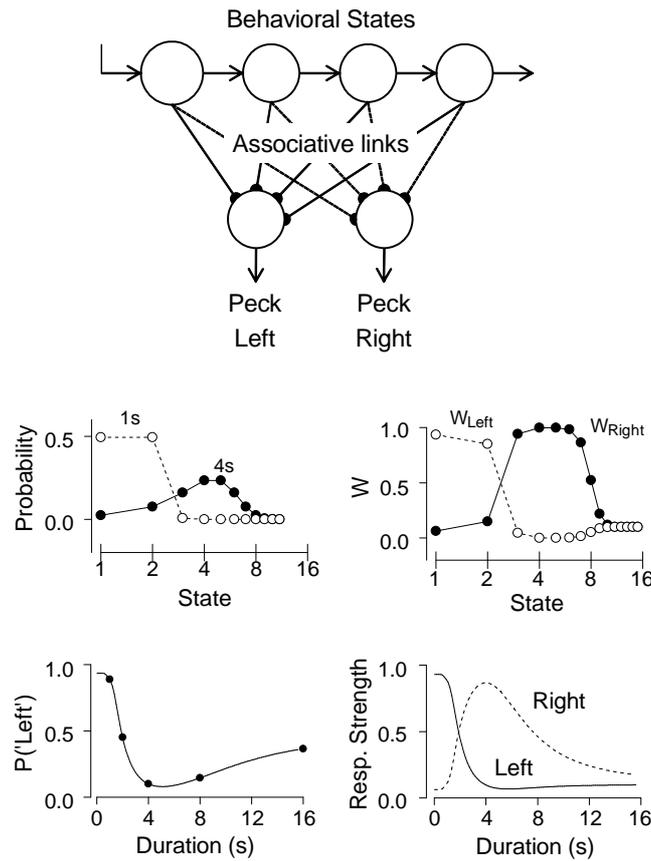


Figure 3. Top. The structure of LeT. After a time marker, a set of states is activated in series. The states are coupled to various degrees (associative links) with the two responses. The strength of each response is determined by associative link of the state active at the end of a sample. Bottom. Simulation results for the task ‘1s→left, 4s→right’. The top left panel shows the probability that state  $n$  is active at the end of 1-s and 4-s samples. The top right panel shows the strength of the associative links connecting state  $n$  with the ‘left’ and ‘right’ responses. The bottom right panel shows the expected strengths of the ‘left’ and ‘right’ responses following samples of different durations. The bottom left panel shows the probability of responding ‘left’ as a function of sample duration.

According to LeT, when the sample is presented, a set of behavioral states is activated in series, first state 1, then state 2, and so on. The rate of activation of successive states remains constant within trials, but varies randomly across trials according to a Gaussian distribution with mean  $\lambda$  and standard deviation  $\sigma$ . At the end of the sample, one of the states is active, say, state  $n$ . That state is linked with the two operant responses, pecking the ‘left’ and ‘right’ keys, and the strengths of the two links,  $W_{\text{Left}}(n)$  and  $W_{\text{Right}}(n)$ , determine the choice response. In fact, the probability of choosing the ‘left’ response equals  $W_{\text{Left}}(n) / [W_{\text{Left}}(n) + W_{\text{Right}}(n)]$ . In addition, these links change with reinforcement and extinction according to a simple linear operator learning rule (Bush & Mosteller, 1955). The model uses

five parameters, the mean ( $\lambda$ ) and standard deviation ( $\sigma$ ) of the speed of activation of the behavioral states, the extinction ( $\alpha$ ) and reinforcement ( $\beta$ ) learning parameters, and the initial value of the associative links ( $W_0$ ). In what follows, all parameters values remained constant at  $\lambda = 1.0$ ,  $\sigma = 0.4$ ,  $\alpha = 0.05$ ,  $\beta = 0.04$ , and  $W_0 = 0.1$ . These value were similar to the values used to fit bisection data in several previous studies (see Machado et al., 2009, for a summary), but other values could be used without changing significantly the model predictions.

Consider the bisection task ‘1s→left, 4s→right’. When a 1-s sample is presented, the active state at the end of the sample is likely to be one of the first states in the series. In fact, if we assume that successive states become active at the average rate of  $\lambda = 1.0$  states per second (with  $\sigma = 0.4$ ), then the first two states are the most likely to be active at the end of the 1-s sample. The open circles in the middle left panel of Figure 3 shows the probability that state  $n$  (with  $n \geq 1$ ) is active at the end of 1-s sample. Similarly, at the end of 4-s sample, the states most likely to be active are states number 4, 5, and neighboring states (filled circles). These state activation curves, wider for 4-s sample than 1-s sample, are the basis of the temporal generalization gradients.

As the animal experiences the reinforcement contingencies, the associative links of the active states change. Thus, because ‘left’ choices are reinforced following 1-s sample, the links connecting the first states with the ‘left’ response will be strengthened and their values will approach 1 (see first two open circles in the middle right panel). In addition, because ‘right’ choices are extinguished following 1-s sample, the links between the first states and the ‘right’ response will be weakened and approach 0 (see first two filled circles). The two curves in the middle right panel show the effect of 20 sessions: States 1 and 2 are associated mostly with the ‘left’ response; states 3 to 8 are associated mostly with the ‘right’ response; and subsequent states, rarely active after 1-s or 4-s samples, maintain their initial link of  $W_0 = 0.1$  with both responses.

Performance depends on the probability distribution of the active state and the profiles of associative links. Combined they determine both the strength of each response after a  $t$ -s sample (see bottom right panel) and the probability of choosing the ‘left’ key following a  $t$ -s sample (see bottom left panel). The former is akin to a temporal generalization gradient and the latter is the familiar psychometric function.

To recapitulate, when a 1-s sample is presented, one of the first two states is likely to be the active state (middle left panel) and because these states became associated mainly with

the ‘left’ response (middle right panel), the strength of the ‘left’ response is greater than the strength of the ‘right’ response (bottom right panel) and the animal tends to choose ‘left’ (bottom left panel). Similarly, when a 4-s sample is presented, one of the next states (3 to 8) is likely to be the active state and because these states became associated mainly with the ‘right’ response, the animal tends to choose ‘right’.

**1.2. The LeT model – specific predictions**

Let us first consider the case of the Relative Upshift and Absolute Upshift groups. The model predicts distinct acquisition and reacquisition curves for the two groups. Figure 4 shows the details.

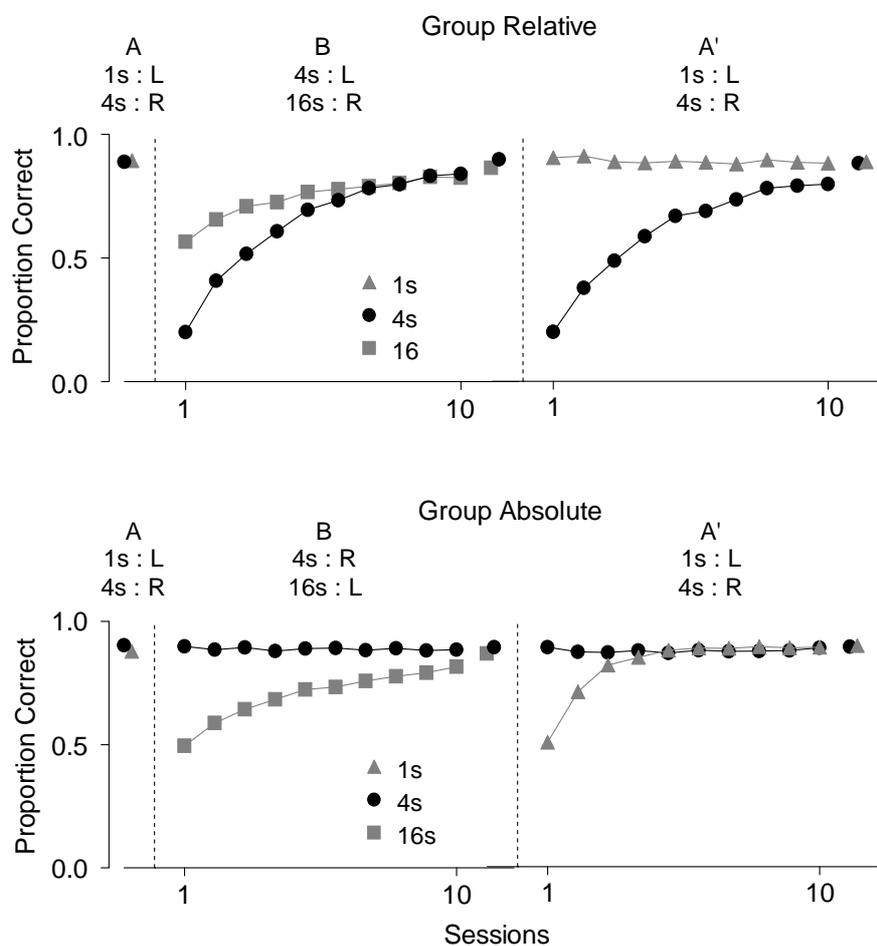


Figure 4. Predictions of the LeT model for the Upshift groups. Top. Proportion of correct responses for the Relative group following each sample (1 s, 4 s, or 16 s) at the end of Phase A, during the first 10 sessions and at the end of Phase B, and during the first 10 sessions and at the end of Phase A'. Bottom. Corresponding predictions for the Absolute group. The dotted vertical lines separate experimental phases.

The top panel corresponds to the Relative Upshift group and the bottom panel to the Absolute Upshift group. In each panel, the sets of data points from left to right show the proportion of correct responses in the last session of Phase A, in the first 10 sessions and in the last session of Phase B, and in the first 10 sessions and in the last session of Phase A'. Of particular relevance to the Relative versus Absolute issue are the acquisition curves during Phases B and A'. Three aspects of these curves are noteworthy. First, consistent with the Absolute Hypothesis, LeT predicts that, during the first sessions of Phase B, the Relative group will perform poorly following the 4-s sample, whereas the Absolute group will perform accurately following the same sample (compare circles in top and bottom panels during Phase B). The reason for the difference is that the states most active following the 4-s sample will have been associated with the 'right' response during Phase A, but during Phase B that response remains the correct response only for the Absolute group. These predictions are the opposite of the results obtained by Church and Deluty (1977). Second, during the first sessions of Phase B, both groups will perform near chance following the 16-s sample (compare squares in top and bottom panels) because the states active at the end of this sample will not have been active during the previous phase and therefore they maintain their initial link strength. Behaviorally one could say that 16 s is practically outside the basin of the 4-s generalization gradient established during the previous phase and therefore the animal remains indifferent between the two choices. Church and Deluty (1977) did not report choice proportions following the 16-s sample. Third, according to LeT the two groups will reach high accuracy levels on both samples, a prediction also at odds with Church and Deluty's findings.

During the first sessions of Phase A', the Relative group again will perform poorly following the 4-s sample but accurately following the 1-s sample. The reason for the latter is temporal generalization – the states that are active at the end of 1-s sample will have been active during some of the 4-s trials of Phase B and, on those trials, their association with the 'left' response will have been further strengthened. In other words, reinforcement of the '4s→left' discriminated operant during Phase B will have generalized to 1 s and this generalization effect will contribute to correct performance on the '1s→left' trials during Phase A'. According to LeT, then, we have here an interesting asymmetry: Whereas the '4s→left' discrimination training in Phase B helps the '1s→left' discrimination training in Phase A', the '4s→right' discrimination training in Phase A does not help the '16s→right'

discrimination training in Phase B. Generalization from 4 s to 1 s is substantially greater than from 4 s to 16 s. We will see another instance of this asymmetry below.

Concerning the Absolute group, performance in Phase A' following the 4-s sample will remain accurate, but performance following the 1-s sample will fall to chance, again because of temporal generalization – on some 4-s trials of Phase B, the states active after 1-s sample will have been active but, unlike for the Relative group, on those occasions their links with the 'left' response will have been weakened. In other words, reinforcement on the '4s→right' trials of Phase B will have generalized to 1 s but this generalization effect will contribute to incorrect performance during Phase A'.

Figure 5 shows the model predictions for the Downshift groups. According to LeT, during Phases B and A', group Relative (top panel) will perform poorly following the 4-s sample, whereas group Absolute (bottom panel) will perform accurately following the same sample. The reasons are the same as for the Upshift groups. Concerning the 1-s and 16-s samples, the Relative group will perform accurately following either sample, but the Absolute group will perform poorly following the 1-s sample during the first sessions of Phase B, and accurately following the 16-s sample throughout Phase A'. The difference between the 1-s and 16-s acquisition curves is another instance of the asymmetry mentioned above, that generalization from 4 s to 1 s is substantially greater than from 4 s to 16 s. In this case, the '4s→left' discrimination training during Phase A harms the '1s→right' discrimination training during Phase B, but the '4s→left' discrimination training during Phase B does not harm the '16s→right' discrimination training during Phase A'.

To summarize, a) performance following the 4-s sample is always disrupted in the Relative group, but never disrupted in the Absolute group; b) performance following the 1-s and 16-s samples is either equal in the two groups or better in the Relative group; and c) due to differences in the degree of overlap between the generalization gradients of 1 s, 4 s, and 16 s, performance following the 1- or 16-s samples differs between the Upshift and Downshift groups. The model's predictions offer a clear standard against which experimental results may be compared.

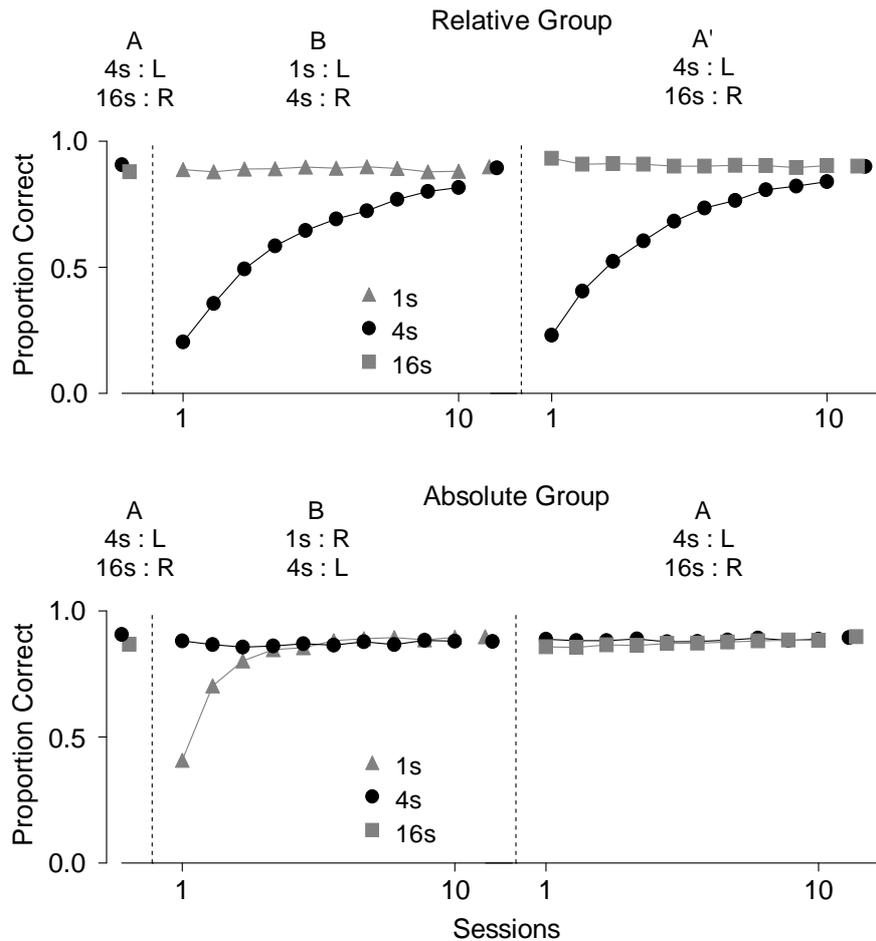


Figure 5. Predictions of the LeT model for the Downshift groups. Top. Proportion of correct responses for the Relative group following each sample (1 s, 4 s, or 16 s) at the end of Phase A, during the first 10 sessions and at the end of Phase B, and during the first 10 sessions and at the end of Phase A'. Bottom. Corresponding predictions for the Absolute group. The dotted vertical lines separate experimental phases.

## 2. Method

### 2.1. Subjects

Sixteen pigeons (*Columba livia*) participated in the experiment. They were housed individually in a colony room with a 12:12 h light:dark cycle with lights on at 8:00 am. Throughout the experiment the pigeons were maintained at 80% of their free-feeding body weight, with free access to water and grit in their home cages. Seven pigeons (P068, P093, P236, P572, P665, P795, and P816) were experimentally naïve, and the remaining nine had experimental histories unrelated to temporal bisection tasks.

## ***2.2. Apparatus***

The experiment used five standard operant chambers from Med Associates, each equipped with three keys and a feeder on the intelligence panel. The keys measured 2.5 cm in diameter, were arranged in a row, 18.5 cm from the floor grid, centered on the panel, and 9 cm apart, center to center. The central key could be illuminated with a white light and the side keys could be illuminated with a red light. The 6 x 5 cm feeder opening was located below the central key, 3.5 cm above the floor grid. A 7.5-W light illuminated the mixed grain when the feeder was activated. On the back panel of the chamber, a 7.5-W houselight provided general illumination. The operant chamber was enclosed by an outer box that contained a fan to circulate air and help to mask extraneous noises. A personal computer programmed in Visual Basic 2005 controlled the experimental events and recorded data. The program interfaced with the Whisker software (Cardinal & Aitken, 2010) to communicate with the chambers and time events with a resolution of 1 ms.

## ***2.3. Procedure***

After the birds learned (or re-learned) to peck the side keys, illuminated with red light, through autoshaping, the experiment began. Each session comprised 60 trials separated by a dark 30-s ITI. Each trial began with the simultaneous illumination of the houselight and the center key with white light. After the sample duration elapsed, the center key was turned off and the side keys were illuminated with red light. Pecking on either side key turned both keylights off. If the choice was correct, the feeder was raised for an individually adjusted duration (range 2 s to 6 s) and then the ITI started; if the choice was incorrect, the ITI started immediately and the trial was repeated (correction method). During the first session, whenever a trial was repeated, only the correct comparison key was presented after the sample. During the second session, after two consecutive errors, only the correct comparison key was presented. From the third session onward, after three consecutive errors, only the correct comparison key was presented. With this arrangement we intended to promote learning while simultaneously reducing the number of correction trials, particularly during the first sessions of each phase. Correction trials were never included in the data analyses.

Table 1. Experimental design. Four groups (Relative Upshift, Absolute Upshift, Relative Downshift, and Absolute Downshift) were exposed to an ABA design. In the three rightmost columns, each cell shows the two sample durations. The left sample was assigned to the ‘left’ key and the right sample to the ‘right’ key.

Trend	Mapping	Pigeon	Phase		
			A	B	A'
Upshift	Relative	PG26	1-4	4-16	1-4
		P572	1-4	4-16	1-4
		P508	4-1	16-4	4-1
		P068	4-1	16-4	4-1
	Absolute	P876	1-4	16-4	1-4
		P435	1-4	16-4	1-4
		P795	4-1	4-16	4-1
		P236	4-1	4-16	4-1
Downshift	Relative	P434	4-16	1-4	4-16
		P454	4-16	1-4	4-16
		P053	16-4	4-1	16-4
		P665	16-4	4-1	16-4
	Absolute	P877	4-16	4-1	4-16
		P093	4-16	4-1	4-16
		P784	16-4	1-4	16-4
		P816	16-4	1-4	16-4

The pigeons were divided into four groups and each group was exposed to three phases according to an ABA design. Table 1 shows the details. Half of the pigeons learned first the discrimination involving the short samples of 1 s and 4 s (Upshift) and the other half learned first the discrimination involving the long samples of 4 s and 16 s (Downshift). Within each of these groups, half belonged to the Relative group and the other half belonged to the Absolute group. The two numbers in each cell of Table 1 represent the sample duration assigned to the ‘left’ and ‘right’ keys, respectively. Thus, as Table 1 shows, the correct choice following each sample was fully counterbalanced across birds. Sessions ended after 30 presentations of each sample (excluding correction trials) in random order.

Each phase continued until a) the proportion of correct choices following each sample equaled at least 90% for three consecutive sessions, and b) a minimum number of sessions

had taken place (15, 20, and 10 for Phases A, B, and A', respectively). The number of training sessions remained similar to that used by Church and Deluty (1977).

### 3. Results

All pigeons learned the discriminations. They required 17.4 sessions on average to complete Phase A (range: 15-24), 20.1 for Phase B (range: 11-25<sup>3</sup>), and 10.8 for Phase A' (range: 10-15).

Figure 6 shows the average data for the Upshift pigeons. The top and bottom panels correspond to the Relative and Absolute groups, respectively. For the Relative group, proportion correct following the 4-s sample decreased to chance in Phase B and below chance in Phase A' and then, in both cases, it increased. Concerning the other sample, in Phase B, proportion correct following the 16-s sample started slightly above chance and tended to be higher than proportion correct following the 4-s sample. In Phase A' proportion correct following the 1-s sample remained as high as in Phase A. The overall pattern of results for this group is consistent with LeT (compare the top panels of Figures 4 and 6).

For the Absolute group, in Phase B, proportion correct decreased to chance following the 4-s sample and started at chance following the 16-s sample. In both cases, it then increased. During Phase A', proportion correct following 1-s sample decreased to chance and then increased rapidly, whereas following 4-s sample it remained relatively high. The overall pattern of results is only partially consistent with LeT. The major discrepancy between data and model is the severe disruption of performance following the 4-s sample during Phase B, which the model did not predict (compare the bottom panels of Figures 4 and 6).

Figure 7 shows the average data for the Downshift pigeons. For the Relative group, proportion correct following the 4-s sample decreased significantly in the first session of Phases B and A' and then it increased with training. Proportion correct following the 1-s sample in Phase B started significantly above chance, and following the 16-s sample in Phase A' remained as high as in Phase A. For the Absolute group, proportion correct following the 4-s sample decreased slightly in the beginning of Phases B and A'. Concerning the other samples, in Phase B, proportion correct following the 1-s sample started significantly below chance and then it increased, whereas in Phase A', proportion correct following 16-s sample

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<sup>3</sup> One pigeon was accidentally moved to Phase A' after 11 sessions, although its proportion correct following each sample was above 90% during the last three sessions of Phase B.

decreased slightly with respect to Phase A. The overall pattern of results for the Downshift pigeons is consistent with LeT (compare Figures 5 and 7).

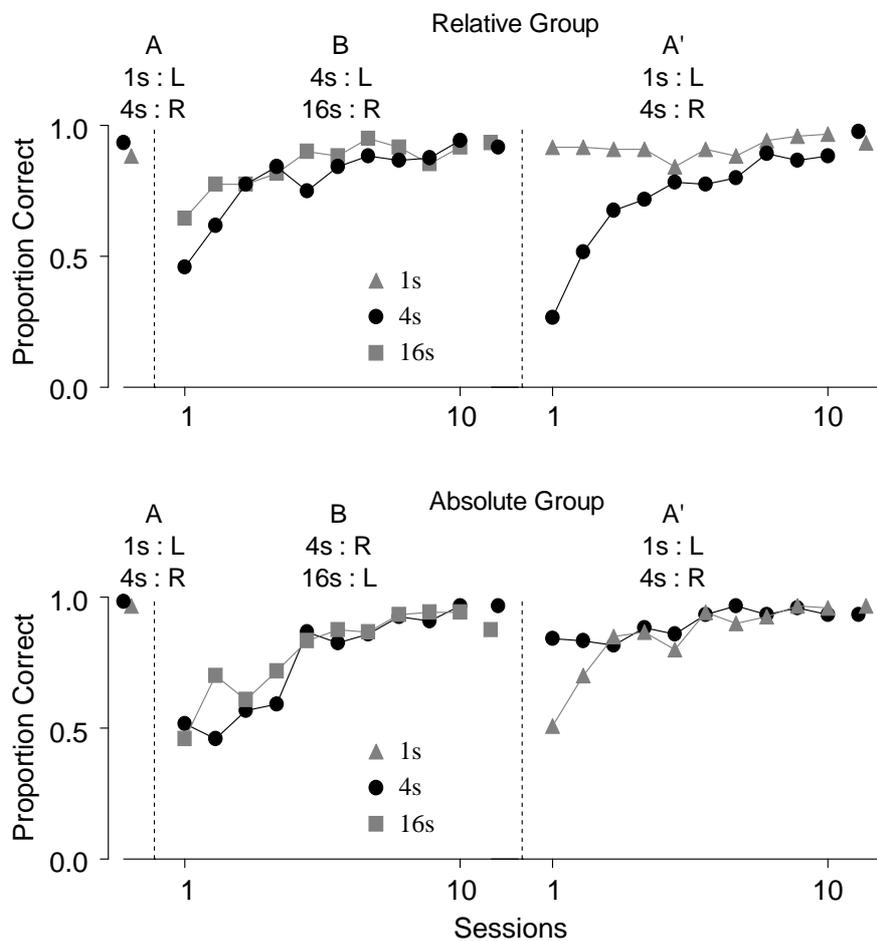


Figure 6. Obtained results for the Upshift groups. Top. Proportion of correct responses for the Relative group following each sample (1 s, 4 s, or 16 s) at the end of Phase A, during the first 10 sessions and at the end of Phase B, and during the first 10 sessions and at the end of Phase A'. Bottom. Corresponding results for the Absolute group. The dotted vertical lines separate experimental phases.

To assess the statistical significance of the foregoing results, we conduct mixed ANOVAS with Mapping (Relative vs. Absolute) or Trend (Upshift vs. Downshift) as the between-subjects factors and Session (10 levels for the first 10 sessions) as the within-subjects factor. To better understand the ANOVA results, Figure 8 re-plots the acquisition curves in a different way. The left and right panels show the acquisition curves for Phases B and A', respectively, and the top, middle, and bottom panels show the acquisition curves for the 4-s, 1-s, and 16-s samples, respectively. The inset graphs show the model's predictions. Consider the 4-s sample. According to LeT, the 2 x 2 x 10 mixed ANOVA should yield the

following significant effects: a) main effect of Mapping because overall the Absolute groups (unfilled symbols) should perform better than the Relative groups (filled symbols); b) a main effect of Session because proportion correct should increase with learning; and, more importantly, c) an interaction between Session and Mapping because the Relative groups should start near indifference and then learn across sessions, whereas the Absolute groups should start at a high value and maintain accurate performance across sessions. For Phase B, the ANOVA yielded only part of the predicted pattern of results, significant effects of Session [ $F(9, 108) = 35.1, p < .001$ ] and Session x Mapping [ $F(9, 108) = 5.28, p < .001$ ], but not of Mapping [ $F(1, 12) = 0.35$ ]; the other effects also were not significant except the three-way interaction Session x Mapping x Trend [ $F(9, 108) = 5.71, p < .001$ ]. The reason for the three-way interaction is that the acquisition curves of the Relative and Absolute groups differed between the Upshift and Downshift conditions. For Phase A', the ANOVA yielded the predicted pattern of results, significant main effects of Sessions [ $F(9, 108) = 20.8, p < .001$ ], Mapping [ $F(1, 12) = 9.08, p = .01$ ], and Sessions x Mapping [ $F(9, 108) = 8.87, p < .001$ ]; all remaining effects were not significant ( $p > .05$ ).

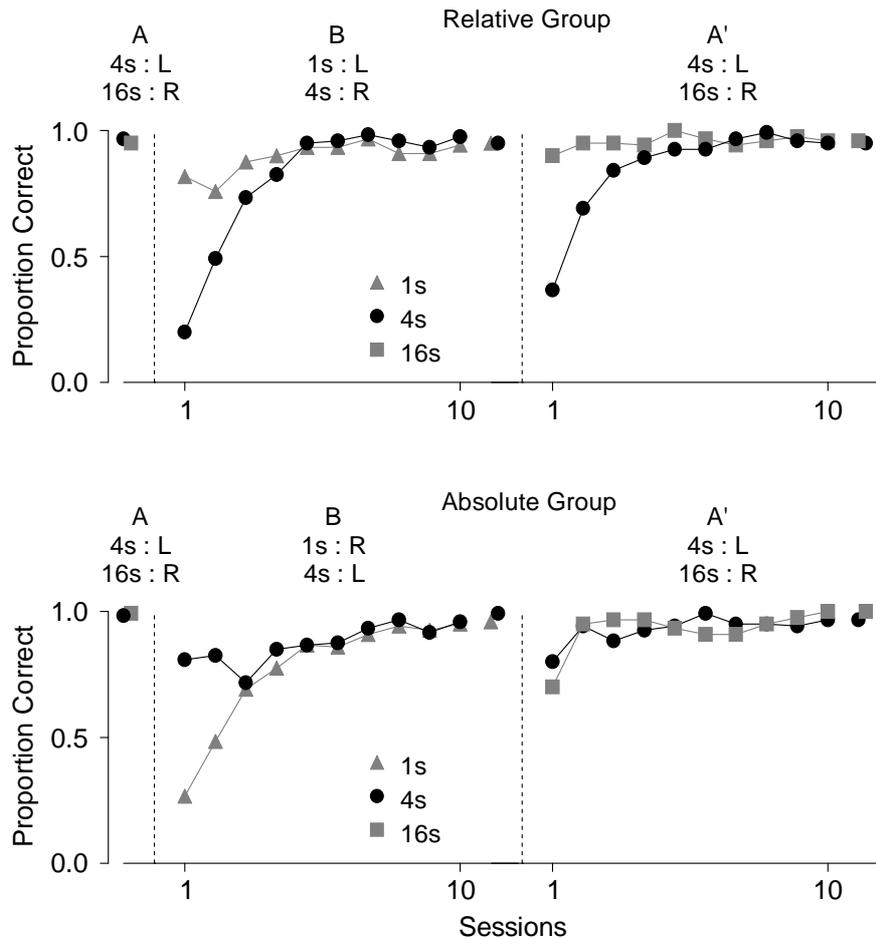


Figure 7. Obtained results for the Downshift groups. Top. Proportion of correct responses for the Relative group following each sample (1 s, 4 s, or 16 s) at the end of Phase A, during the first 10 sessions and at the end of Phase B, and during the first 10 sessions and at the end of Phase A'. Bottom. Corresponding results for the Absolute group. The dotted vertical lines separate experimental phases.

Consider now the 1-s sample. According to LeT, the 2 x 10 ANOVA should yield significant effects of Session (overall improvement with training), Mapping (Relative better than Absolute), and, more importantly, Session x Mapping interaction (group Relative should show accurate performance across sessions, but group Absolute should start at indifference and then improve). The ANOVA for Phase B yielded the predicted pattern, significant effects of Session [ $F(9, 54) = 14.2, p < .001$ ], Mapping [ $F(1, 6) = 17.95, p < .005$ ], and Session x Mapping [ $F(9, 54) = 5.5, p < .001$ ]. The ANOVA for Phase A' yielded significant effects of Session [ $F(9, 54) = 13.2, p < .001$ ] and Session x Mapping [ $F(9, 54) = 10.1, p < .001$ ], but not of Mapping [ $F(1, 6) = 3.08, p = .13$ ].

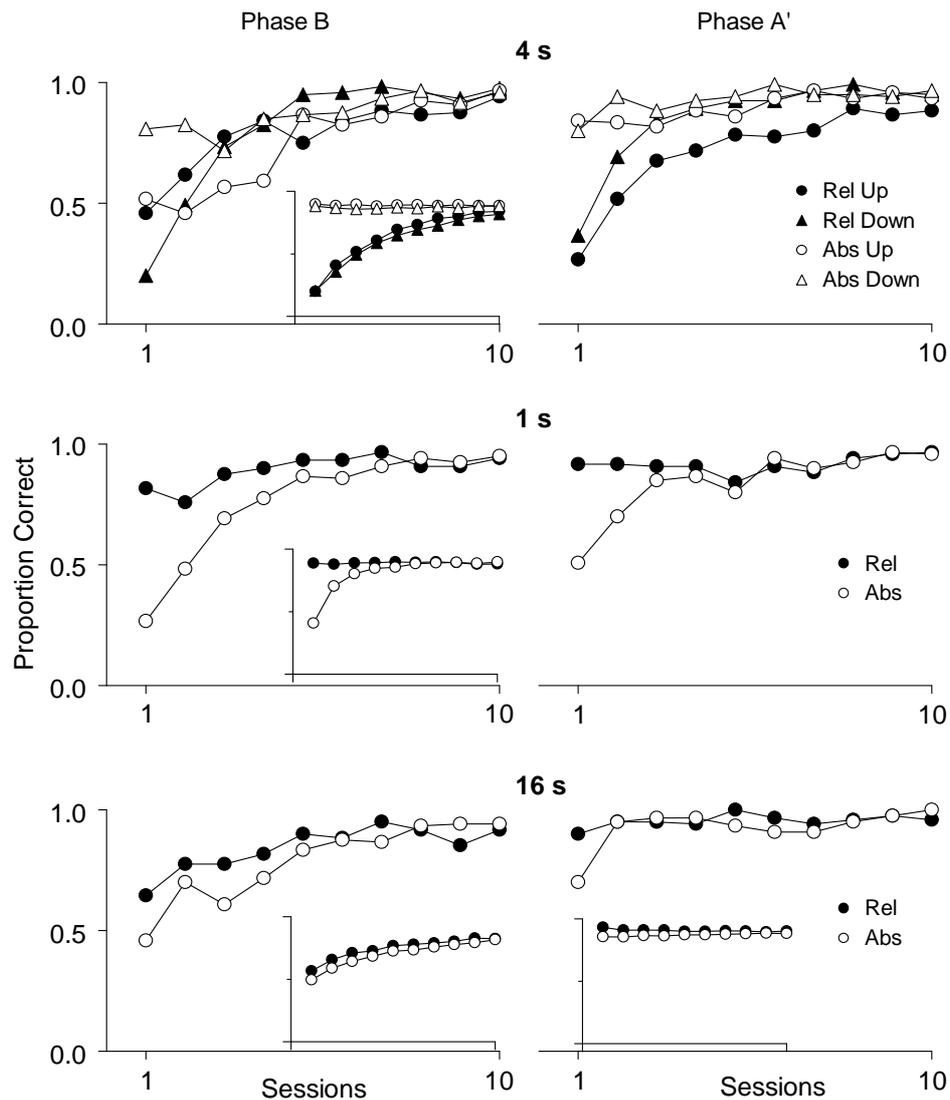


Figure 8. Average acquisition curves for Phases B (left panels) and A' (right panels) following the 4-s sample (top), 1-s sample (middle), and 16-s sample (bottom). The inset graphs show the corresponding model predictions.

With respect to the 16-s samples, LeT predicts that the 2 x 10 ANOVA for Phase B should yield a significant effect of Session, but no effect of Mapping or Session x Mapping. The ANOVA yielded the predicted pattern, for only the Session effect was significant [ $F(9, 54) = 7.6, p < .001$ ]. For Phase A', LeT predicted no significant effects, not even of Session because both groups should perform accurately since the first session. However, the ANOVA yielded a significant Session effect [ $F(9, 54) = 2.7, p = .01$ ] because the first session yielded lower scores than the remaining sessions. In summary, the obtained statistical results were generally consistent with the predicted effects. The major exception occurred in Phase B with group Absolute Upshift following the 4-s sample.

The effects of the two phase transitions were stronger during the first session of each new phase. To better understand these effects, Figure 9 shows side by side the model predictions and the data (mean  $\pm$  SEM) from the first session of Phase B (top four panels) and the first session of Phase A' (bottom four panels). LeT (left panels) predicts always an interaction between sample duration and group such that, for group Relative, proportion correct at 4 s is lower than at the other sample duration, but the opposite is the case for group Absolute. The data showed the predicted interaction: The four between-within ANOVAS with Mapping as the between-subjects factor and Sample Duration as the within-subjects factor all yielded significant interactions at the .05 level. For the Relative group performance was disrupted more following the 4-s sample than the other sample, whereas for the Absolute group the opposite was generally the case. The major discrepancy between model and data occurred during Phase B in the Upshift groups following the 4-s sample (compare top two panels in Figure 9).

The data also revealed differences between the Upshift and Downshift groups, particularly during Phase B. The relevant comparisons are indicated by corresponding letters in the top two panels of Figure 9. As the two a's show, proportion correct following 4-s sample was higher in the Relative Upshift group (.46) than in the Relative Downshift group (.20;  $t(6) = 2.79$ ,  $p = .02$ ). Similarly, the two b's show that proportion correct following 4-s sample was lower in the Absolute Upshift group (.52) than in the Absolute Downshift group (.81;  $t(6) = 2.22$ ,  $p = .03$ ). These differences are not predicted by LeT.

With the other samples, the differences between the Upshift and Downshift groups were similar but less reliable. Thus, as the two c's show, proportion correct following 16-s sample in the Relative Upshift group (.65) was lower than proportion correct following 1-s in the Relative Downshift group (.82), but the difference was not statistically significant ( $t(6) = 1.47$ ,  $p = .10$ ). And as the two d's show, proportion correct following the 16-s sample in the Absolute Upshift group (.46) was higher than proportion correct following the 1-s sample for the Absolute Downshift group (.27), but the difference was only marginally significant ( $t(6) = 1.93$ ,  $p = .05$ ). LeT predicts the same pattern of differences, although more extreme for the Relative groups and less extreme for the Absolute groups.

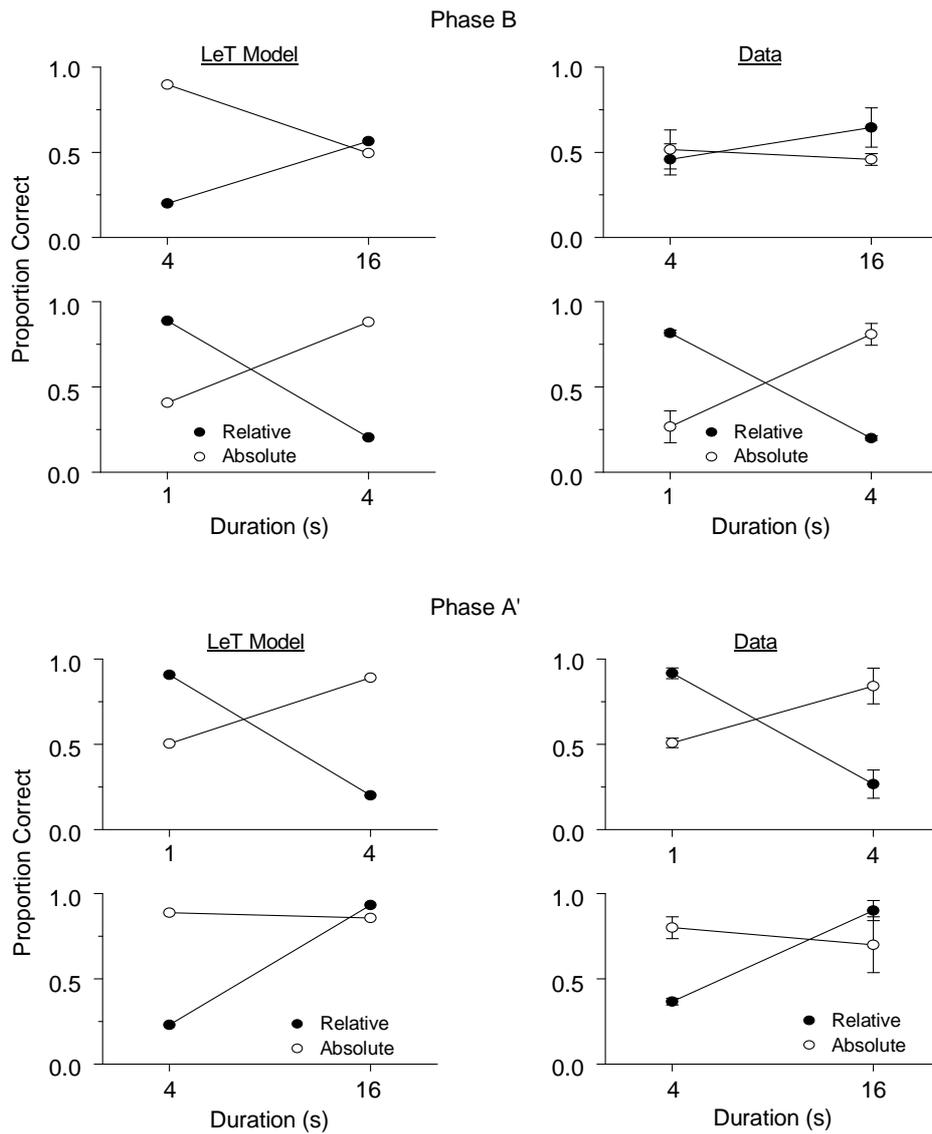


Figure 9. Each row shows the predicted (left) and obtained (right) average proportions of correct responses ( $\pm$  SEM) as a function of sample duration for the Relative and Absolute groups. The data come from the first session of Phase B (top four panels) and Phase A' (bottom four panels).

Most of our results were consistent with the Absolute Hypothesis as the LeT model instantiates it. The differences between the acquisition curves of the Relative and Absolute, Upshift and Downshift groups (Figures 6, 7, and 8), and the overall pattern of results during the first session of a new phase (Figure 9) were generally consistent with LeT. However, there was one major discrepancy, the severely disrupted performance of the Absolute Upshift group following the 4-s sample, a result that LeT did not predict. Figure 10 shows the individual data for this group: Three of the four pigeons showed disrupted performance on the 4-s sample in the first session and one (P795) showed it in the second session;

performance on the 16-s sample started close to indifference, as LeT predicted. It was also the case that for pigeons P876 and P795, there seemed to be a negative covariation during the first sessions between proportion correct following 4-s sample and proportion correct following 16-s sample. We conclude that the major discrepancy between model and data was reliable across pigeons.

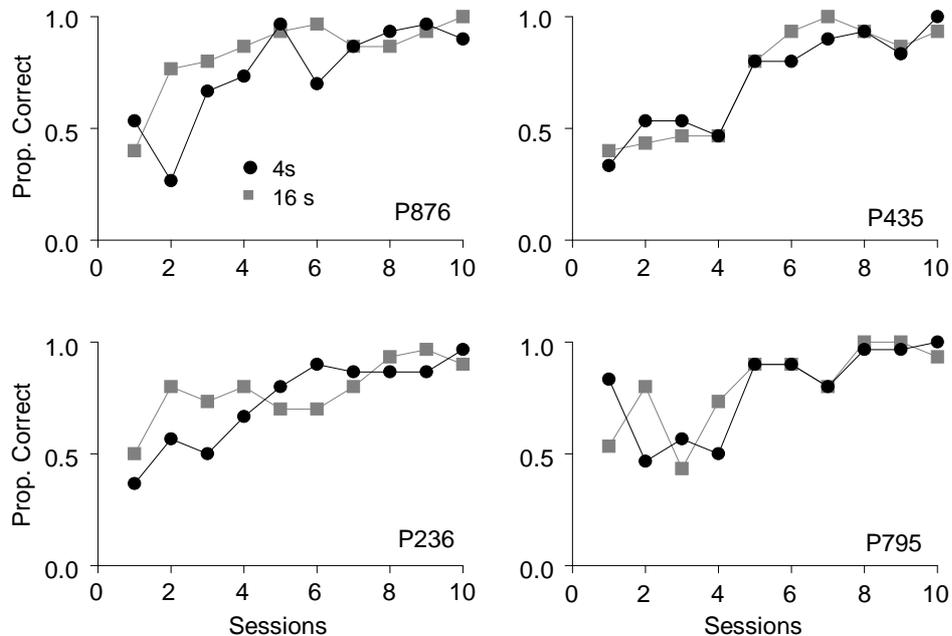


Figure 10. Individual data for the Absolute Upshift group during the first 10 sessions of Phase B. The symbols show proportion correct following 4-s and 16-s samples.

#### 4. Discussion

The present study investigated the issue of Relative versus Absolute stimulus control in the temporal bisection task. We first trained pigeons in one task and then compared how they learned two new tasks, one that maintained the mapping between relative sample durations and the two response keys, and one that reversed it. If the pigeons had learned the relational form of the first task, then they should learn the task that preserved it faster than the task that reversed it. On the other hand, if the pigeons had learned only the absolute form of the task, the opposite should be the case.

The present study improved and extended Church and Deluty's (1977) seminal work by changing the design from AB to ABA – a change that provided two occasions to obtain acquisition curves –, simplifying the subjects' experimental history (i.e., no phase preceded

Phase A), doubling the number of subjects in each group, analyzing the data in greater depth (e.g., we examined the results not only from the 4-s sample but also from the 1-s and 16-s samples), and extending the work to another animal species.

On a more theoretical note, the study also compared the data with the predictions of the Learning-to-Time (LeT) model. The model represents one way of instantiating the Absolute Hypothesis because it shows us what to expect if performance on the bisection task depended exclusively on stimulus generalization gradients (via state activation), and the learning of which key to choose following each sample duration (via associative links); nowhere in the model are sample stimuli represented or categorized relationally as ‘short’ or ‘long’. Moreover, in contrast with other timing models (e.g., SET, BeT, BEM), LeT predicts not only steady state performance but also acquisition. For these reasons, we consider LeT a plausible null hypothesis – only if the empirical evidence clearly rejects it will we entertain the arguably more complex Relational Hypothesis.

In what follows we summarize our empirical findings concerning the Relative and Absolute mappings as well as the Upshift and Downshift trends, compare these findings with the model’s predictions and with Church and Deluty’s (1977) results, and finally discuss their implications for the absolute versus relational issue in the time domain.

#### ***4.1. Relative versus absolute mappings***

Our results showed that in the Relative group performance was always disrupted more following the common (4-s) sample than the other (1-s or 16-s) sample (Figures 6 and 7, top panels). In the Absolute group, the opposite was generally, but not always, the case, that is, performance following the 1-s or 16-s samples was generally disrupted more than performance following the 4-s sample (Figures 6 and 7, bottom panels). These effects were most clear during the first session of each new phase (Figure 9, right panels).

The foregoing results are partly consistent with LeT. On the one hand, LeT correctly predicts that performance will be disrupted mainly following the common sample in the Relative group, and mainly following the other samples in the Absolute group. On the other hand, the model did not predict the severe disruption in performance following the common sample in the Absolute Upshift group. We return to this major discrepancy below.

LeT predicts a difference in the magnitude of the disruptions between the Relative and Absolute groups because these two disruptions have different causes. According to the model, the Relative group chooses the wrong key following the 4-s sample because pecking that key was *directly reinforced* during the previous phase. More specifically, during the

preceding phase the states most likely to be active at the end of the 4-s sample became strongly linked with the (now) incorrect key. In contrast, the Absolute group chooses the wrong key following the 16-s or 1-s samples because of *initial conditions* (16-s sample) or *stimulus generalization* (1-s sample). When the 16-s sample is presented for the first time in Phase B (i.e., Upshift group), the animal makes incorrect choices on about 50% of the trials because the states that are active after 16 s did not become active during the 4-s trials of Phase A and for that reason they maintained their initial (and equal) associations with the two responses. But when the 1-s sample is presented for the first time in Phase B (i.e., Downshift group), the animal makes incorrect choices because the states that are active after 1 s became active during some of the 4-s trials of Phase A and on those trials the association with the (now) incorrect key was strengthened.

Because direct reinforcement biases the associative links more than stimulus generalization or the initial conditions, LeT predicts that the disruption following the 4-s sample in the Relative group will be more severe than the disruption following the 16-s or 1-s samples in the Absolute group (in Figures 4 and 5, compare the first circles of each curve in the top panels with the first triangles and squares of each curve in the bottom panels). The data supported this prediction: Averaged across the first session of Phase B and the first session of Phase A', the proportion of correct choices following the common sample equaled .32 for the Relative group, whereas the proportion of correct choices following the new sample (1 s or 16 s) equaled .48 when for the Absolute group,  $t(14) = 2.52$ ,  $p = .025$ . In fact, the model's predictions for the first session of Phase B and the first session of Phase A' (see Figure 9, left panels) correlate strongly ( $r = .84$ ) with the data (Figure 9, right panels).

#### ***4.2. Upshift versus downshift groups***

The data also revealed a few differences between the Upshift and Downshift groups. These differences are important because they show that performance does not depend exclusively on the ratio between the two sample durations. Although this ratio remained constant for all groups and phases, the magnitude of the disruptions during phase transitions varied. If the ratio of sample durations determines their discriminability, then we conclude that performance in general and the disruptions in particular depend on more than discriminability.

The largest differences between the Upshift and Downshift groups occurred during Phase B and they involved the common, 4-s sample. The LeT model cannot account for these differences because LeT predicts equally severe disruptions for the Upshift and Downshift

Relative groups and no significant disruptions for the Upshift and Downshift Absolute groups. With respect to the other samples, according to LeT the differences between the Upshift and Downshift groups stem from the degree of overlap of the three generalization gradients. Training the '1s→left, 4s→right' mapping during Phase A, for example, will have only a weak effect on the tendency to peck 'right' following the 16-s sample because the gradient centered at 4 s does not extend appreciably to 16 s. Hence, performance during the first session with 16-s sample should be close to chance (see also Siegel, 1986). In contrast, training the '4s→left, 16s→right' mapping during Phase A will have a strong effect on the tendency to peck 'left' following 1-s sample because the gradient centered at 4 s extends appreciably to 1 s; hence performance during the first session with 1-s sample should be above chance.

#### ***4.3. Revisiting Church and Deluty (1977)***

Figure 11 compares our results with those reported by Church and Deluty (1977). For the Relative group, the three curves overlap, showing that rats and pigeons behaved similarly. The average curves had the typical negatively accelerated exponential shape. But for the Absolute group the curves do not overlap, for the pigeon curves are systematically above the rat curve. Interestingly, however, the curve from Phase B has roughly the same shape as the rat curve, concave up during the first sessions and concave down during the last sessions.

The results from the Absolute groups raise two interrelated questions. First, why were the acquisition curves from Phase B concave up initially? And second, why did accuracy following the common sample decrease in the Upshift group if the animals continued to receive food for choosing the same key as in the previous phase? The concave up initial segment may have resulted from the fact that, during the first sessions of Phase B, two pigeons showed negative covariations between the two discriminated operants (see Figure 10, pigeons P876 and P795). When proportion correct following the new sample increased, proportion correct following the common sample decreased.

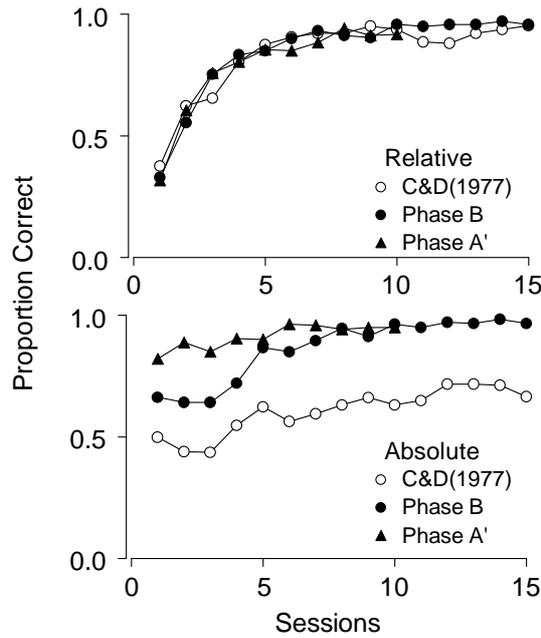


Figure 11. Top. Average proportion of correct responses following the 4-s sample for the Relative group. The three data sets correspond to the rat data from Church and Deluty's (1977) study, and the pigeon data from the present study during Phases B and A'. Bottom. Corresponding data for the Absolute group.

We do not know whether these negative covariations occurred in Church and Deluty's (1977) study and what their causes might be. One possibility is that the extinction periods that necessarily occur during phase transitions reduce temporarily the control exerted by the conditional stimulus and strengthen positional biases. Consider the data from P795 in Figure 10. During the first session of Phase B, pigeon P795 preferred the Right key following the 4-s sample (83% of correct choices) and was indifferent between the two keys following the 16-s sample (53% of correct choices). Presumably because 'right' key choices following the 16-s sample were not reinforced, the pigeon started to choose the 'left' key following these longer samples and receive more rewards for pecking that key. It seems that, at that moment, location gained control over responding and, *regardless of sample duration*, choices became increasingly biased toward the 'left' key. This positional bias was revealed by the worsening of performance following the 4-s sample (47% correct choices in session 2) concomitant with the improvement of performance following the 16-s sample (80% correct choices by session 7). But then the effect of extinction of 'left' choices following the 16-s sample may have had its effect and performance fell to chance in sessions 3 and 4; finally, temporal control by sample duration gradually increased. We have observed similar negative covariations in naïve

pigeons when first exposed to a bisection task. Clearly, the dynamics of the process remain to be worked out, but they are beyond the scope of the LeT model.

Concerning the disruption of performance following the 4-s sample, the challenge is to explain why it happened in the Upshift group but not in the Downshift group in Phase B. The difference between the two groups seems incompatible with both the Absolute and the Relational Hypothesis because none can explain in a principled way why performance following the common sample should be disrupted severely when the other sample is longer than the common sample (Upshift group) but not when it is shorter (Downshift group). We suggest a new account. In the Absolute Upshift group, the new, 16-s sample may have functioned as an extinction trial for the 4-s common sample because a longer interval necessarily includes a shorter interval (see also Russell & Kirkpatrick, 2007, Experiment 1, for a similar idea). If the first 4 s of the 16-s sample functions like an extinction trial for the common sample, then performance following the common sample should approach indifference. In contrast, in the Absolute Downshift group the new, 1-s sample would not function as an extinction trial for the common 4-s sample and therefore performance following the common sample should remain accurate. The account becomes more plausible if one considers that the pigeons may have acquired distinct behavioral patterns during the sample (Machado & Keen, 1999). For example, during Phase A the pigeons from the Absolute Upshift group may have started the trials by approaching the key associated with the 1-s sample, stayed near that key and then, when the sample continued, moved to the key associated with the 4-s sample. During the first session of Phase B, the pigeons from this group would have stayed near the key associated with the 4-s sample during most of the new 16-s sample, perhaps pecked that key at the end of the sample (stimulus generalization) and received no reinforcement. If the interval spent near the key associated with the 4-s sample was functionally similar to an extinction period, proportion correct following the common sample would have decreased, as it did. The foregoing account remains speculative but it can be tested by recording the pigeon's behavior during the sample (e.g., Machado & Keen, 2003) or by defining the comparison stimuli by key color instead of location. If the account is correct, in the latter case the disruptions should not differ between the Upshift and Downshift Absolute groups.

The present study does not support Church and Deluty's (1977) conclusion that a new bisection task is learned faster when it preserves the relational rather than the absolute mapping of the previous task. In fact, the results are more complex because each bisection

task comprises two samples and therefore statements about the learning speed for one sample may not hold for the other sample. In addition, the effects on the new bisection task seem to depend on whether the previous task used longer or shorter sample durations. When the various acquisition curves are taken into account (i.e., Relative and Absolute, Upshift and Downshift), the data seem closer to the Absolute than the Relational Hypothesis.

To conclude, we do not claim that rats and pigeons can learn only about the absolute durations of stimuli. In fact, some studies have already shown that at least pigeons can respond relationally to two temporal intervals (e.g., Dreyfus, 1992; Fetterman & Dreyfus, 1986). But, in contrast with the bisection task, these studies involved explicit training of relational responding with multiple pairs of sample durations. We claim instead that there is no reliable evidence for relational learning in the temporal bisection task. More positively, most of our findings followed the pattern predicted by the LeT model, a simple instantiation of the Absolute Hypothesis. And, though the model failed to account for a subset of the results, its overall goodness of (qualitative) fit suggests that, in the bisection task, temporal control is mostly absolute.

**CHAPTER III<sup>4</sup> – STUDY 2: FURTHER TESTS ON THE RELATIONAL VERSUS ABSOLUTE DISPUTE IN THE TEMPORAL BISECTION TASK**

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<sup>4</sup>This Chapter reproduces the publication

Carvalho, M. P., Machado, A., & Tonneau, F. (in press). Learning in the temporal bisection task: Relative or absolute? *Journal of Experimental Psychology: Animal Learning and Cognition*. Changes were made to the formatting style, but not to the content presented in the original paper.

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### **Abstract**

We examined whether temporal learning in a bisection task is absolute or relational. Eight pigeons learned to choose a 'red' key after a  $t$ -seconds sample and a 'green' key after a  $3t$ -seconds sample. To determine whether they had learned a relative mapping ('short  $\rightarrow$  red, long  $\rightarrow$  green') or an absolute mapping (' $t$ -seconds  $\rightarrow$  red,  $3t$ -seconds  $\rightarrow$  green'), the pigeons then learned a series of new discriminations in which either the relative or the absolute mapping was maintained. Results showed that the generalization gradient obtained at the end of a discrimination predicted the pattern of choices made during the first session of a new discrimination. Moreover, most acquisition curves and generalization gradients were consistent with the predictions of the Learning-to-Time model, a Spencean model that instantiates absolute learning with temporal generalization. In the bisection task, the basis of temporal discrimination seems to be absolute, not relational.

*Keywords:* relational vs. absolute, generalization gradients, temporal bisection, Learning-to-Time model (LeT), pigeons



## 1. Introduction

Gestalt psychologist Wolfgang Köhler proposed that animals are able to respond to relations between stimuli. In one study, Köhler (1918/1938) gave chickens a choice between a bright gray and a dark gray rectangle, and reinforced choosing the bright gray. Afterwards, given a choice between the reinforced bright gray and a new, brighter gray, the birds chose the new brighter gray. Köhler concluded that his subjects had learned to choose the brighter stimulus, and then transposed this relational form to the test trials. Other studies with different species and stimulus dimensions yielded similar results (e.g., Anderson, Awazu, & Fujita, 2004; Manabe, Murata, Kawashima, Asahina, Okutsu, 2009; Pepperberg & Brezinsky, 1991; Riley, Goggin, & Wright, 1983; Saldanha & Bitterman, 1951; Schusterman & Krieger, 1986; Wiegmann, Wiegmann, MacNeal, & Gafford, 2000; Wright, Cook, & Kendrick, 1989; for a review, see Lazareva, 2002).

Spence (1936, 1937) questioned Köhler's interpretations. He reasoned that if, during the initial training, an excitatory gradient formed around the S+ and an inhibitory gradient formed around the S-, the sum of the two gradients could yield a net gradient with an excitatory peak at the new brighter gray. This peak could explain the preference for the new stimulus. According to Spence, we may not need to invoke relational processes if the interaction of simple excitatory and inhibitory generalization gradients predicts transposition (see also Mackintosh, 1974).

However, additional studies showed that the interaction of generalization gradients could not explain all instances of relational responding (e.g., the 'intermediate size problem'; see Reese, 1968; Riley, 1968). It seems that both absolute and relational forms of responding may take place, although it is still unclear which variables determine whether one or the other (or both) occur (see Mackintosh, 1974).

In the present study, we extend the absolute/relational issue to the stimulus dimension of duration. Specifically, we ask whether temporal control in the temporal bisection task, one of the most widely used tasks to study timing, is absolute or relational. To answer the question, we follow Church and Deluty's (1977) rationale: Suppose subjects learn two matching-to-sample tasks sequentially. In task A they learn to choose a 'left' comparison stimulus following a 1-s sample and a 'right' comparison stimulus following a 4-s sample. Successful performance in this task is consistent with two hypotheses. The Absolute hypothesis states that the subjects learned to respond 'left' after the 1-s sample and 'right' after the 4-s sample ('1s→left, 4s→right'). The Relative hypothesis states that the subjects

learned to respond ‘left’ after the short sample and ‘right’ after the long sample (‘short→left, long→right’).

To contrast the hypotheses, the experimenter then divides the subjects into two groups and exposes them to task B. The Absolute group learns the new mapping ‘4s→right, 16s→left’; the Relative group learns the opposite mapping ‘4s→left, 16s→right’. Samples and comparisons are the same, but the mapping differs, and the question is which group learns task B faster. If the discriminations learned in task A rest on the absolute sample durations, the Absolute group will learn task B faster because it can transpose the ‘4s→right’ (absolute) mapping from A to B, whereas the Relative group cannot. However, if the discriminations rest on the relative sample durations, the Relative group will learn task B faster because it can transpose the relative mapping ‘short→left, long→right’ from A to B, whereas the Absolute group cannot.

The results have been mixed: Two studies (Church & Deluty, 1977; Hulse & Kline, 1993) reported evidence more consistent with relational responding, and one study (Carvalho & Machado, 2012; Chapter II here) reported evidence more consistent with absolute responding. Other studies with the bisection task but using a different rationale also reported mixed results, both with animals and humans (Maia & Machado, 2009; Molet & Zentall, 2008; Spínola, Machado, Carvalho, & Tonneau, 2013; Zentall, Weaver, & Clement, 2004).

The reasons for these differences are unclear. The animal species, the sample modality, the amount of training, and the methods of data analyses have varied across studies. Perhaps even more important than these differences may be the fact that hypotheses limited to ordinal statements about speed of acquisition may be too broad and vague to test empirically. In Church and Deluty’s (1977) study, for example, the Relative group learned the 4-s discrimination in task B faster than the Absolute group, but the Absolute group showed slightly better performance during the first session. Moreover, Church and Deluty did not report how fast the two groups learned the 16-s sample discrimination. Hence, the broad conclusion that the data supported the Relational hypothesis is questionable.

Following Carvalho and Machado (2012), we propose an alternative, theoretically guided approach to the absolute/relational issue in the bisection task. In the spirit of Spence (1936, 1937), the approach adopts the simple null hypothesis that seemingly relational forms of responding in the bisection task are reducible to the effects of temporal generalization gradients. If task A produces temporal generalization and if responding to new stimuli depends, at least in part, on this generalization, then performance in task B should be

predictable from the generalization gradients induced by task A. To test this hypothesis, we follow Church and Deluty's (1977) rationale but add generalization tests at the end of each bisection task to determine how well the temporal generalization gradients predict the performance of each group, following each sample, during the next bisection task.

Generalization gradients can predict performance only during the first trials of the new task, before the new contingencies take control of behavior. To predict the acquisition curves beyond the first trials, we need a theory or model that integrates timing and learning. The task is not easy, though, for most timing models deal exclusively with steady-state behavior.

Consider the most influential model, the Scalar Expectancy Theory (SET; e.g., Gibbon, Church, & Meck, 1984; Gibbon, 1991). A pacemaker emits pulses at rate  $\lambda$ , and an accumulator adds the pulses emitted during the to-be-timed interval, the sample in a temporal bisection task. When the sample ends and a response occurs and is reinforced, the number in the accumulator is multiplied by a random variable,  $k$ , and then stored in a memory indexed by the response. Thus, if left and right choices are reinforced after the short and long samples, respectively, the number in the accumulator is stored in the 'left memory' when 'left' is reinforced and in the 'right memory' when 'right' is reinforced. Since  $\lambda$  and  $k$  are random variables, the values stored in each memory will vary across trials and, at the steady state, each memory will contain a distribution of counts that represents the corresponding sample duration. To decide which key to choose on any given trial, the subject takes a sample from each of its two memories,  $X_{\text{Left}}$  and  $X_{\text{Right}}$ , and then compares them with the number in the accumulator,  $X_{\text{Acc}}$ . If the ratio  $X_{\text{Acc}}/X_{\text{Left}}$  is less than the ratio  $X_{\text{Right}}/X_{\text{Acc}}$ , the subject chooses the 'left' key; otherwise, it chooses the 'right' key. This categorical decision rule predicts that the preference for the 'right' key will be sigmoidal, increasing with sample duration from about 0 to about 1, and crossing the indifference point at the geometric mean of the trained samples.

Although SET predicts several properties of steady-state performance, it does not say anything about how the memory contents change with training, particularly when the animal learns a new task. For example, if the 'left' key is correct after a 1-s sample in task A, but after a 4-s sample in task B, SET does not specify how the contents of the 'left memory' change during task B, that is, how the new 4-s sample counts replace the old 1-s sample counts. Without explicit statements about memory dynamics, the model cannot predict acquisition curves. Other timing models are similarly limited to steady-state behavior (e.g.,

the Behavioral Economic Model of Jozefowicz, Staddon, & Cerutti, 2009; the Drift Diffusion Model of Ratcliff & McKoon, 2008).

One model that predicts both acquisition curves and steady state behavior is the Learning-to-Time model (LeT; Machado, Malheiro, & Erlhagen, 2009; Machado, 1997). An outgrowth of Killeen and Fetterman's (1988) Behavioral Theory of Timing, LeT integrates reinforcement, extinction, and temporal generalization processes to predict behavior across tasks. For these reasons, we use LeT to predict the pattern of acquisition curves and the shape of generalization gradients throughout the experiment.

The present study also improved the design followed in previous studies. First, in all of these studies the comparison stimuli were 'left' and 'right' levers or keys. Because location distinguished the alternatives, motor patterns during the sample may have mediated the temporal discriminations (see Carvalho & Machado, 2012). To eliminate the potential confounds introduced by these patterns, we replaced the left-right comparisons by red-green comparisons with their location randomized across trials.

Second, slowing acquisition may reveal more clearly the learning patterns of each group. To that end, we replaced the 1:4 ratio of sample durations used in previous studies (e.g., Carvalho & Machado, 2012; Church & Deluty, 1977) by a 1:3 ratio. Because temporal discrimination follows Weber's law, a smaller ratio should reduce the discriminability of the sample durations and slow the approach to asymptotic performance.

Third, to have more opportunities to examine acquisition, we used an ABAB design. Phases A and B differed in the pair of training samples, 2 s vs. 6 s in one, 6 s vs. 18 s in the other. The successive tasks preserved either the absolute or the relative mapping between samples and comparisons. Then, for each task and mapping, we a) examined whether the generalization gradient obtained at the end of one task predicted performance during the first session of the next task, and b) we compared LeT's predictions against the pigeons' acquisition curves and generalization gradients.

### ***1.1. The Learning-to-Time model***

We describe the model's architecture and then explain qualitatively how it works in two successive bisection tasks (for equations, see Carvalho & Machado 2012; Machado et al., 2009). LeT has three components (see Figure 12, first row), a series of *behavioral states* connected by *associative links* to the two *operant responses*. The onset of the sample activates the first state. After a while, that state becomes inactive and the second state becomes active. After another while, the second state becomes inactive and the third becomes

active, and the process repeats, with the activation passing to the next state in the series. The speed of activation of successive states is a Gaussian random variable,  $\lambda$ , with mean  $\mu_\lambda$  and standard deviation  $\sigma_\lambda$ ;  $\lambda$  is sampled at trial onset.

At the end of the sample, one state will be active and the strengths of its two links – quantities between 0 and 1 – determine the choice probabilities. If the link with one response, say, ‘red’, is stronger than the link with the other response, ‘green’ – in other words, if the links from the active state are biased towards ‘red’ – the probability of choosing ‘red’ will be greater than the probability of choosing ‘green’.

After the choice response, reinforcement or extinction follows. Each of these outcomes changes the links from the active state to the emitted ( $W_E$ ) and non-emitted ( $W_{NE}$ ) response. Reinforcement strengthens  $W_E$  by the amount  $\beta(1-W_E)$  and weakens  $W_{NE}$  by the amount  $\beta W_{NE}$ , where  $\beta > 0$  is a reinforcement parameter; extinction weakens  $W_E$  by the amount  $\alpha W_E$  and strengthens  $W_{NE}$  by the amount  $\alpha(1-W_{NE})$ , where  $\alpha > 0$  is an extinction parameter.

To summarize, the sample duration determines probabilistically the state that is active at the end of the sample, and the reinforcement contingencies, through their biasing effect upon the associative links, determine the choice probabilities. The model uses five parameters,  $\mu_\lambda$  and  $\sigma_\lambda$ , related to state activation,  $\alpha$  and  $\beta$ , related to learning, and  $W_0$ , the link strength of all states before the experiment. For steady state predictions, only two parameters are critical, the ratios  $\sigma_\lambda/\mu_\lambda$  (the “clock’s” coefficient of variation) and  $\alpha/\beta$  (the relative effects of extinction and reinforcement).

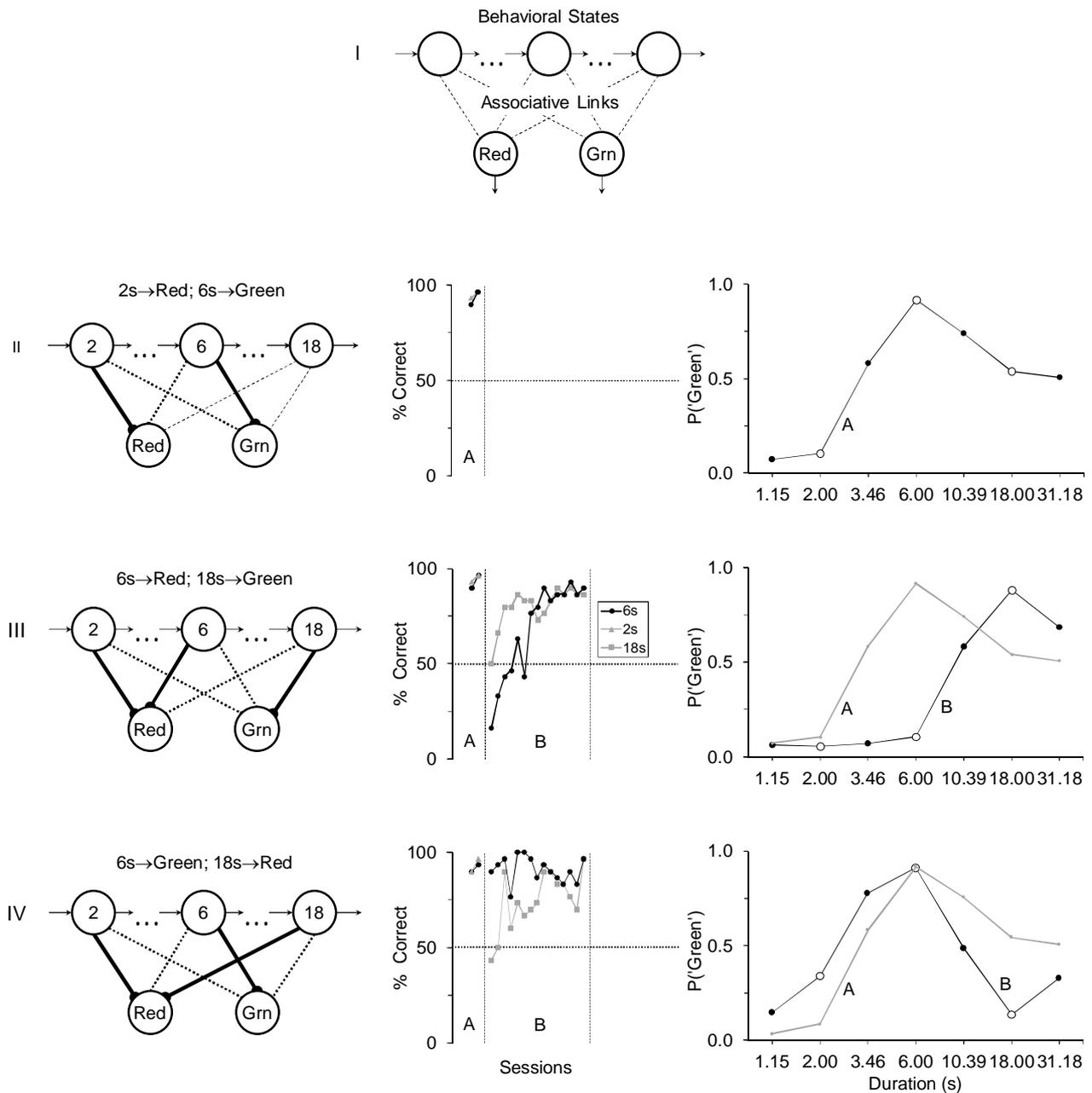


Figure 12. Row I: Structure of the LeT model. A set of behavioral states, activated serially, control the operant responses through vectors of associative links whose strengths change with reinforcement and extinction. Row II: Model predictions for the task '2s → red, 6s → green' (Phase A). The left panel shows the link strengths of the modal states; the middle panel shows the acquisition curves; and the right panel shows the generalization gradients. Row III: Model predictions for Phase B, '6s → red, 18s → green' (Relative group). Row IV: Model predictions for Phase B, '6s → green, 18s → red' (Absolute group).

### 1.2. LeT and successive bisection tasks

To understand the model's predictions, Figure 12 illustrates its typical output at the end of Phase A (2<sup>nd</sup> row) and during a Phase B that preserves either the relative (3<sup>rd</sup> row) or

the absolute (4<sup>th</sup> row) mapping. The left panels single out the three states most likely to be active at the offset of the 2-, 6-, and 18-s samples. We refer to them as modal states 2, 6, and 18, respectively, and to their links with ‘red’ and ‘green’ as, e.g., ‘2→red’ or ‘6→green’. The model predictions do not depend on the specific number of the modal states.

During Phase A, reinforcement strengthens the links ‘2→red’ and ‘6→green’, and extinction weakens the links ‘2→green’ and ‘6→red’; the links from state 18 remain unchanged because state 18 is rarely active after 2- or 6-s samples. At the end of training, the links from states 2 and 6 sustain accurate performance following each sample, a result shown in the middle panel for the last two sessions. The right panel shows the generalization gradient at the end of Phase A. The probability of choosing ‘green’,  $P(\text{‘Green’})$ , is close to 0 when the sample is 2 s or less, increases to approximately 1 as the sample ranges from 2 s to 6 s, and then decreases to chance after the longest samples. The return to chance occurs because the states active after the longest samples were not active during training and therefore preserved their initial, unbiased links with the two responses. The gradient predicts the pattern of choices during the first session of Phase B.

The third row corresponds to a Phase B that preserves the relative mapping. The contingencies ‘6s→red, 18s→green’ change the links from state 6, reversing their bias from ‘green’ to ‘red’, and the links from state 18, biasing them to ‘green’. The links from state 2 retain their bias for ‘red’ because, even though state 2 is seldom active during Phase B, on the few trials it is active the sample is most likely 6-s long and ‘red’ remains the reinforced choice. The middle panel shows the acquisition curves. The percentage of correct responses after the 6-s sample starts below chance (as predicted by the gradient of Phase A) and increases with training, while the percentage of correct responses after the 18 s sample starts at chance (also as predicted by the gradient from Phase A) and increases with training. The right panel shows the gradient at the end of Phase B. With respect to Phase A, the gradient simply shifts to the right.

The fourth row shows a transition that preserves the absolute mapping. Because the link ‘6→green’ is preserved, the percentage of correct choices after the 6-s sample starts close to 100 (as the generalization gradient from Phase A predicted) and remains high, while the corresponding figure for the 18-s sample starts close to chance (also predicted by the gradient from Phase A) and increases subsequently. At the end of Phase B, modal states 2 and 18 are biased toward ‘red’ and therefore the generalization gradient adopts an inverted-v shape, with  $P(\text{‘Green’})$  close to 1 at 6 s and decreasing to 0 both at 2 s (the retained effect of

Phase A) and at 18 s (the effect of Phase B). However, P('Green') at 2 s is not as low as at the end of Phase A because, on the few trials state 2 was active, the contingencies of Phase B biased choice towards 'green', thereby undoing some of the effects of Phase A.

As we show below, LeT predicts distinct acquisition curves and generalization gradients for each phase and mapping of the experiment. We take these curves and gradients, obtained with the same set of parameters, as our null hypothesis. By contrasting them against the pigeon data, we expect to achieve two goals, to clarify the Absolute/Relational issue in the bisection task, and to determine how much data a model based on stimulus generalization, reinforcement, and extinction – a Spencean model – can explain.

## **2. Method**

### ***2.1. Subjects***

Four naïve pigeons (P229, P230, P273, and P451) and four pigeons (P154, P389, P751, P762) with experience in a number discrimination procedure participated in the experiment. Their mean age at the time of the experiment was 6.75 years (range: 3 - 10). They were maintained at 85-90% of their free-feeding weight with grit and water continuously available in their individual home cages. The colony room was under a 13h:11h light-dark cycle, with lights on at 8 a.m.

### ***2.2. Apparatus***

We used four standard operant chambers for pigeons from Med Associates<sup>®</sup>. In the back panel of each chamber, a 7.5-W houselight provided general illumination. In the front panel, a 6 cm high x 5 cm wide feeder opening, centered horizontally and 3.5 cm above the floor grid, provided access to mixed grain. The feeder was illuminated with a 7.5-W light. The front panel also contained three 2.5-cm-in-diameter keys, arranged in a row, 18.5 cm above the grid floor, and 9 cm apart, center-to-center. The center key could be illuminated with a white hue and the side keys could be illuminated with red and green hues. Each chamber was enclosed in a wooden box, itself equipped with a fan that circulated air and helped mask extraneous noises. A personal computer programmed with Visual Basic<sup>®</sup> 2008 and using the Whisker<sup>®</sup> software (Cardinal & Aitken, 2010) controlled the experimental events and recorded the data.

### ***2.3. Procedure***

*General Design.* The pigeons learned two bisection tasks, one using 2-s and 6-s samples, and another using 6-s and 18-s samples. Half of the subjects learned the 2 s vs. 6 s

task first and the 6 s vs. 18 s task next (Upshift subjects) and the other half learned the tasks in the opposite order (Downshift subjects).

The experiment followed an ABAB design. We refer to the four Phases as A, B, A', and B'. For the Upshift subjects, A and A' refer to the 2 s vs. 6 s task, and B and B' refer to the 6 s vs. 18 s task; for the Downshift subjects, A and A' refer to the 6 s vs. 18 s task, and B and B' refer to the 2 s vs. 6 s task.

Following Church and Deluty's (1977) design, we further divided the four Upshift and the four Downshift subjects into two groups, Relative and Absolute, yielding four groups of two pigeons each (see Table 2).

Table 2. Experimental groups and the bisection tasks to which they were exposed across phases.

Phase	Upshift		Downshift	
	Relative	Absolute	Relative	Absolute
A	2s→red, 6s→green	2s→red, 6s→green	6s→green, 18s→red	6s→green, 18s→red
B	6s→red, 18s→green	6s→green, 18s→red	2s→green, 6s→red	2s→red, 6s→green
A'	2s→red, 6s→green	2s→red, 6s→green	6s→green, 18s→red	6s→green, 18s→red
B'	6s→red, 18s→green	6s→green, 18s→red	2s→green, 6s→red	2s→red, 6s→green

Throughout the study, the comparison stimuli were the 'red' and 'green' keylight colors. Which comparison was correct following a given sample was counterbalanced across subjects but, for clarity, we describe the task as if only the mappings shown in Table 2 were used.

*Training.* A training trial began with a 30-s ITI during which all lights were off. After the ITI, the houselight and the center keylight turned on for the duration of the sample. When the houselight and the center keylight turned off, the two side keys turned on, one with 'red' and the other with 'green' light (location counterbalanced across trials). A peck to one of the side keys turned both of them off. If the peck was at the correct comparison, the feeder was activated for 3 s and then the ITI started; if the peck was at the incorrect comparison, the ITI started immediately.

Each session comprised 60 trials, 30 for each sample, presented in random order but with the constraint that no more than four trials of the same sample occurred consecutively. Training continued for a minimum of 15 (Phases A and B') or 20 (Phases B and A') sessions and until the subject achieved at least 80% of correct responses following each sample. A

correction procedure was in effect only during Phase A. Under the correction procedure, an incorrect choice repeated the trial at most three times. If the incorrect response persisted, the fourth trial presented only the correct comparison. The correction trials were not included in data analysis.

*Generalization test.* After the pigeons met the learning criterion, we conducted a single test session with 100 trials, 60 regular trials (30 for each training sample), and 40 test trials. The test trials were equal to the training trials in all details except two: The sample duration differed from the training durations, and choices were not reinforced. The test trials included five different sample durations, each presented on eight trials. The training and test durations equaled (note log spacing) 1.15 s, 2.00 s, 3.46 s, 6.00 s, 10.39 s, 18.00 s, 31.18 s. The 3.46 s and 10.39 s durations correspond to the geometric means of the training samples. The first 10 trials of the test session were always regular training trials, five with each trained duration. After the generalization test session, training resumed for two sessions to reduce potential effects of test and ensure accurate performance to both trained samples before changing phase.

*Transition between phases.* The first session of a new phase (B, A' and B') began with 10 training trials of the previous phase, five with each trained duration, and continued with 60 training trials of the new phase. (Data analyses for the first session of each phase excluded the first 10 trials). From the second session onwards, training proceeded as described in *Training*.

#### **2.4. Model simulation**

To compare LeT with the pigeons' behavior, we conducted two computer simulations for each of the four groups (mimicking the eight subjects in the study), across the ABA'B' phases, with 15 sessions per phase, and the same number of trials per session as the pigeons. Moreover, to isolate the model's response to the reinforcement contingencies of each group and phase, we used the same parameter values for all simulations. They were  $\mu_\lambda = 1.0$ ,  $\sigma_\lambda = 0.3$ ,  $\alpha = .05$ ,  $\beta = .04$ , and  $W_0 = 0.1$ . These values are similar to those used in previous studies (e.g., Carvalho & Machado, 2012), but the model is robust to parameter changes. For each training session, we obtained the percentage of correct responses following each sample, and for each test session, we obtained the proportion of responses to 'green' following each sample. Acquisition curves and generalization gradients defined the model's predicted output for each phase.

### 3. Results

All pigeons mastered the two discriminations of each phase taking on average 26.4 sessions in Phase A, 23 in Phase B, 20 in Phase A', and 15 in Phase B'. To compare the acquisition rates in each phase, we examined the number of sessions required to meet the 80% criterion on the 6-s common sample and on both samples. With respect to the 6-s sample, two-tailed *t* tests revealed that the Absolute group needed fewer sessions than the Relative group in Phases B ( $\bar{x} = 2.0$  vs.  $\bar{x} = 6.5$ ,  $t(6) = 3.25$ ,  $p = .017$ , Cohen's  $d = 2.3$  with 95% CI = [0.37, 4.13]) and B' ( $\bar{x} = 1.25$  vs.  $\bar{x} = 4.5$ ,  $t(6) = 3.28$ ,  $p = .017$ , Cohen's  $d = 2.31$  with 95% CI = [0.38, 4.16]). The Upshift and Downshift groups did not differ in Phases B, A', and B' (all  $p$ 's > .05). With respect to both samples, the Relative and the Absolute groups differed only in Phase B, with the Relative group meeting the criterion in fewer sessions than the Absolute group ( $\bar{x} = 7.75$  vs.  $\bar{x} = 16.0$ ,  $t(6) = 4.01$ ,  $p = .007$ ,  $d = 2.84$  with 95% CI = [0.70, 4.88]). The Upshift and Downshift groups did not differ in any phase ( $p$ 's > .05).

In summary, the Absolute group acquired the correct response to the 6-s sample faster than the Relative group, a result at odds with Church and Deluty (1977) and Hulse and Kline (1993). However, the Relative group acquired the correct responses to both samples faster than the Absolute group. This last result stemmed, at least in part, from tradeoffs in the acquisition of the correct responses. For some subjects, particularly in the Absolute groups, while the correct response to one sample increased, the correct response to the other sample decreased, until both responses met the learning criterion. Below we show acquisition curves with these tradeoffs, and in the Discussion we elaborate on this finding.

#### 3.1. Relative groups

*Relative Upshift.* Figure 13 shows the individual data (top two rows) and the model's predictions (bottom row). The percentage of correct responses after the 6-s sample decreased after each phase transition and then increased with training. This result is consistent with LeT (cf. bottom row). With respect to the other training samples, in Phase B, performance after the 18-s sample started somewhat above chance for pigeon P762, as LeT predicts, but close to 100 for pigeon P154, a result inconsistent with LeT. In subsequent phases, performance following the 2-s (A') and 18-s (B') samples remained always close to 100, a result also consistent with LeT.

The generalization gradients for each pigeon were roughly ogival. In Phase A, P('Green') was close to 0 for 2-s and shorter samples, increased as the sample ranged from 2 to 6 s, and then reached 1 for longer samples. In Phase B, the ogives shifted to the right so

that  $P(\text{'Green'})$  remained close to 0 up to 6 s and then increased to 1 at 18-s or longer samples. The gradients of Phases A' and B' were roughly similar to the gradients of Phases A and B, respectively.

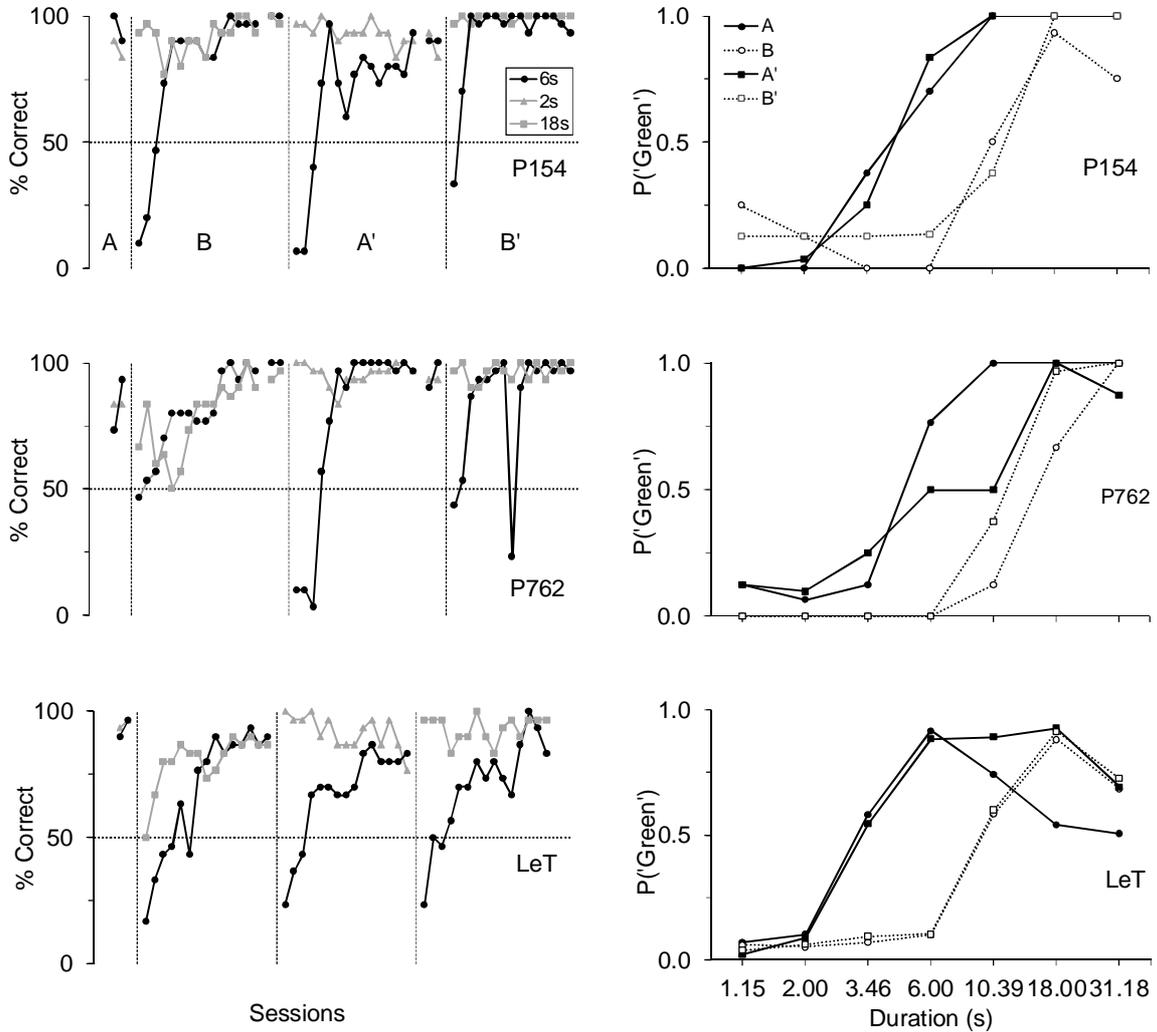


Figure 13. Acquisition curves (left) and generalization gradients (right) for the two pigeons of the Relative Upshift group (top and middle rows) and corresponding model predictions (bottom row).

With two exceptions, the pigeon gradients were consistent with LeT. The first exception was the value of  $P(\text{'Green'})$  at the longest samples, particularly in Phase A. Whereas the pigeons' gradients remained close to 1, LeT's gradients decreased to chance. The second exception was the peak-shift-like effect observed in Phases A and A' when the longest samples occasioned more 'green' responses than the 6-s sample. LeT does not predict this effect.

To measure the match between model and data, we fitted the model to the four data sets of each pigeon simultaneously (i.e., 28 data points) and then computed the variance accounted for,  $\omega^2$ . It equaled .75 for P154 and .63 for P762.

*Relative Downshift.* The acquisition curves (Figure 14, top rows) show that correct performance decreased severely after the 6-s sample, but remained accurate after the other samples. Both patterns are consistent with LeT (cf. bottom panel). In Phase B', pigeon P451 showed the aforementioned tradeoffs, for performance at the 2-s sample decreased as performance at the 6-s sample increased.

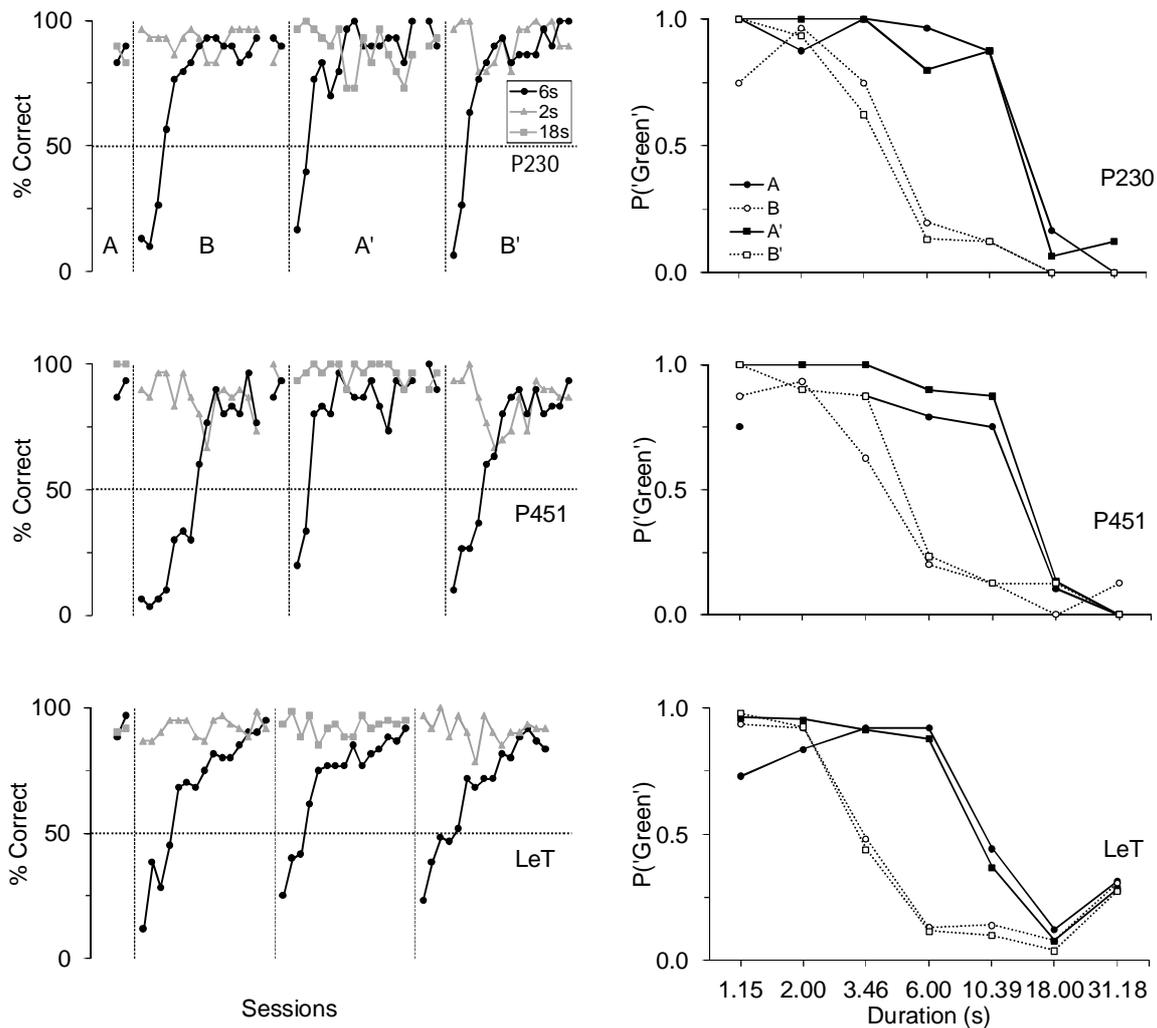


Figure 14. Acquisition curves (left) and generalization gradients (right) for the two pigeons of the Relative Downshift group (top and middle rows) and corresponding model predictions (bottom row). Due to a programming error, the 2-s sample was not presented in the generalization test session of Phase A for P451.

With respect to the generalization gradients, in Phase A, the gradient decreased for durations within the trained range of 6 s and 18 s. The gradient then shifted to the left in Phase B, returned to the right in Phase A' (but this time retaining the high value at the shortest samples), and finally shifted to the left again in Phase B'. The generalization gradients were also broadly consistent with LeT (for P230,  $\omega^2 = .81$ ; for P451,  $\omega^2 = .80$ ). But there were inconsistencies between model and data in Phase A, for durations shorter than 6 s occasioned at least as many 'green' responses as the 6-s sample, whereas LeT predicts a return to indifference, and in Phases B and B', for durations longer than 6 s occasioned more 'red' responses than the 6-s sample (the peak-shift-like effect).

### **3.2. Absolute groups**

*Absolute Upshift.* Figure 15 shows that at the beginning of each phase, the pigeons' performance after the 6-s sample was always significantly above chance, a result consistent with LeT. Their performance after the 18-s sample in Phase B and the 2-s sample in Phase A' was less accurate than after the 6-s sample, a result also consistent with LeT. However, LeT did not predict performance significantly *below* chance, as both pigeons showed in Phase B and pigeon P751 showed in Phase A'. In Phase B', performance of pigeon P751 on the 18-s sample was accurate since the first sessions, as LeT predicted, but that of pigeon P229 started at chance, a result LeT did not predict. Acquisition tradeoffs occurred in Phases B and A' for pigeon P229.

The generalization gradients in Phase A were ogival and approached 1 at samples longer than 6 s. At the end of the remaining phases, the gradients approached the inverted-v shape that LeT predicted with the mode at or close to 6 s. Except for the high value of P('Green') at the two longest samples in Phase A, the generalization gradients were broadly consistent with LeT (for P229,  $\omega^2 = .63$ ; for P751,  $\omega^2 = .71$ ).

The low percentages of correct responses after the 18-s (Phase B) and the 2-s samples (Phase A'), although inconsistent with LeT, were consistent with the generalization gradients obtained in the preceding phases. In Phase A, the two individual gradients showed a high value of P('Green') at the 18 s duration, which predicts the close-to-zero percentage of correct responses ('red') observed at the beginning of Phase B. Similarly, in Phase B, the gradient of P229 showed a high value of P('Green') at the 2 s duration, which predicts the below chance percentage of correct responses ('red') observed at the beginning of Phase A'.

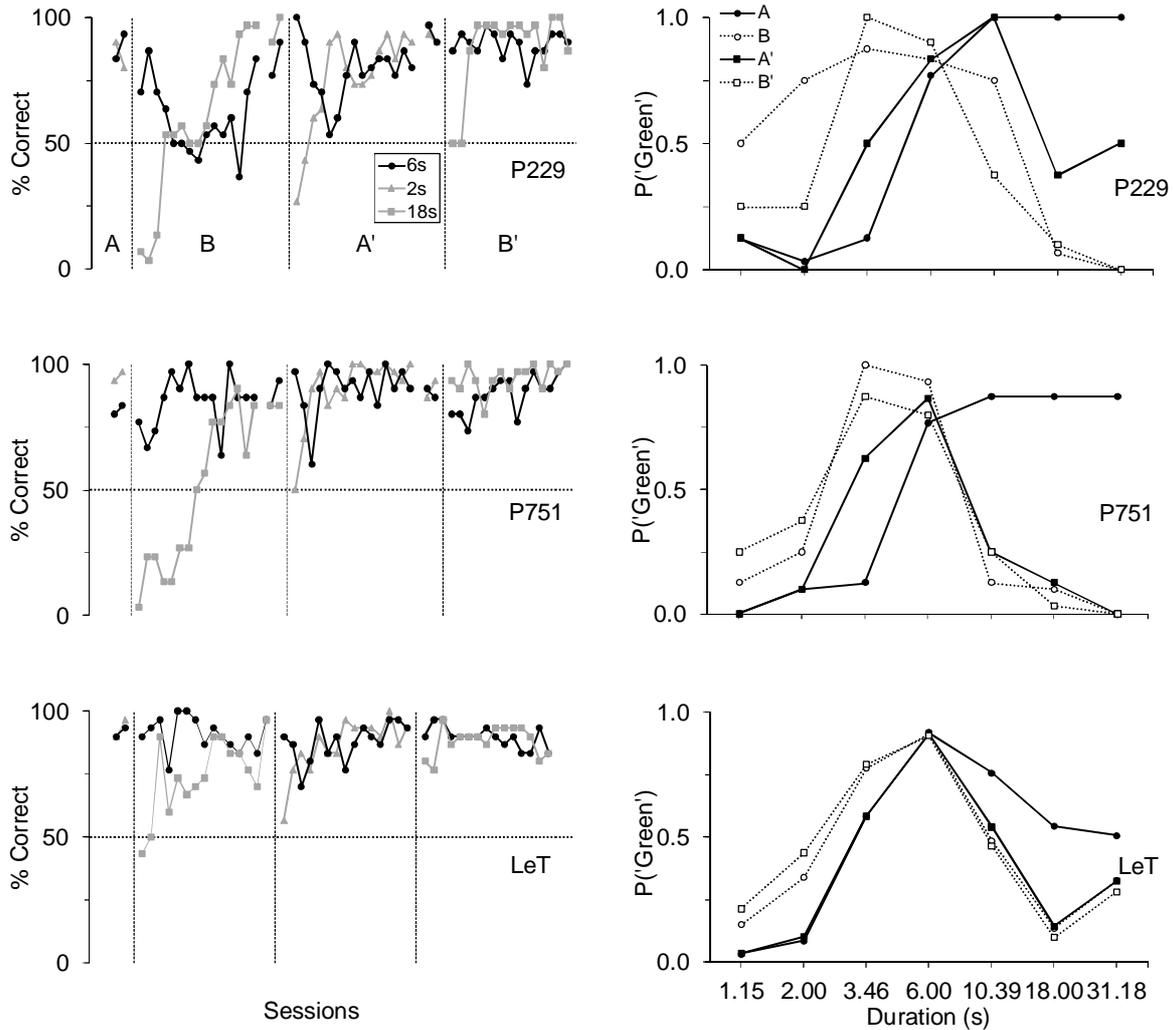


Figure 15. Acquisition curves (left) and generalization gradients (right) for the two pigeons of the Absolute Upshift group (top and middle rows) and corresponding model predictions (bottom row).

*Absolute Downshift.* In Phases B and B' (Figure 16, top rows), performance started high, as LeT predicted, but then, in Phase B, it followed a u-shaped curve that was particularly pronounced in pigeon P389, another instance of tradeoffs. In the first sessions of Phase A', pigeon P273 showed a percentage of correct responses significantly below chance. This result was the most inconsistent with LeT. Correct responses after the 2-s sample began markedly below chance in Phase B, and close to chance in Phase B'. Correct responses after the 18-s sample started at chance in Phase A' and then increased, smoothly for pigeon P389, erratically for pigeon P273.

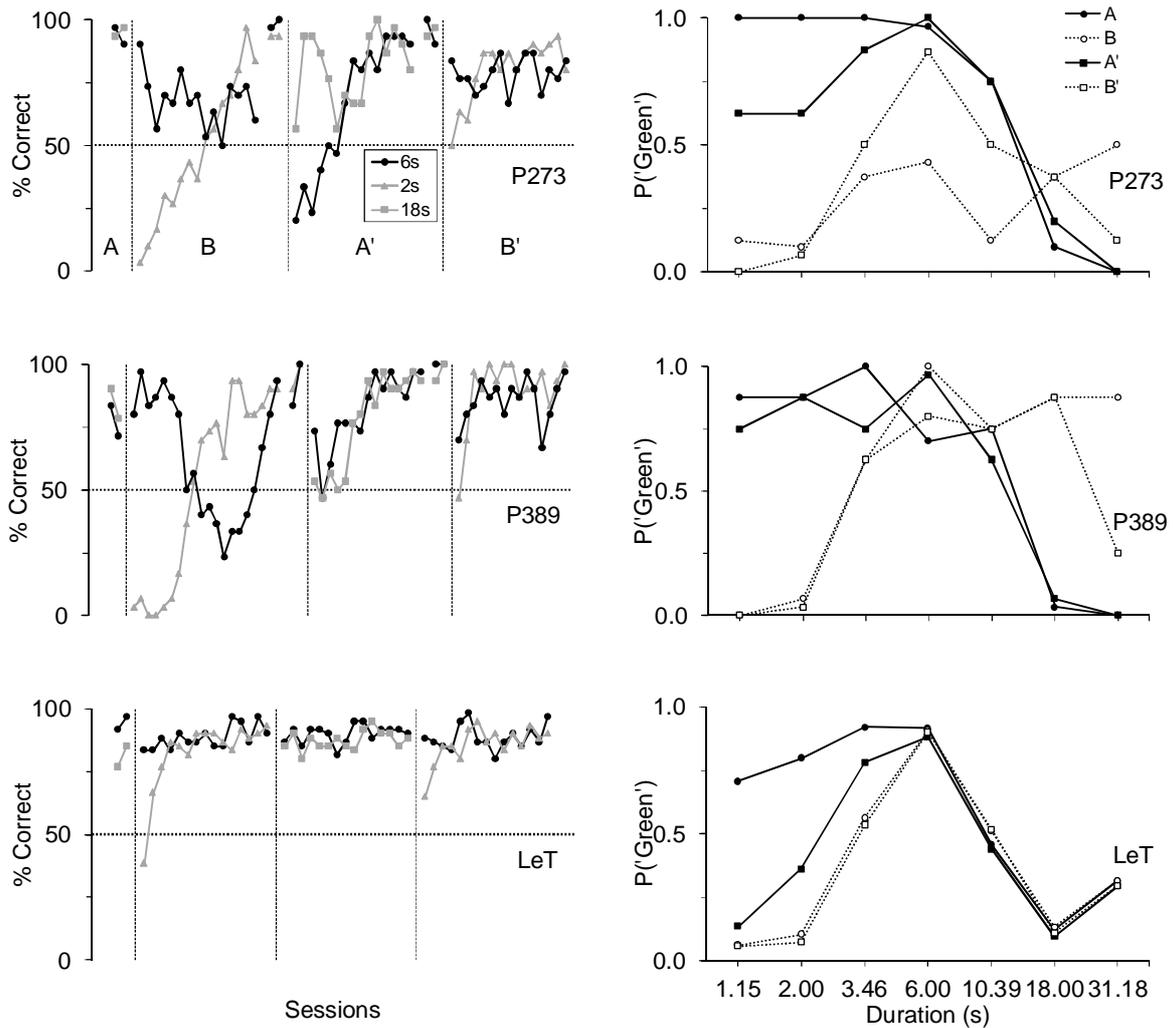


Figure 16. Acquisition curves (left) and generalization gradients (right) for the two pigeons of the Absolute Downshift group (top and middle rows) and corresponding model predictions (bottom row).

At the end of Phase A the two gradients were descending ogives, as LeT predicted, but with higher left limbs. In Phase B, pigeon P273 showed marked bias for the 'red' key, and both pigeons showed relatively high values at 18-s and longer samples. In the last two phases, the gradients differed between the two pigeons. For P273 the gradients in Phases A' and B' were roughly inverted-v shaped as LeT predicted. For P389 the gradients were a descending (A') and an ascending (B') ogive, the latter with a low value at the longest duration. Consistently,  $\omega^2$  was smaller for the Absolute Downshift (.57 for P273, and .35 for P389).

### 3.3. Aggregate data

The LeT model predicted three main results concerning the acquisition curves. First, at each phase transition, performance following the 6-s common sample should be below chance in the Relative groups but above chance in the Absolute groups. In the top row of Figure 17, the symbols show the percentage of correct responses following the 6-s sample during the first session of Phases B, A', and B' predicted by the model (left panel) and obtained with the pigeons (right panel). With one exception, the pattern of results is consistent with the model.

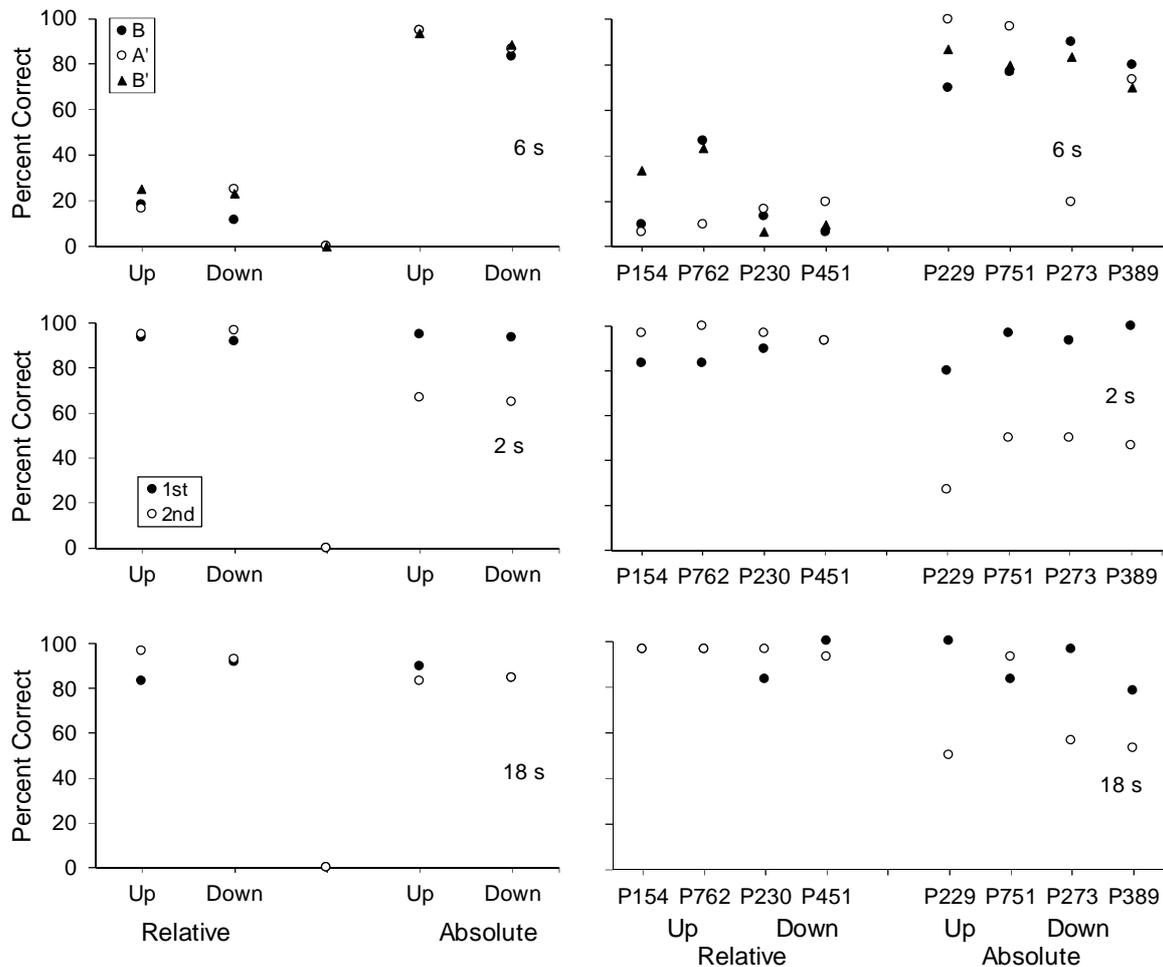


Figure 17. The symbols show the percentage of correct responses following the 6-s, 2-s and 18-s samples in the first session of Phases B, A', and B', as predicted by the model (left) and as observed in the pigeons' performance (right).

Second, there should be some generalization from the 6-s sample to the 2-s sample. Therefore, training with the 6-s and 18-s samples in one phase should affect the choices the pigeons learned to make after 2-s sample in the preceding phase. However, the effect should

be positive for the Relative groups, and negative for the Absolute groups. In addition, the positive effects should be small because of a ceiling in choice proportion, whereas the negative effects should be large.

The middle panels of Figure 17 show percent correct after the 2-s sample during two sessions, the last session of the first phase with that sample (filled circles) and the first session of the second phase with that sample (empty circles). The difference between the two data points reveals the effect of the training phase that occurred between the two sessions. The Relative groups showed small positive differences, whereas the Absolute groups showed large negative differences.

Third, according to LeT there should be less generalization from the 6-s sample to the 18-s sample. Therefore, training with 2-s and 6-s samples in one phase should not affect the choices learned in a previous phase with the 18-s sample. The bottom panel of Figure 17 shows that all four pigeons from the Relative groups and one pigeon (P751) from the Absolute groups corroborated the prediction, but the other pigeons showed a significant loss in performance.

Concerning the generalization gradients, LeT predicted two main results. First, the gradients obtained at the end of one phase should predict choice during the beginning of the next phase. Figure 18 plots the choice proportions obtained during the first session of a new phase against the proportion predicted by the generalization gradient from the previous phase. For seven of the eight pigeons (except P389), a linear function described the data well; the correlations averaged .96 (range: .91-.99) and the slopes averaged 0.95 (range: .71-1.14). The same analysis but using only the first half of the session of the new phase yielded similar results, an average correlation of .96 and slope of 1.0.

Second, the gradients for the Relative and Absolute groups should differ markedly in shape. To check this prediction, we averaged the gradients from the Upshift and Downshift groups after rotating the gradients from the Downshift groups 180° around the 6-s vertical line. The rotation aligned the trends of the two gradients and made their averaging meaningful. The symbols in Figure 19 show the results.

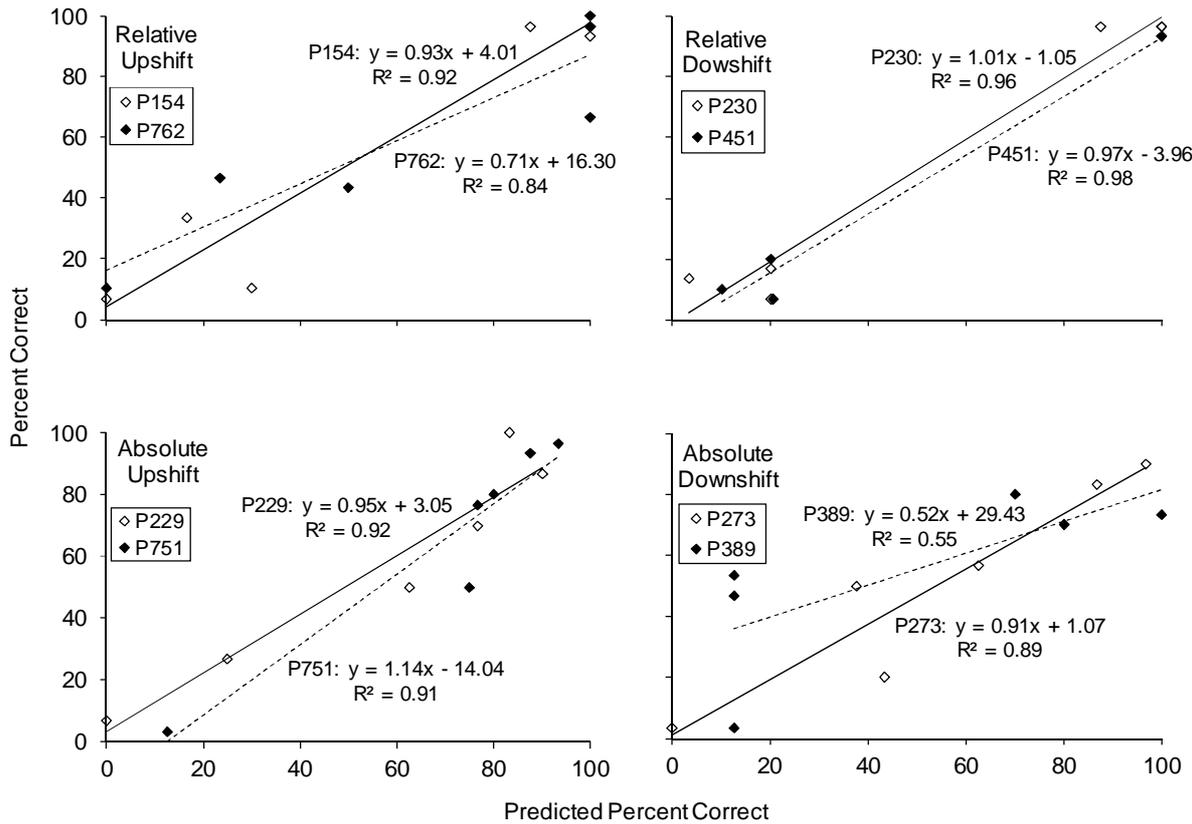


Figure 18. The symbols show the percentage of correct responses observed during the first session of Phases B, A', and B', plotted against the values predicted from the generalization gradient of the previous phase. The lines are the best-fitting regression lines.

In addition, we asked whether LeT could fit *simultaneously* the four generalization gradients of each pigeon by a) varying only its two critical parameters, the ratios  $\sigma_\lambda/\mu_\lambda$  and  $\alpha/\beta$ , and b) using only the two points of each gradient corresponding to the training samples of each phase. Each of these two points represented 30 trials, whereas the data from any other sample represented eight trials. The lines in Figure 19 show the results.

The average gradients of the Relative groups (top row) were shifted ogives, increasing from about 0 to about 1 and with bisection points close to the geometric mean of the trained samples. LeT fit the gradients well except at the longest samples in Phase A ( $\omega^2 = .79$  in A,  $.99$  in B,  $.93$  in A', and  $.96$  in B'). For the Absolute groups (bottom row), the average gradients changed across phases from an ogive to an inverted v-shaped curve with a mode at 6 s. The main local discrepancy between model and data occurred again at the right tail of the gradient from Phase A. The  $\omega^2$  values equaled  $.83$ ,  $.59$ ,  $.69$ , and  $.74$  in Phases A, B, A' and B',

respectively. For both data and model, the bisection points were close to the geometric mean of the trained samples.

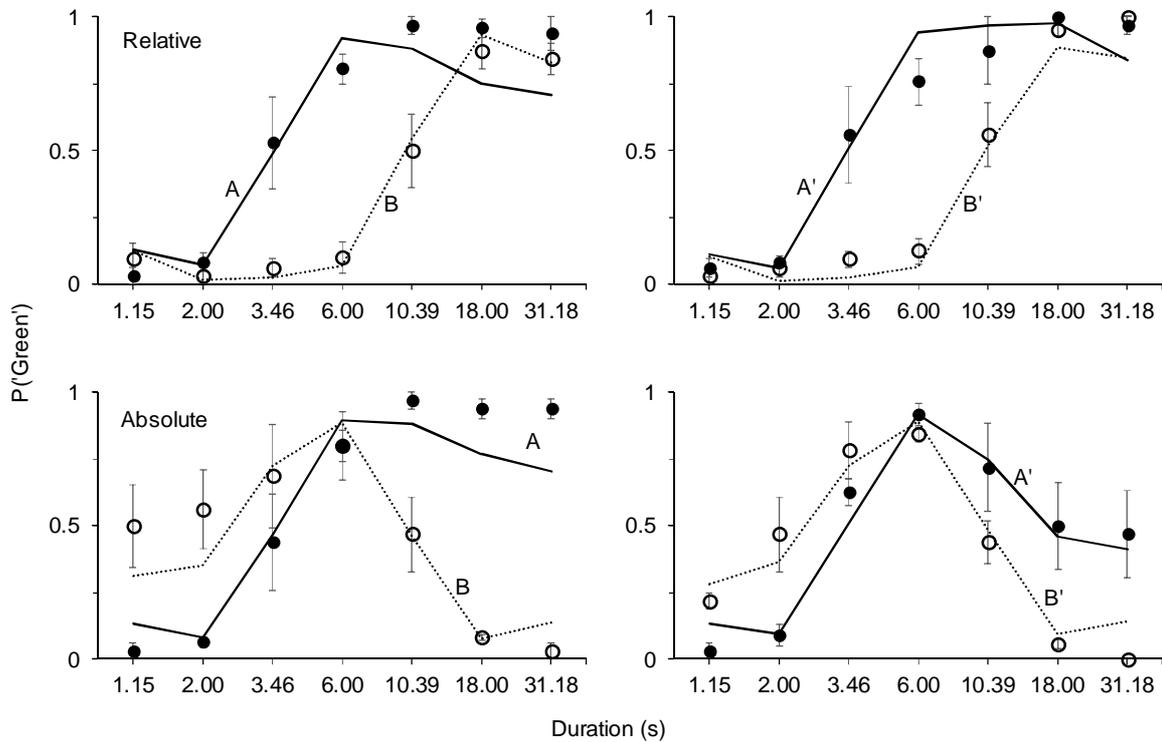


Figure 19. The symbols show the average ( $\pm$ SEM) generalization gradients for the Relative (top) and Absolute (bottom) groups. The lines are the average of the individual gradients fit by the LeT model. The data from the Downshift pigeons were reflected around the 6-s vertical line before averaging them with the data from the Upshift subjects. The left panels show data from Phases A and B, and the right panels show data from Phases A' and B'.

#### 4. Discussion

In the present study, we extended Spence's approach to the time domain. That is, we attempted to explain seeming forms of relational responding in the bisection task by means of temporal generalization and the combination of temporal generalization gradients. We proceeded through a series of increasingly more demanding tests. In the first test, we used the generalization gradient obtained at the end of one phase to predict choice at the beginning of the next phase. In this case, we did not need a theoretical model to predict that the values of P('Green') at the end of one phase should be close to the values of P('Green') during the first session of a new phase. The data confirmed the prediction. For most pigeons and phases, the

correlations between the two sets of values were positive and strong, and the least-squares regression lines had slopes close to 1.

In two other tests, we attempted to predict the pattern of the acquisition curves after each phase transition and the shape of the generalization gradients at the end of each phase. In these cases, we needed a theoretical model to specify how the tendencies to choose the comparisons following the trained samples change with the reinforcement contingencies of each phase, and how they generalize to other samples. The LeT model served this purpose. It operationalized the Spencean approach – with its processes of temporal generalization (state dynamics), reward following (learning rules), and temporal memory (associative links from the states to the responses) – and predicted the pattern of acquisition curves and the shape of the generalization gradients. We proposed it as a null hypothesis.

In what follows, we assess how well LeT fared as a null hypothesis and then address the implications of its fits and misfits of the data to our understanding of the absolute/relational issue in the temporal bisection task.

#### ***4.1. Generalization gradients***

For Phase A, LeT predicted a gradient that, within the range of the two training samples, increased monotonically from about 0 to about 1 and that, outside the range, approached .5. For the remaining phases, LeT predicted shifted ogives for the Relative groups and inverted v-shaped curves for the Absolute groups. The data were broadly consistent with these predictions (see Figures 13-16, and 19).

But there were two systematic deviations. First, in Phase A, obtained and predicted gradients differed at sample durations outside the training range. LeT predicted a return to indifference, but the pigeons showed a sustained preference for the ‘short’ key after the shortest test samples and for the ‘long’ key after the longest test samples.

Second, given any reasonable value for the Weber fraction (in LeT, the ratio  $\sigma_\lambda/\mu_\lambda$ ), the generalization gradient induced by the 18-s sample should not overlap the gradient induced by the 2-s sample. In model terms, the set of states active after the 18-s sample and the set of states active after the 2-s sample should have few or no elements in common. Therefore, if the contingencies associated with the 6-s sample do not change across phases (Absolute groups) the behavior occasioned by the 18-s sample in one phase should be retained during training with the 2-s sample in the next phase. Although some gradients strongly supported this prediction (e.g., the gradients for P751 in Figure 15 and the other inverted v-shaped gradients in Figures 15 and 16), others showed more changes than

expected (the bottom panel of Figure 17 summarizes the discrepancies). These discrepancies contrast with the mostly correct predictions concerning the 2-s sample (see Figure 17 middle panel).

The discrepancies between model and data concerning the shape of the generalization gradients pose a difficult problem. On the one hand, monotonic generalization gradients with sustained low and high tails outside the training range (as in Phase A) suggest simple categorical decision rules of the sort “choose ‘red’ after samples below 3.5 s and ‘green’ after samples above 3.5 s”. Such rules occur in the leading timing model, Scalar Expectancy Theory. On the other hand, non-monotonic gradients (e.g., inverted v-shaped gradients) rule out such categorical decision rules. To illustrate, if a pigeon learns the mapping ‘2s→red, 6s→green’ in Phase A, its strong tendency to choose ‘red’ at the end of 2-s and shorter samples agrees with a categorical decision rule. If it then learns the mapping ‘6s→green, 18s→red’ in Phase B, a similar categorical rule entails a tendency to choose ‘green’ at the end of 6-s and shorter samples, eliminating the tendency acquired in Phase A to choose ‘red’ after 2-s and shorter samples<sup>5</sup>. Hence, any evidence that the pigeon preserved, albeit incompletely, the tendencies acquired during Phase A – evidence such as an inverted v-shaped gradient – would seem to reject simple categorical decision rules.

Other studies have found both gradient shapes. Using rats, Russell and Kirkpatrick (2007) and Siegel (1986) reported non-monotonic gradients with tails that approached indifference outside the trained range, as LeT predicts. Using pigeons, Vieira de Castro, Machado, and Tomanari (2013) reported monotonic gradients with non-decreasing tails, gradients consistent with simple categorical decision rules but inconsistent with LeT. Future experiments should investigate the reason for these differences across studies and discover when one or the other type of gradient obtains. Future analyses should also answer two theoretical questions: a) how can we modify a model such as LeT to mimic categorical-like decision rules, and b) how can we modify a model such as SET or other categorical-based models to account for the retention of learning across temporal tasks. The present findings suggest a partial answer. A categorical rule seems to apply when the animal first experiences sample durations outside the trained range (Phase A); a non-categorical rule seems to apply when the animal has previously experienced those sample durations (subsequent phases).

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<sup>5</sup> For this reason, SET *always* predicts shifted ogives in the bisection task.

#### ***4.2. Acquisition curves***

According to LeT, at each phase transition, the Relative groups should show more errors after the 6-s sample than after the 2-s or 18-s samples; the Absolute groups should show the opposite pattern. Again, most results were consistent with the predicted trends, but a few were not. Some of the inconsistencies stem from the model incorrectly predicting the shape of the gradient outside the training range. If at the end of Phase A the model predicted indifference after the 18-s sample but the pigeons strongly preferred ‘green’, a fortiori the model also predicted incorrectly the acquisition curve for the 18-s sample at the beginning of Phase B. However, other inconsistencies were of a different sort. The Absolute Downshift pigeons showed acquisition curves with more errors after the 6-s than the 18-s sample in Phase A’. These results were the most inconsistent with LeT (see Carvalho & Machado, 2012, for a similar finding).

Although we do not know why the Absolute Downshift pigeons made a large number of errors after the 6-s sample in Phase A’, we note that during the preceding phase they also showed acquisition curves with pronounced tradeoffs (see Figure 16). These tradeoffs occurred also in the Relative groups (cf. Figure 13, pigeon P762 in Phase B; Figure 14, pigeon P451 in Phase B’), but they seemed to be more frequent or pronounced in the Absolute groups (in addition to P273 and P389, see also Figure 15, P229 in Phases B and A’). In Carvalho and Machado’s (2012) study it was also the case that the pigeons that showed the acquisition curves most at odds with LeT, also showed “a negative covariation during the first sessions between proportion correct following 4-s sample and proportion correct following 16-s sample” (p. 37) – in other words, tradeoffs.

Blocks of sessions during which the discriminative behavior after two or more samples co-varies negatively have occurred in other studies. Vyazovska, Teng and Wasserman (2014) reported negative covariations in a go/no go task with 16 stimuli, defined by four binary dimensions (large/small, circle/square, bright/dark, and with a horizontal/vertical bar), with one stimulus positive (e.g., a large circle with a bright background and a horizontal bar) and the other 15 negative. Some pigeons showed severe upswings and downswings in response rate to the negative features, which occasioned large changes in the discrimination ratios across sessions. The authors described these findings as *attentional* tradeoffs and related them to some pigeons’ limited capacity to process multiple stimulus dimensions. The same authors did not find as large changes in discrimination ratios in a simultaneous discrimination task (Teng, Vyazovska, & Wasserman, 2015).

Carvalho and Machado (2012) advanced a more specific hypothesis to explain the tradeoffs. The bisection task involves two conditional discriminative stimuli, the sample durations, and two simple discriminative stimuli, the keylight colors. The tradeoffs could be due to competition between the two classes of stimuli triggered by extinction. Take the case of pigeon P389 (Figure 16). The pigeon learned the mapping '6s→green, 18s→red' in Phase A and then the mapping '2s→red, 6s→green' in Phase B. In the first sessions of Phase B, the pigeon experienced massive extinction for choosing 'green' after the 2-s sample. Such extinction episodes, and the occasional reinforcements for choosing 'red' after the 2-s sample, could have enhanced stimulus control by the keylight colors while reducing stimulus control by the sample durations. The net effect could be a strong tendency to choose 'red' *regardless of sample duration*, a generalized bias for 'red' that would have increased correct responses following the 2-s sample and decreased correct responses following the 6-s sample – the tradeoff revealed in Figure 16. This competitive dynamic may also involve some degree of hysteresis because reinforcement for choosing 'red' seems to become more effective *for several sessions* (more than 10 in Figure 16) than reinforcement for choosing 'green'.

This account of acquisition tradeoffs is speculative, but its emphasis on extinction seems consistent with another finding. For some pigeons and phases, performance at the currently long sample (6 s when the samples were 2 s and 6 s, 18 s when they were 6 s and 18 s) decreased during the generalization test sessions, even though correct responses continued to be reinforced. Pigeon P273 from group Absolute Downshift showed the clearest example. In the generalization test session of Phase B (see Figure 16), P('Green') after the 6-s sample equaled .43, a value noticeably below the proportions observed in the previous (.76) and following (.93) sessions (see also Figure 13, both pigeons in Phase A, pigeon P762 in Phases B and A'; Figure 14, both pigeons in Phase B; Figure 15, P229 in Phases A and A'). This test effect explains why we described the resulting gradient not as peak-shift but as 'peak-shift-like': The higher value of P('Green') at a sample different from the trained sample seemed to be due to the disruption of performance at the trained sample and not only to a shift in the duration that yields the highest probability of responding 'green'.

Alternatively, we could interpret the peak-shift-like effect in terms of Adaptation Level theory (see Thomas, 1993). Assume that training with '2s→red, 6s→green' sets the pigeon's adaptation level (AL) at the geometric mean, 3.5 s. The pigeon would then associate the samples perceived as below that level (2 s) with 'red', and those perceived as above (6 s) with 'green'. If during testing the AL increased to the geometric mean of all samples, 4.7 s,

the discriminability of the 6-s would decrease and that of the 2-s sample would increase, although the latter effect would be hard to detect because of a ceiling effect. Testing after training with the 6 s and 18 s samples would yield a similar result.

Our data were partly consistent with the account. The number of correct responses after the 6-s sample was on average 8.4% ( $\approx 2.5$  trials out of 30) less during the generalization test sessions than during the two sessions that preceded and followed them (matched pair t-test,  $t(7) = 7.97$ ,  $p < .001$ ,  $d = 2.8$ , 95% CI = [1.2, 4.4]). However, the decrease was much stronger when 6 s was trained with 2 s than with 18 s (27% vs 6.7%;  $t(7) = 2.6$ ,  $p < .05$ ,  $d = 0.91$ , 95% CI = [0.05, 1.72]), an asymmetry not predicted by AL. Moreover, it is also unclear how to derive the inverted-v shaped gradients from the AL theory.

Future research should investigate these alternative accounts, how extinction may trigger acquisition tradeoffs or disrupt performance during generalization tests, particularly following long samples, and how new samples may change the pigeon's AL. Clarifying these issues may help us understand better the Absolute/Relative nature of stimulus control in the bisection task.

We conclude with some thoughts about the original questions: Which group, Relative or Absolute, learns the bisection tasks faster? And, more broadly, is stimulus control in the temporal bisection task absolute or relational? The answer to the first question depends on whether we focus on the 6-s sample (advantage of the Absolute group), or both samples (advantage of the Relative group). More decisively, perhaps, because the acquisition curves from the two groups followed distinctly different patterns at each phase transition, the question of which group learns faster is, if not devoid of theoretical interest, at least secondary to our understanding of these patterns.

Concerning the second question, given that a Spencean model such as LeT predicted the major trends in the data, we conclude that the current data in the temporal bisection task remains consistent with the absolute (null) hypothesis. However, our conclusion must be tempered by three factors, the relatively small number of pigeons included in the present study, the occasional peak-shift-like effects that seem consistent with AL's relational account, and the fact that other studies have shown that pigeons respond relationally when explicitly trained to do so with multiple pairs of samples (e.g., Dreyfus, 1992; Fetterman & Dreyfus, 1986). Whether relational responding in the bisection tasks occurs with more training, or training with more than two pairs of samples remains an open question. If this

### Chapter III – Further tests on the relational vs. absolute dispute in the temporal bisection task

proves to be the case, then the challenge will be to articulate how the two forms of responding, absolute and relational, actually combine.

**CHAPTER IV<sup>6</sup> - ANIMAL TIMING: A SYNTHETIC APPROACH**

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<sup>6</sup> This Chapter reproduces the submitted article

Carvalho, M. P., & Machado, A., & Vasconcelos, M. (submitted). Animal timing: A synthetic approach. *Animal Cognition*.



## **Abstract**

Inspired by Spence's seminal work on transposition, we propose a synthetic approach to understand the temporal control of operant behavior. The approach takes as primitives the temporal generalization gradients obtained in prototypical concurrent and retrospective timing tasks, and then combines them to synthesize more complex temporal performances. The approach is instantiated by the Learning-to-Time (LeT) model. The chapter is divided into three parts. In the first part, we review the basic findings concerning the generalization gradients observed in fixed-interval schedules, the peak procedure, and the temporal generalization procedure, and then describe how LeT explains them. In the second part we use LeT to derive by gradient combination the typical performances observed in mixed fixed interval schedules, the free-operant psychophysical procedure, the temporal bisection task, and the double temporal bisection task. We also show how the model plays the role of a useful null hypothesis to examine whether temporal control in the bisection task is relative or absolute. In the third part, we identify a set of issues that must be solved to advance our understanding of temporal control, including the shape of the generalization gradients outside the range of trained stimulus durations, the nature of temporal memories, the influence of context on temporal learning, whether temporal control can be inhibitory, and whether temporal control is also relational. These issues attest to the heuristic value of a Spencean approach to temporal control.

*Keywords:* timing, temporal generalization gradients, Learning-to-Time (LeT) model, Spencean approach



## 1. Introduction

The concept of temporal generalization gradient may unify a large body of research on animal timing. In fact, most studies on animal timing of the last four decades have dealt, directly or indirectly, with temporal generalization gradients; on the empirical side, with the factors that determine their properties, like overall shape, symmetry, location, tails, and height; on the theoretical side, with models of the processes that engender them (e.g., Catania, 1970; Church, 2003, 2004; Church, Meck, and Gibbon, 1994; Dews, 1970; Gallistel, 1990; Gibbon, 1991; Gibbon, Church, & Meck, 1984; Killeen & Fetterman, 1988; Lejeune & Wearden, 2006; Lejeune, Richelle, & Wearden, 2006; Machado, 1997; Machado, Malheiro, & Erlhagen, 2009; Meck, 1983; Meck & Church, 1984; Platt, 1979; Platt & Davis, 1983; Roberts, 1981, 1998; Staddon & Higa, 1999; Zeiler & Powell, 1994).

Experimental research on the determinants of temporal generalization gradients and theoretical research on the causal processes of these gradients define an *analytic* approach to understanding temporal generalization. Within the analytic approach, the gradients themselves are what needs to be explained, the *explanandum*. Less pursued has been its converse, a *synthetic* approach, wherein temporal generalization gradients are used to explain other behavioral phenomena; they become the *explanans*.

In this chapter, we advance a synthetic approach to timing. That is, we take as primitives a set of well-known and reasonably consensual findings concerning temporal generalization gradients, and then use these primitives to explain seemingly more complex performance. Like a chemist, we attempt to synthesize more complex performance based on a few principles governing simple performance or, equivalently, given a complex performance we attempt to reduce it to the interplay of simpler performances. The approach extends to the time domain Spence's (1936, 1937, 1942) seminal idea that excitatory and inhibitory gradients may combine to produce unexpected results such as transposition, or seemingly relational forms of responding.

The choice of what counts as a primitive and what counts as a derivative is to some extent arbitrary – different researchers are likely to make different choices (e.g., whereas Köhler (1938) conceived of relational forms of stimulus control as primitives, Spence (1936, 1937, 1942) conceived of them as derivatives). However, any choice of primitives must be accompanied with a set of principles or rules to combine them. Without these rules, the synthetic approach cannot work. A well-defined set of primitives with explicit rules of derivation defines a theoretical model.

Our synthetic approach to timing is instantiated by the Learning-to-Time (LeT) model (Machado et al., 2009; Machado, 1997), a quantitative model of the causal processes of timing in animals. An outgrowth of Killeen and Fetterman's (1988) Behavioral Theory of Timing (BeT), LeT has been used to interpret research findings, relate results that seem to have little in common, contrast timing models, and ask new questions that require empirical answers. But perhaps the model's most important feature is that it qualifies as a plausible and parsimonious instance of the synthetic approach; plausible because, as we shall see, it relies on three fundamental principles of learning, reinforcement, extinction, and generalization, to account for temporal performance; and parsimonious because it operationalizes those principles in relatively simple ways (e.g., linear learning rules; small number of free parameters). Going one step further, we propose to consider LeT a *null hypothesis* in the animal timing domain. This means that we propose the model as a standard against which to compare alternative models; to reject the null and accept these alternative models – in other words, to entertain different and perhaps more numerous or complex sets of principles – we should require an equal degree of explicitness and consistency and a better account of experimental results.

This chapter is divided into three parts. In the first part we review the concepts of temporal generalization and temporal generalization gradients, central to our synthetic approach. We focus on studies with animals exposed to two types of operant conditioning procedures, those involving concurrent timing and retrospective timing. The prototype of concurrent timing procedures is the Fixed-Interval (FI) reinforcement schedule (Skinner, 1938), or its close relative, the Peak procedure (Catania, 1970; Roberts, 1981); the prototype of retrospective timing procedures is the Temporal Generalization task (Church & Gibbon, 1982). The generalization gradients obtained with the two prototypes define our primitives, the building blocks of the synthetic approach. The explanation of how these gradients come about according to LeT introduces the principles or rules that subsequently will be used to synthesize more complex performances.

Although we use a quantitative model to instantiate the synthetic approach, in the present study we focus more on its qualitative features than on its quantitative fits to specific data sets. At this early stage of the synthetic approach, a qualitative analysis may be more fundamental because it focuses on the model's core assumptions abstracted (as much as possible) from their precise mathematical formulations. To illustrate, the LeT model assumes a learning process whereby the strength of associative links increases with reinforcement and

decreases with extinction. We focus more on this qualitative feature than on the fact that LeT assumes a *linear* rule (Bush & Mosteller, 1955) as a first-order approximation to the quantitative, dynamic properties of the learning process. The empirical counterpart of our focus on qualitative model features is our focus on idealized (frictionless, we might say) research findings, that is, on data patterns and trends abstracted from their natural noisy background.

In the second part, we show the synthetic approach at work. That is, we use the primitives to derive some familiar results obtained with more complex procedures, including mixed FI-FI schedules and the free-operant psychophysical procedure in the domain of concurrent timing, and simple and double temporal bisection procedures in the domain of retrospective timing. We chose these procedures and their corresponding results not only to illustrate the synthetic approach, but also to identify some of the thorny problems that any timing theory must solve. To close this part, we use the synthetic approach to examine a new research issue, whether temporal control in the bisection task is relational or absolute. This case study illustrates in a concrete way what it means to consider LeT a null hypothesis.

In the third and last part, we summarize the synthetic approach and then discuss some of the issues it brings to the forefront of timing research. To broaden the scope of the study, we analyze each issue both in the light of LeT and in the light of another better-known model of timing, Scalar Expectancy Theory (SET; e.g., Gibbon, 1991). Some of these issues remain empirically unresolved, whereas others remain theoretically controversial, but all seem to be crucial to advance our understanding of timing. Hence, they can be viewed as a road map for future research to further extend and test our simple Spencean hypothesis – complex temporally regulated behavior may result from the interaction of simple temporal generalization gradients.

## **2. Part I: The temporal generalization gradients in prototypical procedures**

When a stimulus sets the occasion in which a response is reinforced, the stimulus comes to control the response – the probability or rate of the response increases when the stimulus is present, and decreases when the stimulus is absent. But stimulus control is never completely selective for other stimuli may also control the response, albeit to a lesser extent. When an animal responds in the presence of stimuli  $S_1, S_2, \dots, S_n$  because its responses were reinforced in the presence of stimulus  $S_+$ , stimulus generalization has taken place. Moreover,

when  $S_1, S_2, \dots, S_n$  differ from  $S_+$  along a continuous dimension – say light wavelength or tone frequency – the function relating a measure of response strength such as rate or probability to  $S_1, S_2, \dots, S_n$  defines a generalization gradient.

Figure 20 shows two classical examples. Guttman and Kalish (1956) reinforced four groups of pigeons for pecking a key illuminated with a different light (see  $S_+$  in Figure 20a), and then, in subsequent tests, illuminated the key with lights of different wavelengths ( $S_1, S_2, \dots, S_n$ ), and recorded the number of pecks at each light. The generalization gradients of each group peaked at the  $S_+$  and then decreased with the difference between the value of the other stimulus and the value of  $S_+$ . Jenkins and Harrison (1960) alternated periods with and without a 1000-Hz tone, and reinforced pigeons for pecking at a key only during the periods with the tone. Subsequently, they varied the frequency of the tone and obtained the pitch generalization gradient shown in Figure 20b. As for wavelength, the gradient peaked at the  $S_+$  and decreased with the difference between the test and the  $S_+$  frequencies (for a review, see, e.g., Ghirlanda & Enquist, 2003).

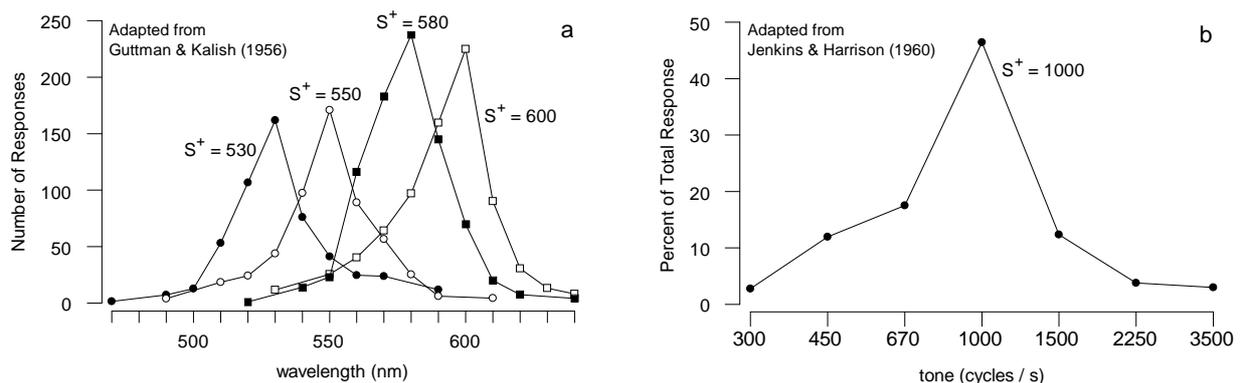


Figure 20. Panel a: Wavelength generalization gradients obtained by Guttman and Kalish (1956) with four groups of pigeons. Panel b: Example of a tone generalization gradient obtained by Jenkins and Harrison (1960) also with pigeons.

### 2.1. Fixed-interval schedule and the peak procedure

Temporal generalization occurs when the  $S_+$  is an interval of time, say a T-seconds interval, measured from the onset of a timer marker, and  $S_1, S_2, \dots, S_n$  are other temporal intervals, measured from the same time marker. Consider a FI T-seconds reinforcement schedule (see Figure 21a). On each trial, a time marker such as the illumination of a key for a pigeon initiates the interval. Responses during the T-seconds interval are not reinforced (the minus symbols in the figure); the first response after T seconds is reinforced (the plus

symbol), and then the next interval begins. Because most reinforced responses occur shortly after T, the pigeon does not experience intervals much longer than T (shaded range).

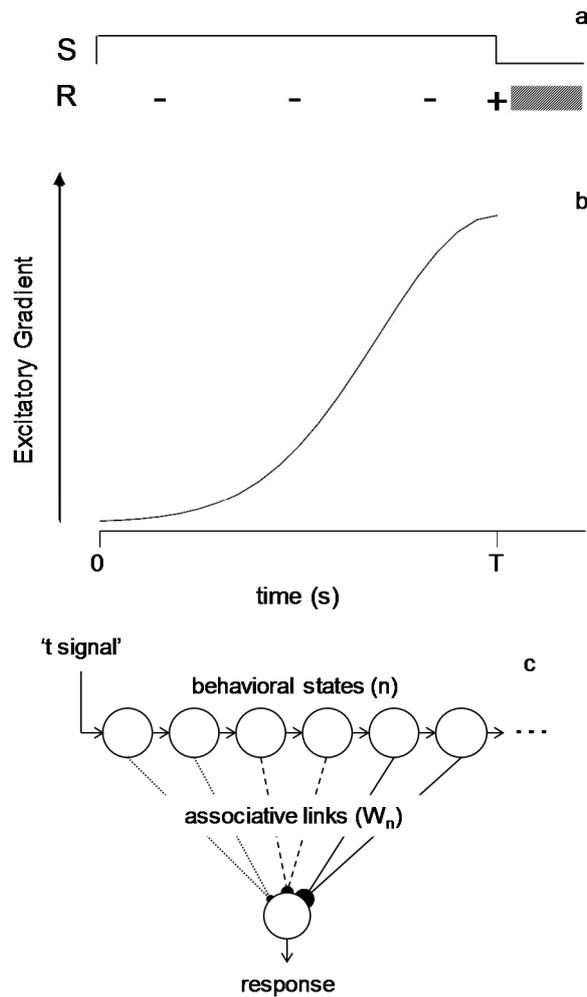


Figure 21. Panel a: A Fixed Interval T-seconds trial. The ‘S’ row shows Stimulus onset and offset. In the ‘R’ row, the minus symbols stand for extinction of Responses at times  $t < T$ ; the plus symbol stands for the moment T after which responding is reinforced; and the shaded area stands for intervals not experienced by the subjects. Panel b: Hypothetical excitatory gradient for a FI task. Panel c: The Learning-to-Time (LeT) model as applied to the FI task. States become active serially. Each state is linked to the operant response. The dotted, dashed, and solid lines represent increasingly strong links.

How do the effects of reinforcement at T seconds since trial onset generalize to other intervals? With respect to intervals shorter than T, performance on each trial at the steady state answers the question: On the average, response rate,  $R(t)$ , is zero or low at the beginning of the trial and then increases according to a roughly ogive function until the end of the trial; typically, the rate reaches its maximum around  $t = T$ . Figure 21b shows a stylized FI temporal generalization gradient.

Researchers have attempted to identify the factors that influence the shape of the gradient, and thus have studied the effect of a number of independent variables such as the absolute value of  $T$ , the magnitude of the reinforcer, and the amount of training on a number of dependent variables such as the duration of the initial pause, the pattern of responding on individual trials (break-and-run versus scallop), or the running rate (e.g., Dews, 1970, 1978; Guilhardi & Church, 2004; Lejeune & Wearden, 1991; Lowe & Harzem, 1977; Lowe, Harzem, & Spencer, 1979; Richelle & Lejeune, 1980; Schneider, 1969; Wynne & Staddon, 1988). When they compared the response rate gradients obtained with different values of  $T$ , they found that these gradients superimpose when the independent and dependent variables are scaled, the former with respect to  $T$  and the latter with respect to the maximum response rate during the interval (e.g., Dews, 1970). Known as *scale invariance*, this is perhaps the most robust property of temporal generalization gradients. In fact, it is the foundation stone of arguably the most influential model of animal and human timing, SET (Gibbon, 1977, 1991; Gibbon et al., 1984).

The FI temporal generalization gradient is consistent with a simple and intuitive hypothesis: Reinforcement at  $T$  engenders a hypothetical excitatory gradient over the interval from zero to  $T$ , a gradient that peaks at  $t = T$  and then decreases to a low value at  $t = 0$ ; responding starts when the excitatory gradient exceeds a noisy threshold,  $\Theta$ . The LeT model formalizes this simple hypothesis.

Figure 21c shows the three components of the LeT model, a series of behavioral states, numbered  $n = 1, 2, 3, \dots$ ; a set of links from the states to the operant response, each with a strength or weight denoted by the variable  $W(n)$ ; and the operant response itself. The model works as follows: The time marker (e.g., the illumination of a keylight in a FI schedule with pigeons) activates the first state. After a while, the first state becomes inactive and the second state in the series becomes active; after another while, the second state becomes inactive and the third state becomes active. We may picture the dynamic process as a wave that sweeps across the states, activating each one in series. The speed of the wave – the number of states activated per unit of time – remains constant within a trial, but varies from trial to trial. It is modeled as a Gaussian random variable with mean  $\mu_\lambda$  and standard deviation  $\sigma_\lambda$ .

While a state is active, the strength of its link determines whether the subject responds: If that strength exceeds a threshold,  $\Theta$ , the subject responds, otherwise it does not.

At the beginning of training, the link strength of state  $n$ ,  $W(n)$ , equals a constant,  $W_0$ . To ensure that responding occurs throughout the first trial, we set  $W_0 > \Theta$ .

At the end of the trial, the active state at reinforcement – state  $n^*$  – sees its link strengthened, whereas all previous states, active in extinction, see their links weakened, and all subsequent states, inactive during the trial, see their links unchanged. In symbols,  $W(n)$  increases for  $n = n^*$ , decreases for  $n < n^*$ , and does not change for  $n > n^*$ . LeT assumes one of the simplest mathematical forms for the changes in  $W$  with reinforcement and extinction, the Bush and Mosteller (1955) linear operator rule (see Machado et al., 2009, for details).

According to LeT the temporal generalization gradient results from the link strengths,  $W(n)$ , changed during training with reinforcement and extinction. The key idea is that, at the steady state,  $W(n)$  quantifies the degree of temporal overlap between the activation of state  $n$  and the delivery of reinforcement. Hence, the set of  $W$  values plays the role of the hypothetical excitatory gradient mentioned above. The links of the first states decrease to zero because they correlate negatively with reinforcement – when they are active, reinforcement rarely occurs<sup>7</sup>. The links of subsequent states increase because their active period is more likely to coincide with reinforcement. In fact, one of the states will have the strongest link and for that reason we call it the modal state for interval  $T$ . Finally, the states further down the series retain their initial link because they remain inactive during training. The link profile predicts that average response rate will be zero at trial onset and then increase as an ogive until the time of reinforcement (Machado et al., 2009).

Reinforcement at  $T$  may have effects on intervals longer than  $T$ . To see them, the experimenter needs to omit the reinforcer and extend the trial. Surprisingly, these effects remain poorly understood. A few studies (Machado & Cevik, 1998; Monteiro & Machado, 2009) and non-systematic observations (Ferster & Skinner, 1957) report that response rate remains high for intervals significantly longer than  $T$ , perhaps on the order of  $10T$ ; for even longer intervals, behavior may oscillate, with pauses and periods of sustained responding alternating (Crystal & Baramidze, 2006; Kirkpatrick-Steger, Miller, Betti, & Wasserman, 1996; Machado & Cevik, 1998; Monteiro & Machado, 2009). For our present purposes, the important point is that the gradient after  $T$  seems to differ significantly from the gradient before  $T$ .

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<sup>7</sup> Another possibility is to decrease the link strength to a negative value. The difference may be important to explain some experimental findings through summation of temporal generalization gradients. We return to this issue in the final section.

A high and sustained gradient after T does not follow from the simple excitatory gradient hypothesized above (Figure 21b), for that gradient would presumably decrease to zero as the interval grows beyond T and becomes increasingly more distinct from T. But it does follow from the gradient of link strengths that LeT predicts because as we move from the modal state in both directions, to previous states and to subsequent states, W decreases to different asymptotes. For previous states, W decreases to zero, but for subsequent states, W decreases to  $W_0$ . Because  $W_0$  is greater than the threshold, responding is sustained when those later states become active following intervals longer than T.

The asymmetry of the temporal generalization gradient around T shows that the moment of reinforcement is not the only determinant of the shape of the gradient. This idea becomes clearer when we compare an FI T-seconds schedule with the equivalent peak procedure. The moment of reinforcement remains the same, but in the peak procedure FI trials alternate with longer trials, say 4T-seconds long, that end without reinforcement. In most studies, after an intertrial interval, a tone or light is turned on until either a reinforcer occurs at approximately T seconds (FI or food trials), or the trial ends after 4T seconds elapse (empty trials). As Figure 22a shows, the peak procedure is similar to a FI in the interval from zero to T, and differs from it in the interval from T to 4T. Typically, at the steady state average response rate increases from  $t = 0$  to  $t = T$  and then it decreases for  $t > T$  (see Figure 22b); sometimes response rate increases again as t approaches 4T (e.g., Roberts, Cheng, & Cohen, 1989). The curves for different values of T also are scale invariant. On individual empty trials, the animals start to respond sometime before T, and stop to respond sometime after T; on some trials they may start to respond again at the end of the trial (Church et al., 1994; Kirkpatrick-Steger et al., 1996; Sanabria & Killeen, 2007).

Following the analytical approach, several studies have examined the factors that affect the shape of the gradient, its mode (peak time), the amount of responding at the mode (peak rate), its symmetry around T, or its changes with the nature of the time-marker, for example (e.g., Roberts, 1981; Roberts, 1998; Roberts, Cheng, & Cohen, 1989; Church et al., 1994). Other studies have examined the effects of interrupting the stimulus that signals the onset of the trial (gap procedure; e.g., Roberts, 1981, 1998; Cabeza de Vaca, Brown, & Hemmes, 1994; Kaiser, Zentall, & Neiman, 2002). But for our purposes the main lesson learned from the peak procedure is that, for the generalization gradient to decrease past T, the animal must experience intervals longer than T in extinction.

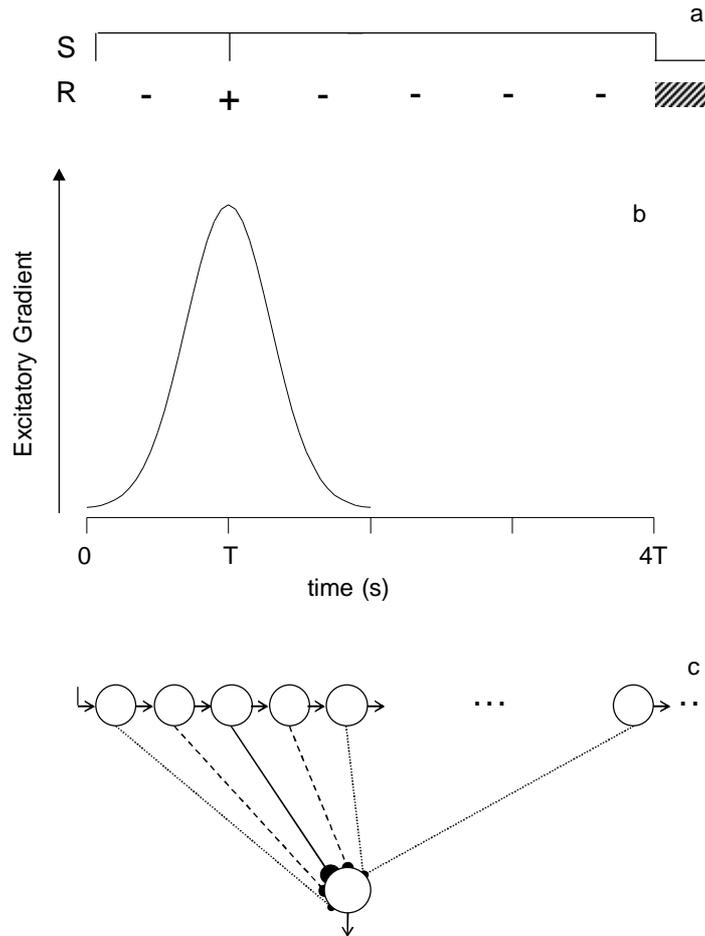


Figure 22. Panel a: A Peak procedure trial and its reinforcement (at T) and extinction (at  $t < T$  and  $t > T$ ) contingencies. Panel b: Hypothetical Gaussian excitatory gradient for the peak task. Panel c: Profile of link strengths predicted by LeT. Only a subset of states is shown. The link strengths increase from the ‘initial’ states, active at the beginning of the trial, to the modal state at T, and then decrease for ‘late’ states, active after T.

According to LeT (Figure 22c), as we move from the FI to the peak procedure, no new causal processes are required to explain the shape of the new generalization gradient. The experience of extinction for intervals longer than T introduces a negative correlation between reinforcement and the states activated after the modal state. Hence, the link strengths of those states decrease from  $W_0$  to zero; when they fall below the threshold  $\Theta$ , responding stops. At the steady state the link strengths (the excitatory gradient) increase from zero (first states) to the highest  $W$  (modal state) and then decrease to zero (states active during empty trials) before they increase again to  $W_0$  (states inactive even during empty trials). LeT predicts that the response rate generalization gradient will increase from  $t = 0$  to  $t = T$ , decrease from  $t = T$  to about  $t = 2T$  and then, depending on the amount of training, it may

increase again or remain low until  $t = 4T$ . The model also predicts that response rate *will* increase if the experimenter extends the empty trials significantly beyond the value used during training,  $4T$  in the foregoing example (see Monteiro & Machado, 2009). This prediction, which remains to be tested systematically, shows that we need to explore the shape of the temporal generalization gradients beyond the intervals used during training, intervals longer than  $T$  in the FI schedule, and intervals longer than the empty trials in the peak procedure. Only by examining these boundary conditions, as we may call them, will we know the full effects of reinforcement at  $T$  and extinction before and after  $T$ . Without such knowledge, our understanding of the very primitives of the synthetic approach will remain incomplete and the scope of the approach will remain limited. In the meantime, we conclude that the generalization gradient for FI schedules is not simply the left limb of the gradient for the corresponding peak procedure; it is different for values of  $t$  greater than  $T$ .

## ***2.2. The temporal generalization task***

The two procedures presented above are the prototype of concurrent timing tasks; by responding as the critical interval elapses, the animal reveals its temporal generalization gradient. Next, we consider the prototype of retrospective timing tasks, tasks in which the animal responds only after an interval ends. We set up the FI equivalent in a retrospective timing task as follows: We present a stimulus with duration  $T$ , and when the stimulus ends, we illuminate a key or insert a lever to allow the animal to respond, and then reinforce its response. Surprisingly, perhaps, this non-differential procedure engenders no temporal control (e.g., Elsmore, 1971; Spetch & Cheng, 1998). The contrast with FI schedules, during which a target response is only occasionally reinforced, suggests that the temporal control of an operant response may require some form of differential reinforcement. Hence, the prototype of retrospective timing tasks, and the correct analog of the FI schedule, is the *temporal generalization procedure*. In its simplest form (see Figure 23a) the experimenter presents a stimulus that lasts for  $T$  or  $TS$  seconds, with  $TS < T$ . When the animal responds at the end of the stimulus, the experimenter reinforces the responses that follow  $T$  (the S+) and extinguishes the responses that follow  $TS$  (the S-; Church & Gibbon, 1982; Reynolds & Catania, 1962). In this conditional discrimination task, the duration of the sample signals

whether a response will be reinforced. In the terminology of Switalski, Lyons, and Thomas (1966), the procedure is an instance of intra dimensional discrimination training<sup>8</sup>.

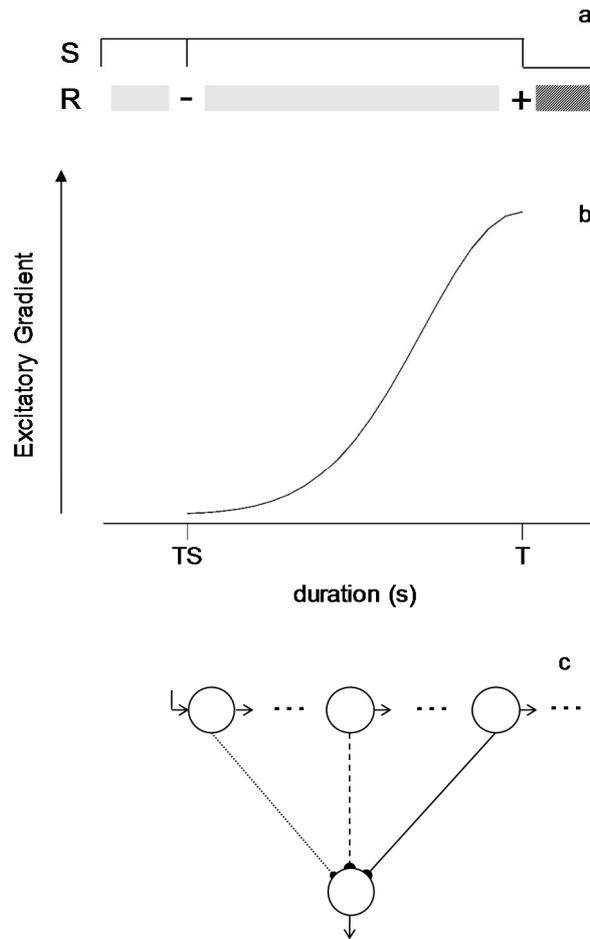


Figure 23. Panel a: A Temporal Generalization trial and its contingencies. The response is reinforced after the longer, T-seconds sample, and extinguished after the shorter, TS-seconds sample; the grey areas stand for the periods when responding is not allowed; the shaded area stands for intervals the subjects do not experience. Panel b: Hypothetical excitatory gradient for a temporal generalization task. Panel c: Profile of link strengths predicted by LeT.

The correlation between sample duration T and reinforcement engenders a temporal generalization gradient that is similar to the FI gradient: Within the trained range, response rate or probability increases from TS to T (Figure 23b; Church & Gibbon, 1982; Reynolds &

<sup>8</sup> Although temporal control in operant procedures seems to require some form of differential reinforcement, it is still unclear whether the differential reinforcement must be with respect to two or more distinct stimulus durations (intra dimensional discrimination training, as in the foregoing example with T and TS), or whether it suffices to reinforce a response following a stimulus with a particular duration and not to reinforce the response (or reinforce a different response) following the absence of the stimulus (inter dimensional discrimination training); Jenkins and Harrison's (1960) study in Figure 1 shows the latter for tone frequency (see Russell & Kirkpatrick, 2007; Vieira de Castro, Vasconcelos, & Machado, in press).

Catania, 1962); the gradient also is scale invariant (e.g., Church & Gibbon, 1982). Although we think that a gradient obtained with sample durations outside the range of the trained durations will be similar to the FI gradient (i.e., low for  $t < TS$  and high for  $t > T$ ), we do not know of any study that examined the issue (see Church & Gibbon, 1982, Study 2).

If we add a third stimulus duration (TL) with  $TS < T < TL$  and reinforce responses after T but not after TS or TL (see Figure 24a), we obtain the retrospective timing task equivalent to the peak procedure. The animal experiences reinforcement at T together with extinction at intervals shorter and longer than T, resulting in a scale invariant Gaussian-like gradient with its mode at T (Figure 24b).

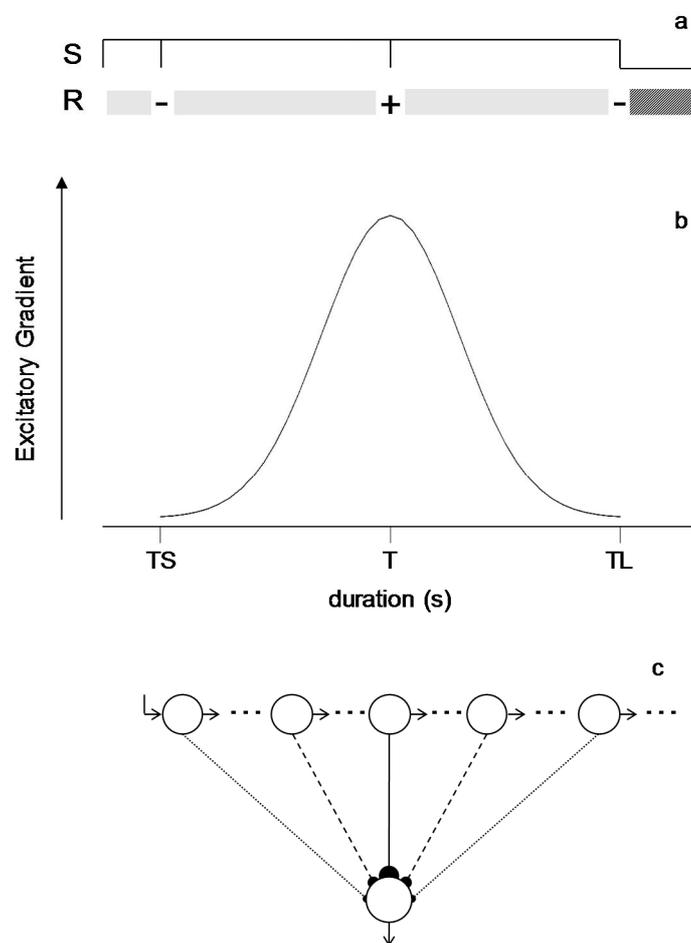


Figure 24. Panel a: A three sample Temporal Generalization trial. Responses are extinguished after the shortest TS and the longest TL samples, and reinforced after the intermediate T samples. Panel b: Hypothetical excitatory gradient for the task. Panel c: Profile of link strengths predicted by LeT. Compare with Figure 23.

In terms of causal processes, the bell-shaped generalization gradient may result from an excitatory gradient that is highest at T (the S+) and decreases, towards TS and TL (the S-)

or from an excitatory gradient centered at T plus two inhibitory gradients, one centered at TS and the other centered at TL. The LeT model assumes the former alternative.

For LeT, the generalization gradient expresses once again the profile of link strengths acquired during training. Reinforcement strengthens the links connecting the states active at T with the operant response, and extinction weakens the links connecting the states active at TS and TL with the operant response (Figures 23c and 24c, respectively). Although LeT invokes no new causal processes, we note that, like other timing models, it does not explain why temporal control requires differential reinforcement with at least one temporally defined S+ and one temporally defined S- (see Russell & Kirkpatrick, 2007; Vieira de Castro, Vasconcelos, & Machado, in press).

### **3. Part II: The synthetic approach at work**

#### ***3.1. Concurrent timing: Mixed fixed-interval schedules and the serial nature of temporal memories***

A simple modification of the peak procedure illustrates the potential of generalization gradients to synthesize more complex temporally regulated performance. Suppose that we replace the empty trials of the peak procedure by trials that also end in reinforcement. The new schedule is a *mixed FI T<sub>1</sub>-FI T<sub>2</sub>* schedule with two distinct reinforcement moments, T<sub>1</sub> and T<sub>2</sub>. On a proportion *p* of the trials, reinforcement occurs at T<sub>1</sub> seconds since trial onset; on the remaining trials, reinforcement occurs T<sub>2</sub> seconds since trial onset (Catania & Reynolds, 1968; Ferster & Skinner, 1957; Leak & Gibbon, 1995; Lima, 2010; Whitaker, Lowe, & Wearden, 2003, 2008). No signal announces the duration of the current trial. Figure 25 shows the temporal gradient obtained by Leak and Gibbon (1995) using a mixed FI 10s-FI 120s schedule. The response-rate generalization gradient is bimodal, with one mode close to 10 s and another at 120 s. Moreover, the two ascending limbs superimpose if scaled with respect to 10 s and 120 s, respectively (Leak & Gibbon, 1995; see also Ferster & Skinner, 1957, pp. 597-605). More important is the fact that on the longer trials, the animal generally starts responding before 10 s, stops responding after 10 s, starts responding again sometime later, and then continues responding until the end of the trial (Leak & Gibbon, 1995). As Ferster and Skinner (1957) put it, “a well-marked priming exists after the shorter interval, and a falling-off into a curvature appropriate to a longer interval” (Ferster & Skinner, 1957, p. 597).

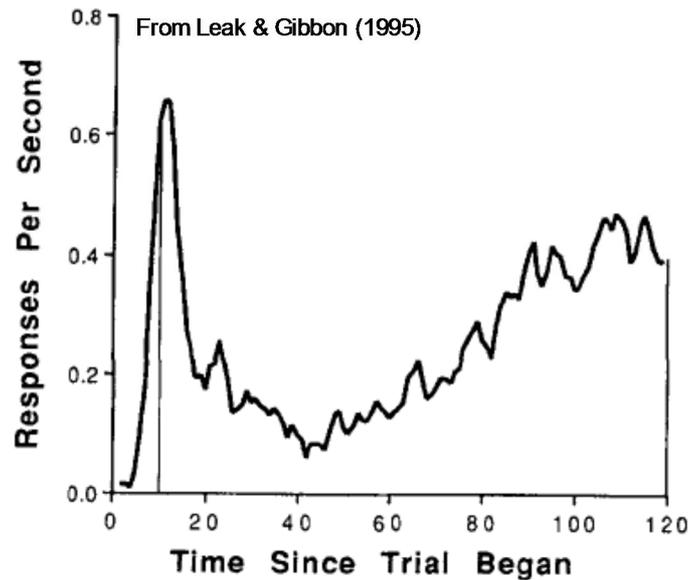


Figure 25. Generalization gradient obtained by Leak and Gibbon (1995) with a group of pigeons exposed to a Mixed FI 10s-FI 120s schedule. The gradient is bimodal (one mode at 10 s and another at 120 s) and shows the scalar property. The minimum response rate occurs close to 35 s, the geometric mean of 10 and 120.

Consider a mixed schedule with parameters similar to the peak procedure that we described above, that is, a mixed FI T-FI 4T. As its name shows, the schedule combines two FI schedules and therefore we could try to synthesize its gradient from the gradients engendered by the two FI schedules, the primitives. We would fail because the correct ingredients are not those from the separate FI schedules, but the gradient engendered by a T-seconds peak procedure and the gradient engendered by a FI 4T-seconds schedule. As Figure 26a shows, the reinforcement contingencies in the mixed FI-FI schedule are similar to the contingencies during the peak procedure, for in both cases the reinforced moment T is flanked by two directly experienced extinction intervals; the second reinforcement moment at 4T brings in the FI gradient.

Figure 26b shows three excitatory gradients: a Gaussian gradient that corresponds to a peak procedure with reinforcement at T, a left Gaussian gradient that corresponds to a FI 4T schedule, and a gradient obtained by adding the other two. This third gradient has the same shape as the generalization gradient observed in mixed schedules with widely separated reinforcement moments (see Machado et al., 2009, for quantitative details).

Figure 26c illustrates how the LeT model handles this procedure. Because the states active around T and 4T correlate positively with reinforcement and the remaining ones with

extinction, the generalization gradient will increase from  $t = 0$  to  $t = T$ , decrease from  $t = T$  to about  $t = 2T$  as in a typical peak procedure, and then increase again as  $t$  approaches  $4T$ .

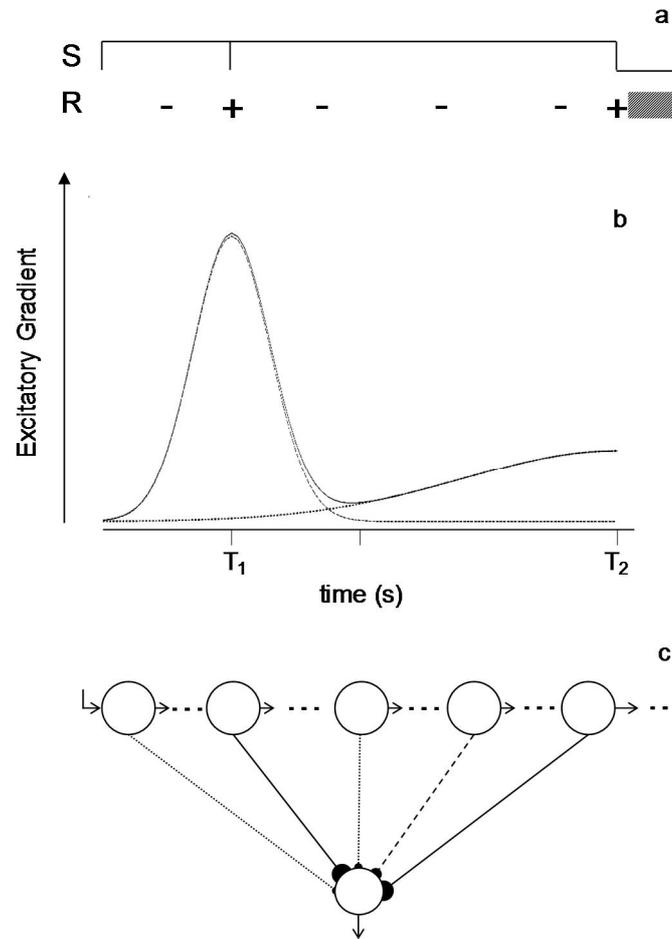


Figure 26. Panel a: A Mixed FI-FI trial with its contingencies. Panel b: Three excitatory gradients, a Gaussian gradient from a peak procedure with reinforcement at  $T_1$ , a half Gaussian gradient from a FI  $T_2$  schedule, and the sum of the two gradients. Panel c: Profile of link strengths predicted by LeT. Two states have the strongest links with the response, the modal states at  $T_1$  and  $T_2$ .

Mixed FI-FI schedules are important in the study of timing because they show how generalization gradients may combine to produce new forms of temporally regulated behavior. Moreover, they also challenge timing models that concentrate the effects of reinforcement in distinct memory stores (e.g., SET). When the *same* response is reinforced at two different moments, say  $T$  and  $4T$ , these models explain the bimodal generalization gradient by assuming two different memories, memory A representing the effects of reinforcement at  $T$  and sampled at trial onset, and memory B representing the effects of reinforcement at  $4T$  and sampled later into the trial. The problem is that the models do not explain how the two memories are created, populated, and accessed. That is, they do not

explain how the representation of a particular interval is stored in memory A rather than memory B, or how a particular temporal sample is retrieved from memory B rather than memory A. As Machado (1997) argued, SET's account of the bimodal generalization gradient in mixed FI-FI schedules is circular because the model postulates two memory stores to explain the temporal discrimination, but the appropriate use of these stores presupposes the temporal discrimination. We will see below other expressions of the same logical problem (see also Machado et al., 2009).

### ***3.2. Concurrent timing: The free operant psychophysical procedure and the distributed nature of temporal memories***

The last concurrent timing procedure that we analyze, the *free-operant psychophysical procedure (FOPP)*, introduces a second operant response into the experimental situation and further illustrates how separate gradients may combine to produce a generalization gradient. Figure 27a shows the details. Responses on a 'left' key are reinforced unpredictably (i.e., according to a variable interval, VI, schedule) *only* during the first half of a T-seconds trial; responses on a 'right' key are reinforced also unpredictably (according to a VI schedule) *only* during the second half of the trial. No stimulus signals the middle of the trial, the moment 'left' responses cease to be reinforceable and 'right' responses become reinforceable.

Typically, at the steady state, two response rate generalization gradients are obtained, one for each operant (Figure 27b). The rate on the 'left' key starts high and then decreases, whereas the rate on the 'right' key starts low and then increases. When the VI's are equal the gradients intersect at time  $t^*$  close to the middle of the trial ( $t^* \approx T/2$ ). The relative response rate gradient, defined by the proportion of 'right' responses at each trial moment, follows a roughly ogive curve. At trial onset it is close to 0, around the middle of the trial it reaches .5, and at the end of the trial it is close to 1. Importantly, when the VI's differ, the rate gradients shift in predictable directions. If the VI for the 'left' key is richer, the gradients shift to the right (the animal stays longer on the 'left' key) and the relative rate gradient crosses indifference at  $t^* > T/2$ ; if the VI for the 'left' key is poorer, the gradients shift to the left (the animal changes to the 'right' key earlier) and the relative rate gradient crosses indifference at  $t^* < T/2$  (e.g., Bizo & White, 1995; Machado & Guilhardi, 2000).

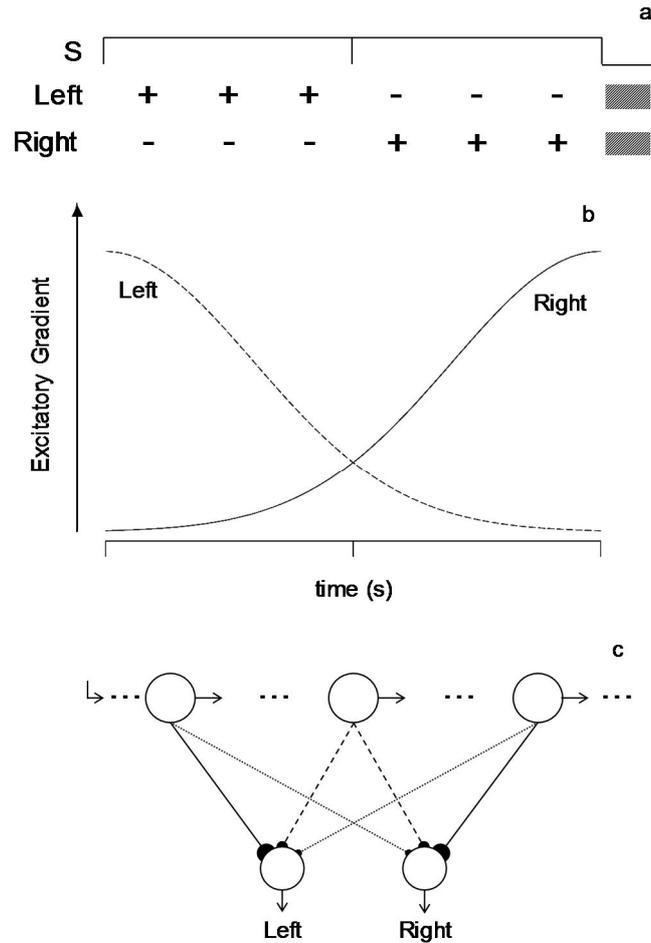


Figure 27. Panel a: A trial of a Free-Operant Psychophysical Procedure (FOPP) and its contingencies. ‘Left’ responses are reinforced during the first half of the trial and extinguished during the second half. ‘Right’ responses have the opposite contingencies. Panel b: Hypothetical excitatory gradients for ‘left’ and ‘right’ responses. Panel c: Profile of link strengths predicted by LeT. Each state is linked to both responses. ‘Initial’ states are linked strongly with ‘left’ and weakly with ‘right’; ‘late’ states are linked strongly with ‘right’ and weakly with ‘left’. When the VI’s are equal, ‘intermediate’ states are linked equally to both responses.

According to LeT, the causal processes remain the same as for the other procedures, except that in the FOPP each state is linked to two operant responses, the ‘left’ and ‘right’ key pecking (Figure 27c). Because the link strengths express the overlap between state activation and reinforcement, the states active during the beginning of the trial become linked strongly with the ‘left’ response and weakly with the ‘right’ response, and conversely, the states active during the end of the trial become linked strongly with the ‘right’ response and weakly with the ‘left’ response; when the VI’s are equal, the ‘intermediate’ states that are active around the middle of the trial become linked equally with both responses (see middle

circle in Figure 27c). Hence, when the VI's are equal the relative rate on the 'right' key at time  $t$  is ogival and crosses .5 close to the middle of the trial. However, when the VI's differ, the reinforcement contingencies bias the links of the 'intermediate' states towards the richer operant and, as a consequence, the two response-rate gradients and the ogival relative gradients shift in the expected direction (Machado & Guilhardi, 2000; see also Bizo & White, 1995, Guilhardi, MacInnis, Church, & Machado, 2007).

The FOPP procedure is important for yet another reason. The reinforcer for each operant response distributes uniformly across the corresponding interval, the first half of the trial for 'left' key pecks, and the second half of the trial for 'right' key pecks. Therefore, the moments of reinforcement for each operant remain the same regardless of the absolute value of the VI schedules. If the temporal generalization gradients depended exclusively on these moments, they should not shift when the VI's change from, say, favoring the 'left' key to favoring the 'right' key. Because they shift, it seems that at least two variables affect the gradients: the moments of reinforcement and the frequency of reinforcement at those moments. In LeT these variables map onto the state active at reinforcement and its link strength (see Machado & Guilhardi, 2000; Machado et al., 2009).

Somewhat analogous to the FOPP is the midsession reversal task, which can be conceived of as a session-wide or single trial FOPP. Typically, in a simultaneous discrimination procedure, the animal faces two options,  $S_1$  versus  $S_2$ ; responses to  $S_1$  are reinforced in the first half of the session and responses to  $S_2$  are reinforced in the second half (for an extension to a 3-stimuli / 2-reversals procedure, see McMillan & Roberts, 2015). The optimal strategy in this task is to attend only to the local rate of reinforcement: choose  $S_1$  until the first unreinforced response to  $S_1$  and then reverse preference and choose  $S_2$  until the end of the session (a win-stay, lose-shift strategy). Surprisingly, animals commit two types of errors around the moment of reversal, they anticipate the reversal and choose  $S_2$  when  $S_1$  still is the reinforced option, and they persevere after the reversal and continue to choose  $S_1$  after  $S_2$  has become the reinforced option.

After Cook and Rosen (2010) first reported the midsession reversal effect, a flurry of studies ensued (e.g., Laude, Stagner, Rayburn-Reeves, & Zentall, 2014; McMillan, Kirk, & Roberts, 2014; McMillan & Roberts, 2012, 2015; Rayburn-Reeves, Laude, & Zentall, 2013; Rayburn-Reeves, Molet, & Zentall, 2011; Rayburn-Reeves & Zentall, 2013; Stagner, Michler, Rayburn-Reeves, Laude, & Zentall, 2013). Most of their authors have interpreted the effect in terms of animals timing the duration of the session up to the reversal (e.g., Cook

& Rosen, 2010; McMillan & Roberts, 2012), which is consistent with the pattern of errors and plausible. Because most midsession reversal experiments comprise around 80 trials per session with 5- to 6-s ITI's, rats and pigeons would be timing an interval of about four minutes, which is feasible. However, how temporal control by the time marker (seemingly, the session onset) combines with the situational control by the trial outcome remains to be worked out.

### 3.3. *Retrospective timing: Simple bisection*

We illustrate the synthetic approach to retrospective timing first with the simple bisection procedure, and then with the double bisection procedure. In the *simple bisection* procedure (see Figure 28a), a trial begins with one of two samples that differ only in duration: a short TS sample (e.g., a 1-s light) or a long TL sample (e.g., 4-s light). After the sample, two responses  $R_1$  and  $R_2$  (say pecking a 'red' or a 'green' key) are simultaneously available. Choice of  $R_1$  following TS and of  $R_2$  following TL are reinforced. After the animal learns the mappings 'TS $\rightarrow$  $R_1$ , TL $\rightarrow$  $R_2$ ', the experimenter presents new sample durations,  $t$ , ranging from TS to TL, and measures the subject's choices of, say,  $R_2$ . The function relating the probability of choosing  $R_2$  given a  $t$ -seconds sample,  $P(R_2|t)$ , defines a temporal generalization gradient, also known as the *psychometric function*.

The prototypical gradient is ogival, starting close to 0 at  $t = \text{TS}$  and ending close to 1 at  $t = \text{TL}$ . Moreover, in animals, the duration  $t^*$  following which the subject is indifferent between  $R_1$  and  $R_2$  (i.e.,  $P(R_2|t^*) = P(R_1|t^*) = .5$ ), called the Point of Subjective Equality (PSE) or the bisection point, tends to be at the geometric mean of the trained durations ( $\text{GM} = \sqrt{\text{TS} \cdot \text{TL}}$ ; Catania, 1970; Church & Deluty, 1977; Stubbs, 1976). It is also the case that the gradients obtained with TS-TL pairs with the same ratio (e.g.  $\text{TS}_1 = 1$  vs.  $\text{TL}_1 = 4$ , and  $\text{TS}_2 = 4$  vs.  $\text{TL}_2 = 16$ ) superimpose when  $t$  is scaled with respect to  $\text{TS}_i$ , another instance of scale invariance. Figure 29 from Church and Deluty (1977) shows an example.

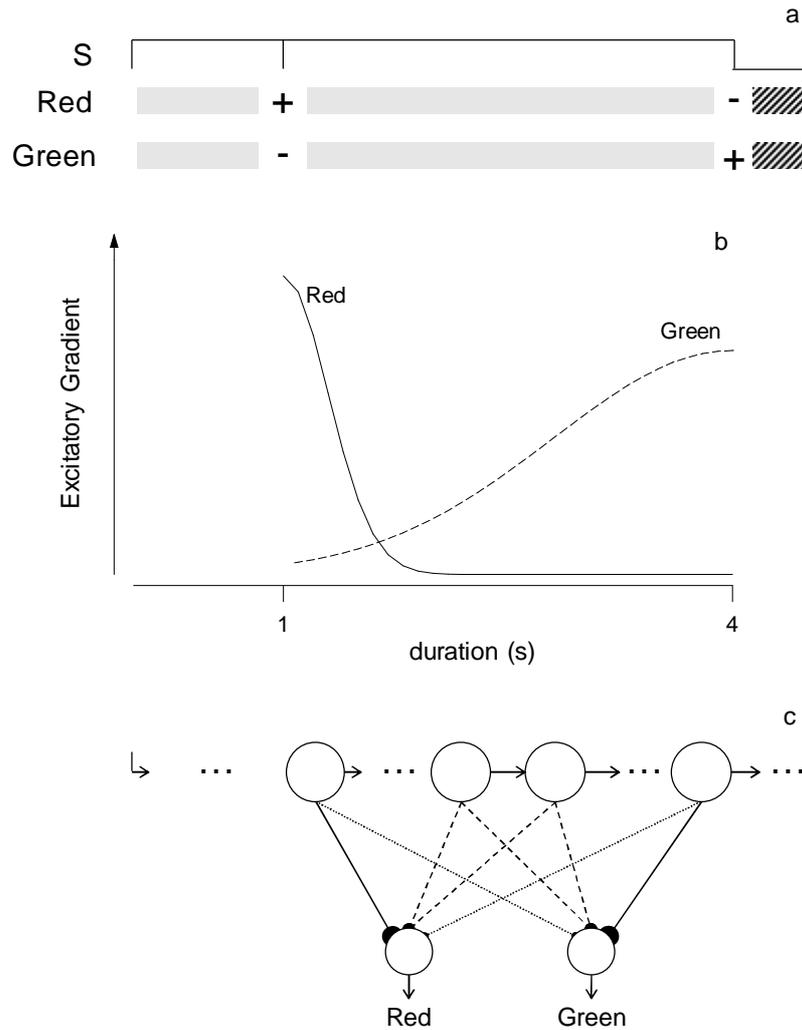


Figure 28. Panel a: A Simple Bisection trial and its contingencies. Responses on ‘red’ and ‘green’ keys are reinforced after the short and long samples, respectively. Panel b: Hypothetical excitatory gradients for ‘red’ and ‘green’ responses. Panel c: Profile of link strengths predicted by LeT. ‘Initial’ states are linked strongly with ‘red’ and weakly with ‘green’; ‘late’ states are linked strongly with ‘green’ and weakly with ‘red’. Subsequent states retain their initial link strength.

Within the analytic approach, the temporal generalization gradient obtained with the bisection procedure may be one of the most extensively investigated. Researchers have found that its shape is affected by a variety of factors such as the ratio of sample durations (e.g., Church & Deluty, 1977), sample modality (e.g., Wearden, Edwards, Fakhri, & Percival, 1998; Wearden, Norton, Martin, & Montford-Bebb, 2007), drugs (e.g., Meck, 1983; Odum, Lieving, & Schaal, 2002), and neurological conditions (e.g., Brown et al., 2011; Carroll, Boggs, O’Donnell, Shekhar, & Hetrick, 2008; Caselli, Iaboli, & Nichelli, 2009; Merchant, Luciana, Hooper, Majestic, & Tuite, 2008).

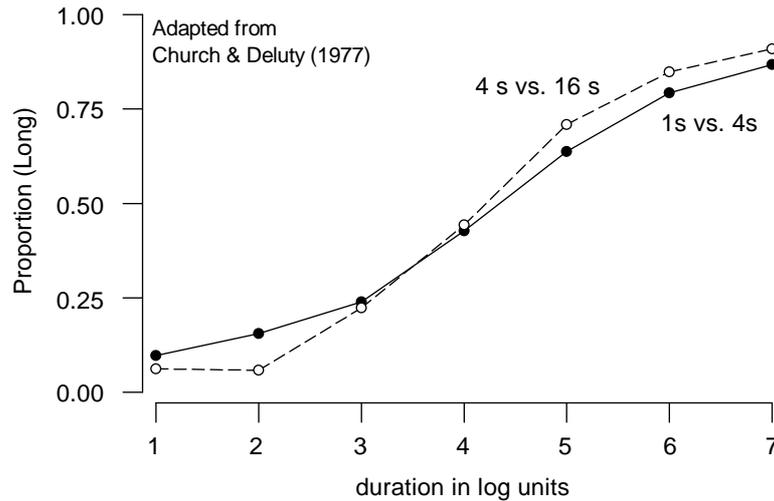


Figure 29. Temporal generalization gradients obtained by Church and Deluty (1977) with rats in two simple bisection tasks, one with 1 s vs. 4 s samples, and the other with 4 s vs. 16 s samples. The gradients follow an ogive curve, cross indifference at the geometric mean of the training samples, and overlap when plotted in a common scale.

The measured gradient may result from two excitatory gradients (Figure 28b), one related to response  $R_1$  and having TS as the S+ and TL as S-, and the other related to  $R_2$  and having TS as the S- and TL as the S+ (see Machado & Pata, 2005; Vieira de Castro & Machado, 2012; Vieira de Castro, Machado, & Tomanari, 2013).

LeT instantiates the preceding hypothesis (Figure 28c). At the beginning of training, each state is linked equally to  $R_1$  and  $R_2$ . During training, and given the reinforcement contingencies of the task, the states most active following the TS sample will become strongly linked to  $R_1$  and weakly linked to  $R_2$ , whereas the states most active following the TL sample will become weakly linked to  $R_1$  and strongly linked to  $R_2$ . At the steady state the two vectors of link strengths will express the overlap between state activation and reinforcement for each response. They predict a temporal generalization gradient that increases with  $t$ , has a bisection point close to the geometric mean of TS and TL, and is scale invariant (see Machado et al., 2009).

LeT accounts well for the psychometric function when the test stimuli are within the trained range (Machado, 1997; Machado et al., 2009), but the model has difficulties when the test stimuli are outside the trained range ( $t < TS$  or  $t > TL$ ). For according to LeT, durations significantly shorter than TS or significantly longer than TL activate states whose associative strengths did not change during training, and therefore preserved their initial, unbiased links with the two responses. Hence, as the test sample decreases below TS or increases above TL,

the predicted gradient approaches indifference. According to LeT, then, the full generalization gradient  $P(R_2|t)$  is polytonic: a) It decreases as  $t$  increases from  $t = 0$  to  $t = TS$ ; b) it increases like an ogive from about 0 to about 1 as  $t$  increases from  $t = TS$  to  $t = TL$ ; and finally, c) it decreases to .5 as  $t$  increases above  $TL$ .

Few studies have investigated the shape of the generalization gradient in the simple bisection procedure for test durations outside the trained range. Moreover, their results have been inconsistent (Russell & Kirkpatrick, 2007; Siegel, 1986; Vieira de Castro & Machado, 2012; Vieira de Castro et al., 2013). Some studies found polytonic gradients with increasing tails at the shortest durations ( $t < TS$ ), decreasing tails at the longest durations ( $t > TL$ ), or both effects (see Russell & Kirkpatrick, 2007; Siegel, 1986, Study 2; Vieira de Castro et al., 2013). However, the results of other subjects in the same studies and the results of other studies have found gradients with tails at the longest durations that remained at least as high as at  $TL$  (Siegel, 1986, Study 1; Vieira de Castro & Machado, 2012). We do not know the causes of this between-subjects and between-studies variability.

### ***3.4. Retrospective timing: Double temporal bisection and a context effect***

The model's generalization-based approach accounts also for the data of the *double bisection* procedure. Originally developed by Machado and Keen (1999) to contrast LeT with SET, the double bisection procedure combines two simple bisections. In one bisection, a response, say, pecking a 'red' key, is correct following a 1-s sample, and another response, pecking a 'green' key, is correct following a 4-s sample (see Figure 30a, left panel); the subject learns the mapping '1s→red; 4s→green'. In the other bisection, pecking a 'blue' key is correct following a 4-s sample, and pecking a 'yellow' key is correct following a 16-s sample (Figure 30a, right panel); the subject learns the mapping '4s→blue; 16s→yellow'. Figure 30b shows the hypothetical generalization gradients.

Critically, the 4-s sample is common to both bisections, but the correct comparison ('green' and 'blue') differs. After the animal learns the two mappings, the experimenter runs generalization tests with samples that range from 1 s to 16 s, and with the 'green' and 'blue' keys as comparisons.

Several studies have shown that, given a choice between 'green' and 'blue', the preference for 'green' increases with the sample duration (Arantes & Machado, 2008; Machado & Arantes, 2006; Machado & Keen, 1999; Machado & Oliveira, 2009; Machado & Pata, 2005; Oliveira & Machado, 2008, 2009). Figure 31 shows this finding.

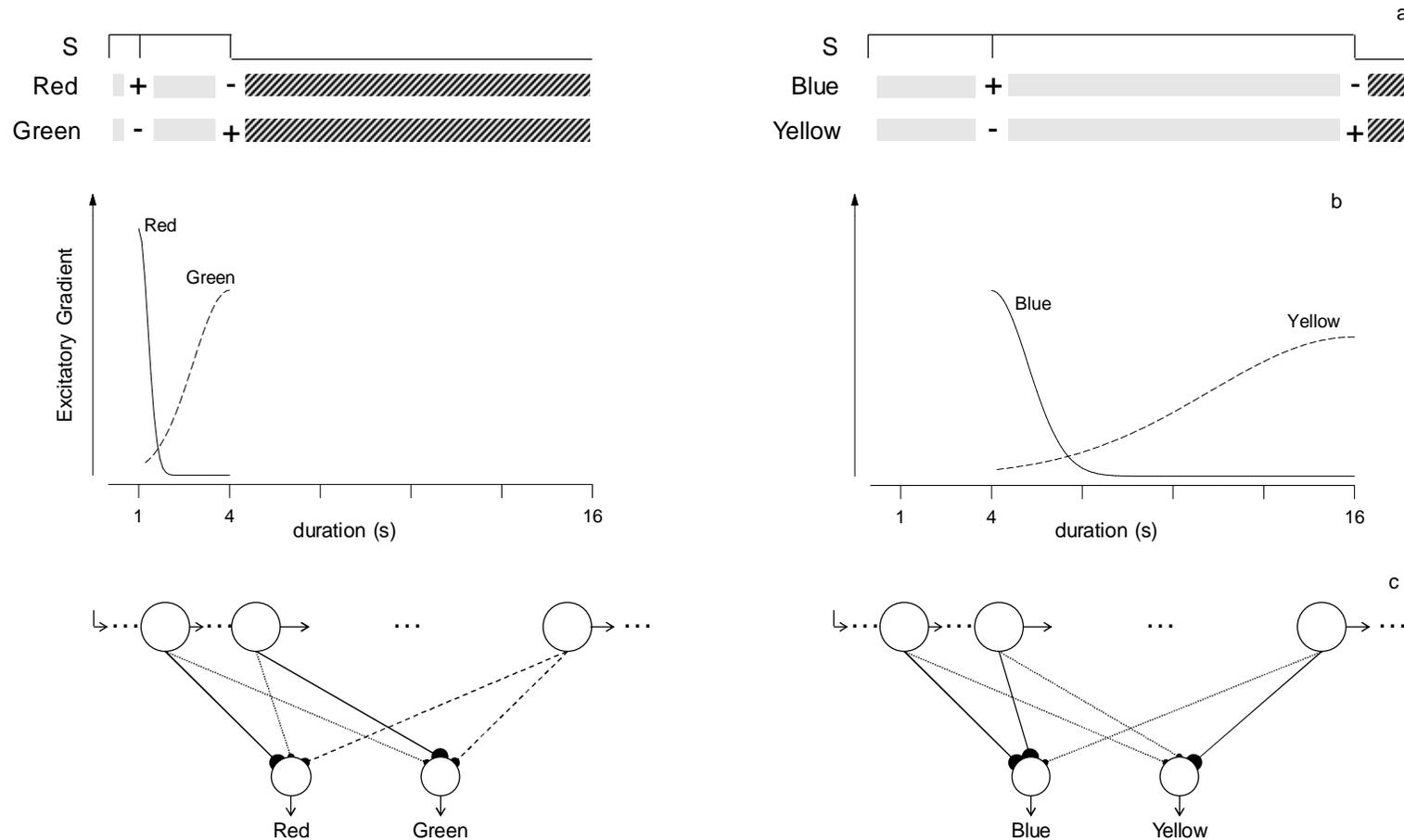


Figure 30. Panel a: A Double Bisection procedure and its contingencies. The subject learns two simple bisection tasks. In one (left), ‘red’ and ‘green’ responses are reinforced after 1-s and 4-s samples, respectively. In the other (right), ‘blue’ and ‘yellow’ responses are reinforced after 4-s and 16-s samples, respectively. Panel b: Hypothetical excitatory gradients for ‘red’ and ‘green’ responses (left) and for ‘blue’ and ‘yellow’ responses (right). Panel c: Profile of link strengths predicted by LeT.

We named the result a context effect because of how LeT explains it. According to the model, the difference in the sample contexts in which ‘green’ and ‘blue’ are reinforced and extinguished is critical. Initially, all states are linked equally to ‘blue’ and ‘green’. But during training the choice of ‘green’ is extinguished when the early states are active (the effect of 1-s sample; Figure 30c, left panel), whereas the choice of ‘blue’ is extinguished when the late states are active (the effect of 16-s sample; Figure 30c, right panel). Therefore, at the end of training, the early states are linked more strongly to ‘blue’ than ‘green’, whereas the late states are linked more strongly to ‘green’ than ‘blue’. These asymmetries in the excitatory gradients for ‘green’ and ‘blue’ predict that during testing the preference for ‘green’ over ‘blue’ should increase with the sample duration, the context effect.

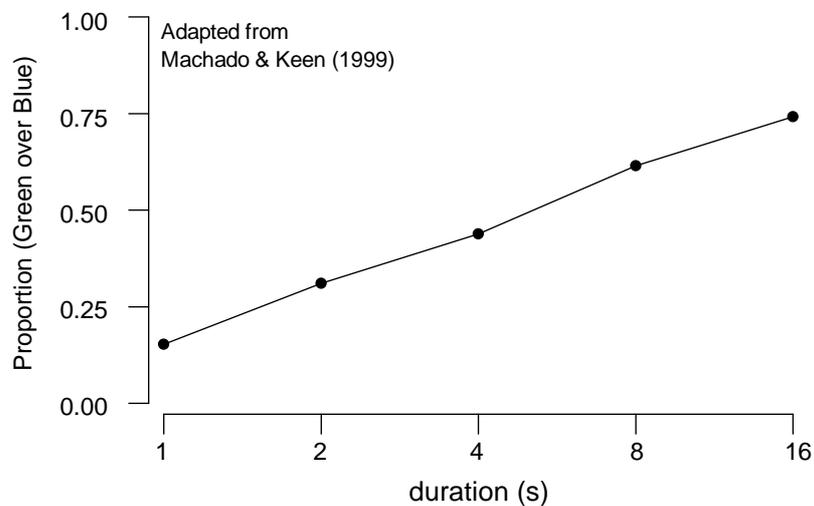


Figure 31. The context effect obtained by Machado and Keen (1999) after training pigeons in a double bisection task. Given a choice between ‘green’ and ‘blue’, the keys associated with the 4-s sample but in different sample contexts, preference for ‘green’ increases with sample duration.

Two studies show more directly how generalization gradients predict the context effect. Vieira de Castro et al. (2013) used the prototypical double bisection procedure described above, but before running the ‘blue’ vs. ‘green’ test, they obtained two generalization gradients. After the ‘2s→red, 6s→green’ training, they obtained the gradient for ‘green’ over ‘red’ with samples ranging from 0.7 to 51.4 s (Figure 32a). Similarly, after the ‘6s→blue, 18s→yellow’ training, they obtained the gradient for ‘blue’ over ‘yellow’ with samples also ranging from 0.7 to 51.4 s (Figure 32a)<sup>9</sup>. Finally, they used these two gradients to predict the gradient of ‘green’ over ‘blue’. Although the magnitude of the context effect

<sup>9</sup> The gradients in Figure 32a show the inconsistency mentioned before: Whereas the gradient obtained after the 2 s vs. 6 s training (filled circles) shows a decreasing right limb, the gradient obtained after the 6 s vs. 18 s training (empty circles) shows a sustained left limb.

was smaller than in previous studies, the predicted gradient matched qualitatively the obtained gradient (Figure 32b).

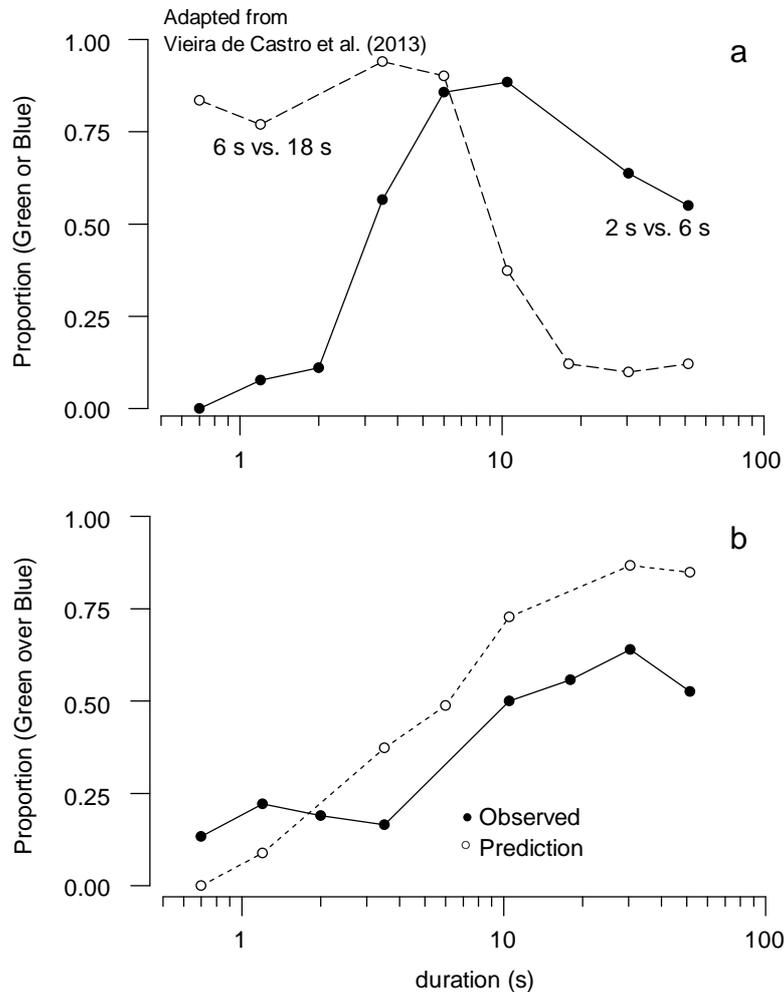


Figure 32. Panel a: Generalization gradients obtained by Vieira de Castro et al. (2013) after training pigeons in a double bisection tasks with 2 s vs. 6 s samples in one task, and 6 s vs. 18 s samples in the other. ‘Green’ and ‘blue’ were reinforced after the 6-s sample, but ‘green’ was extinguished after the 2-s sample and ‘blue’ after the 18-s sample. Panel b: Obtained gradient for ‘green’ over ‘blue’ (the context effect), and the gradient predicted from the two gradients in Panel a.

Vieira de Castro and Machado (2012) simplified the double bisection procedure to obtain separate ‘green’ and ‘blue’ gradients that were not “contaminated” by the competing ‘red’ and ‘yellow’ responses. In the first bisection, after 1-s or 4-s samples, pigeons chose between a ‘green’ key and a key with a ‘vertical’ bar. They received food for choosing ‘green’ after the 4-s sample, but not after the 1-s sample; they never received food for choosing the ‘vertical’ bar, a comparison used only to force the pigeons to attend to the choice keys. As in a go/no-go task, the pigeons suppressed pecking to ‘green’ after the 1-s

sample and pecked ‘green’ after the 4-s sample. Next, to obtain the first gradient, the experimenters presented samples that ranged from 1 s to 16 s and measured response rate on ‘green’ (see Figure 33a).

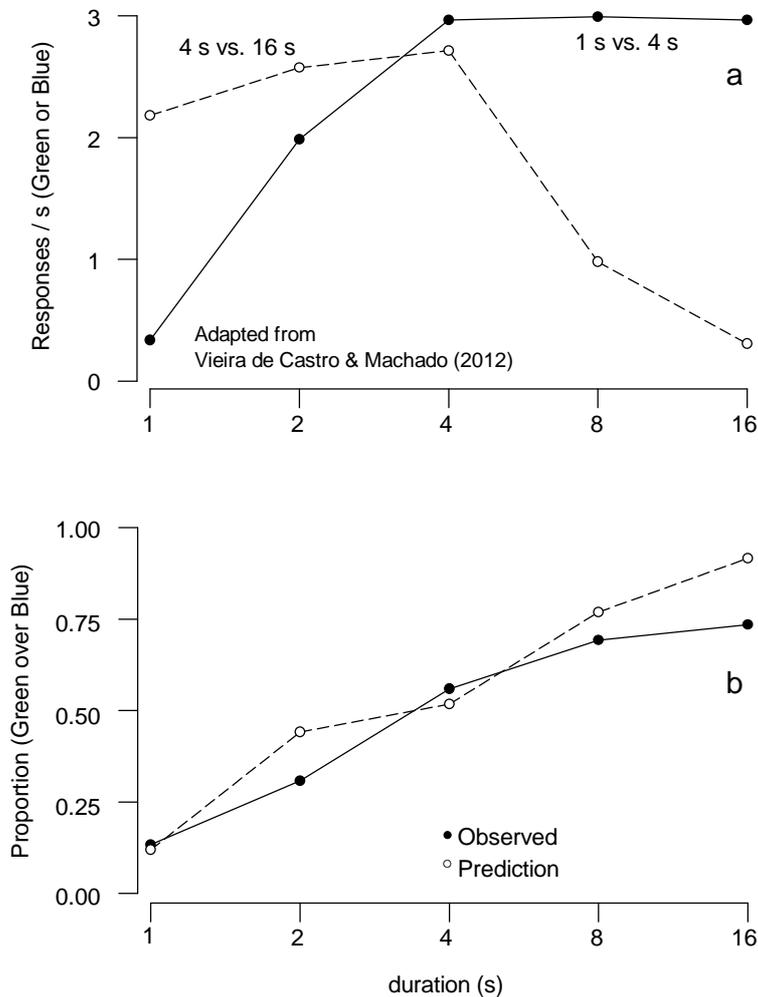


Figure 33. Panel a: Generalization gradients obtained by Vieira de Castro and Machado (2012) in a double bisection, go/no-go task, with 1 s vs. 4 s samples in the first task, and 4 s vs. 16 s samples in the second task. ‘Green’ and ‘blue’ were reinforced after the 4-s sample, but ‘green’ was extinguished after the 1-s sample and ‘blue’ after the 16-s sample. Panel b: Obtained gradient for ‘green’ over ‘blue’ (the context effect), and the gradient predicted from the two gradients in Panel a.

The pigeons then learned the second bisection, with 4- and 16-s samples, and a ‘blue’ key and a key with a ‘horizontal’ bar as comparisons. They received food only for choosing ‘blue’ after the 4-s sample. At the end of training, the experimenters obtained the second gradient (see Figure 33 a).

In the final test, the pigeons chose between ‘green’ and ‘blue’. The issue was whether the two separately obtained gradients could be combined to predict the gradient in the final

test. Figure 33b shows that the relative heights of the separate gradients at each sample duration indeed predicted the final gradient.

The various studies with the double bisection procedure (reviews in Machado et al., 2009, and Machado & Oliveira, 2009) reveal the explanatory power of the synthetic approach, its capacity to account for complex performance by means of temporal generalization gradients combined in relatively simple ways.

### ***3.5. A case study: Searching for relational temporal control with LeT as the null hypothesis***

The context effect could be interpreted differently, in terms of subjects responding to the relative durations of the samples. In each bisection task, one sample is short and the other is long. Since ‘green’ was correct following the long sample in the first task, and ‘blue’ was correct following the short sample in the second task, the pigeons may have learned the relational rules ‘long→green’ and ‘short→blue’ and then *transposed* them to the test trials; hence, the context effect.

The issue of whether temporal control in the bisection task is relational or absolute deserves closer scrutiny because our Spencean approach, instantiated by the LeT model, accounts for a reasonably large number of experimental findings by assuming only absolute control with temporal generalization. Any evidence for relational temporal control that is irreducible to the combination of generalization gradients would imply that LeT is if not wrong at least incomplete; an alternative model would seem to be called for. Hence, we propose to examine the “relational vs. absolute” issue with LeT as a plausible null hypothesis. Our analysis of the evidence will also qualify as a new case study of the synthetic approach to timing.

In addition to the double bisection studies, several studies have suggested that rats (Church & Deluty, 1977), starlings (Hulse & Kline, 1993), pigeons (Zentall, Weaver, & Clement, 2004), and humans (Molet & Zentall, 2008) categorize the training samples of the bisection task as either short or long and use these categories on subsequent test trials. The studies have adopted one of two different rationales and designs. Figure 34 shows the first, introduced by Church and Deluty (1977). In Phase A, one group of four rats learned the mapping ‘1s→left, 4s→right’ (Figure 34a, left panel). Then, in Phase B, half of the rats, the Relative group learned the new mapping ‘4s→left, 16s→right’, which preserves the relative assignments ‘short→left, long→right’ (Figure 34a, middle panel). The other half, the

Absolute group, learned the new mapping '16s→left, 4s→right', which preserves the absolute assignment '4s→right' (Figure 34a, right panel). A second group of four rats learned the same discriminations but in the opposite order, initially the '4s→left, 16s→right' mapping (Phase A), and then, after the group was divided into two, half learned the relational-preserving mapping '1s→left, 4s→right', whereas the other half learned the absolute-preserving mapping '4s→left, 1s→right' (Phase B). The preserved mapping, Relative or Absolute, and the training order, Upshift (from 1 s : 4 s to 4 s : 16 s) or Downshift (from 4 s : 16 s to 1 s : 4 s), defined four groups of two rats each, Relative Upshift, Relative Downshift, Absolute Upshift, and Absolute Downshift. If animals learn the relative value of the samples during Phase A, then, in Phase B they should learn faster a task that preserves the relative assignment than one that preserves the absolute assignment. On the other hand, if rats learn only the absolute value of the samples, the opposite should be the case. At issue then is which group learns faster the task in Phase B.

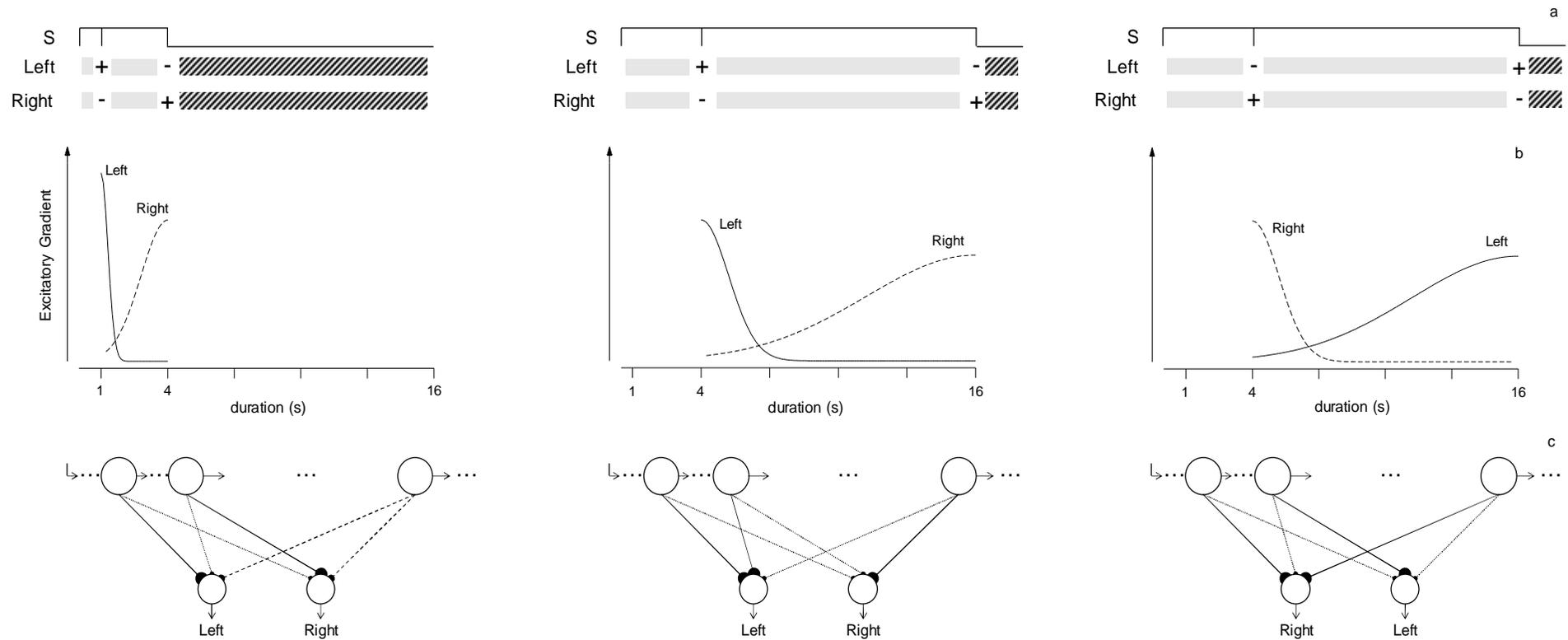


Figure 34. Panel a: The two types of bisection trials used in some studies about relational temporal control. In the first bisection task (left), ‘left’ and ‘right’ responses are reinforced after 1-s and 4-s samples, respectively. In the second bisection task, for the Relative group (middle) ‘left’ and ‘right’ responses are reinforced after 4-s and 16-s samples, respectively; for the Absolute group (right) ‘left’ and ‘right’ responses are reinforced after 16-s and 4-s samples, respectively. Panel b: Hypothetical excitatory gradients for each response in each task. Panel c: Profile of link strengths predicted by LeT. In the second task, the Relative group reverses the link strengths from the modal state at 4 s (cf. middle circle in middle panel).

Based exclusively on correct responses to the 4-s sample during Phase B, both Church and Deluty (1977) and Hulse and Kline (1993) concluded that subjects learn the relative value of stimuli because the Relative group (averaged across the Upshift and Downshift groups) learned the second task faster than the Absolute group. Surprisingly, in both studies the Absolute group had not mastered the second bisection task even after 10 sessions (see Figure 35a and 35b). The authors did not report performance on the 1-s or 16-s samples.

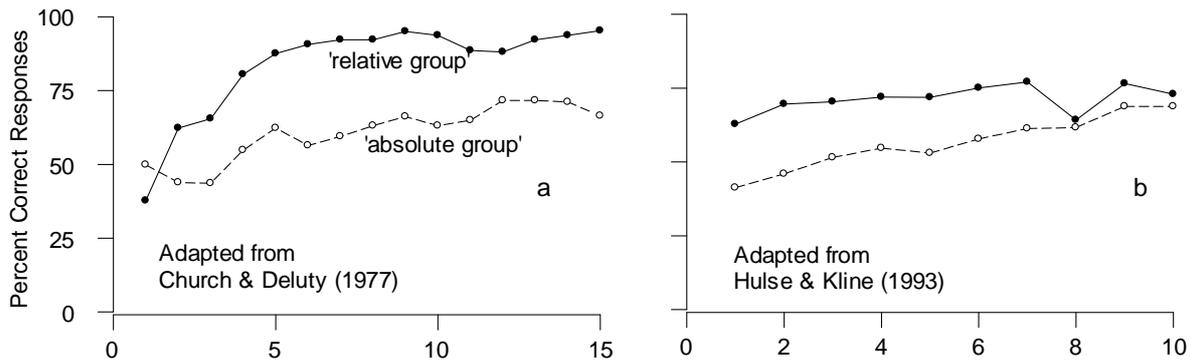


Figure 35. Acquisition curves for the Relative (full circles) and Absolute (empty circles) groups in the second bisection task. Panel a: Results obtained by Church and Deluty (1977) with rats. Panel b: Results obtained by Hulse and Kline (1993) with starlings.

Carvalho and Machado (2012; Chapter II here) extended the procedure to pigeons but improved Church and Deluty's design by a) doubling the number of subjects ( $N = 16$ ), b) adding a third phase during which each pigeon was re-exposed to its first bisection task (ABA' design), c) examining the results also for the 1-s and 16-s samples, and d) comparing the data with the predictions of the LeT model. Figure 8 (Chapter II) summarizes their findings. The pigeons showed little evidence of relational learning. At the beginning of Phase B, correct responses to the 4-s sample were at or below chance in the Relative group, but at or above chance in the Absolute group; similar results were obtained in Phase A'. Moreover, with few exceptions, the LeT model predicted well the acquisition pattern of both groups not only following the 4-s sample, but also following the 1-s and 16-s.

To understand the model's predictions, we label the states that tend to be active after the 1-s sample as 'early', those that tend to be active after the 4-s sample as 'intermediate', and those that tend to be active after the 16-s sample as 'late' (Figure 34c). After the '1s→left, 4s→right' training, the early states are strongly linked to 'left' and weakly linked to 'right'; the intermediate states are strongly linked to 'right' and weakly linked to 'left'; and the late states are linked equally to both responses. This link profile determines how pigeons

choose when the second task begins (Figure 34c, left panel). Consider the Relative group with the new mapping ‘4s→left, 16s→right’: The links from the early states will not change because these states will rarely be active; the links from the late states will be biased toward ‘right’; and the links from the intermediate states *will invert the bias acquired in the first task*, weakening the links to ‘right’ and strengthening the links to ‘left’ (Figure 34c, middle panel). This inversion explains why the proportion of correct responses following the 4-s sample decreases in the first sessions of the second and third bisections. Now consider the Absolute group with the new mapping ‘4s→right, 16s→left’: The links from the early states also will not change because they are rarely active; the links from the late states will be biased toward ‘left’; and the links from the intermediate states *will remain biased* toward ‘right’ (Figure 34c, right panel). Therefore, the proportion of correct responses following the 4-s sample remains above chance in the first sessions of the second and third bisections. Similar reasons explain the model’s predictions for the 1-s and 16-s samples (see Carvalho & Machado, 2012, for an extended discussion).

In a follow-up study, Carvalho, Machado and Tonneau (in press; Chapter III here) used ‘red’ and ‘green’ keylight colors as comparisons, introduced another phase (ABA’B’ design) to better study the acquisition patterns, and attempted to predict choice on the first session of each phase based on the generalization gradient obtained at the end of the preceding phase. Their results were generally consistent with their previous findings and again offered little support for relational learning in the bisection task. Moreover, the generalization gradients obtained at the end of four phases were broadly consistent with LeT. Figure 19 (Chapter III) shows the average data and model fits. Because these gradients have important implications for our conceptions of temporal learning and memory in the bisection task, we return to them below.

Zentall et al. (2004) approached the relational issue with a different rationale and design. Pigeons learned separately two bisections: ‘2s→red, 8s→green’ and ‘4s→vertical, 16s→horizontal’. Then, on test trials, they chose between ‘red’ and ‘green’ following 4-s sample, and between ‘vertical’ and ‘horizontal’ following 8-s sample. The 4-s sample had never been presented with the ‘red’ and ‘green’ comparisons, and the 8-s sample had never been presented with the ‘vertical’ and ‘horizontal’ comparisons. If the pigeons had not learned the relative value of stimuli during training, they should be indifferent between ‘red’ and ‘green’ following the 4-s sample (the geometric mean of 2 and 8) and between ‘vertical’ and ‘horizontal’ following the 8-s sample (the geometric mean of 4 and 16). But if the

pigeons had learned to categorize the trained samples as short and long, and associated these categories with the correct comparisons (i.e., short with ‘red’ and ‘vertical’, long with ‘green’ and ‘horizontal’), then responding should be biased toward ‘red’ following the 4-s short sample and toward ‘horizontal’ following the 8-s long sample. As Figure 36 shows, the results were mixed because if the pigeons preferred ‘red’ over ‘green’ following the 4-s sample, they were indifferent between ‘horizontal’ and ‘vertical’ following the 8-s sample.

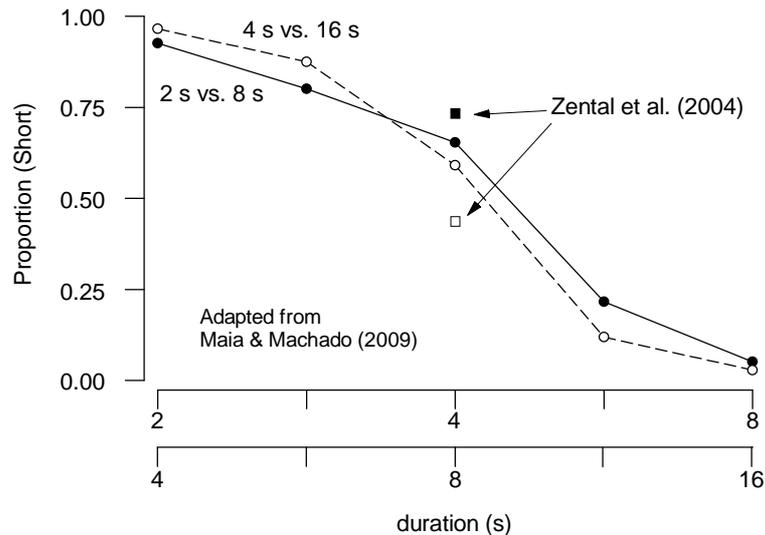


Figure 36. Pigeons learned two bisection tasks, one with a ‘2s→red, 8s→green’ mapping, and the other with a ‘4s→horizontal, 16s→vertical’ mapping. Next they were exposed to new test samples but with the same comparisons. Zentall et al.’s (2004) data show the preference for ‘red’ over ‘green’ following the 4-s sample (filled squares), and the preference for ‘horizontal’ over ‘vertical’ following the 8-s sample. Maia and Machado’s (2009) data show how the preference for ‘red’ (filled circles) or ‘horizontal’ (empty circles) varied with sample duration.

Maia and Machado (2009) enriched the testing procedure by including other sample durations besides the geometric mean of the training samples. They found that the pigeons preferred ‘red’ over ‘green’ following the 4-s sample, but also ‘vertical’ over ‘horizontal’ following the 8-s sample. That is, they chose the key associated with short equally often after the 4-s and 8-s samples. The generalization gradients obtained with each pair of comparisons almost superimposed (Figure 36).

Maia and Machado (2009) also showed that LeT could reproduce the psychometric functions obtained with each pair of comparisons with a slight bias for the short comparison at 4 s and 8 s. Our causal account runs as follows. The sets of states active after the 2-s and 4-s samples have more common elements than the sets active after the 4-s and 8-s samples and

these common elements bias choice toward the ‘red’ comparison. Similarly, the sets of states active after the 4-s and 8-s samples have more common elements than the sets active after the 8-s and 16-s samples and these common elements bias choice toward the ‘vertical’ comparison. According to LeT, then, the serial activation of the states and the link between these states and the operant responses account for both Zentall et al.’s (2004) and Maia and Machado’s (2009) results. More to the point, performance in the temporal bisection task seems broadly consistent with a model that assumes that reinforcement and extinction at specific time moments generalize to neighboring moments. The evidence remains consistent with the null hypothesis as instantiated by LeT.

#### 4. Part III: Conclusion

We proposed a synthetic approach to interval timing in animals, an approach grounded on the idea that temporal generalization gradients may combine to produce complex forms of temporally regulated behavior. Correlatively, we suggest that to explain apparently complex behavior, researchers may consider the combination of temporal generalization gradients as a useful null hypothesis.

Several models could be used to instantiate the null hypothesis, including the well-known and influential Scalar Expectancy Theory. We chose the Learning-to-Time (LeT) model, with which we have worked since 1997 (Machado, 1997), for the following reasons. Like its predecessor, Killeen and Fetterman’s (1988) Behavioral Theory of Timing, LeT is based on well-established principles of reinforcement and extinction and accords with Weber’s law for timing, hence it is *plausible*. LeT has accounted well for data from a variety of experimental situations (e.g., concurrent and retrospective timing with one or two responses), hence, it has a modicum of *depth* and *breadth*. LeT has helped us to look at apparently disconnected procedures and data through the same lens, hence it is *integrative*. LeT is framed in mathematical language and predicts not only acquisition patterns but also steady-state performance; hence it is *clearer* and empirically *more sensitive* than purely verbal models. But perhaps its most significant feature is that the model operationalized in a relatively straightforward way the Spencean approach, explaining both its primitives (how animals acquire temporal generalization gradients) and their derivatives, how these gradients interact to predict known and sometimes surprising results (e.g., context effects). As Killeen

(1999) put it, “models are go-betweens”, and the LeT model has served us well in going back and forth between data and our sense of understanding temporal performance.

Our basic tenet is that many apparently complex phenomena in the timing domain may be explicable either by simple phenomena or by their combination in a Spencean fashion. Certainly, many key questions remain unanswered about temporal generalization gradients, both as *explanandum* and *explanans*. We summarize four of them below because we believe that to advance our understanding of timing and build more powerful quantitative causal models and theories we will have to answer them satisfactorily. Moreover, to show their broad pertinence to our understanding of timing, we examine the questions according to the LeT and SET models. Our exam will also show the heuristic value of the synthetic approach proposed here.

#### ***4.1. The shape of generalization gradients outside the trained range***

What is the shape of temporal generalization gradients outside the range of trained durations? A response reinforced at T-seconds since a time marker, but extinguished before T, will increase in strength as time elapses from 0 to T, but how strong will it be significantly after T? Models such as LeT and SET assume that the effect of reinforcement at T-seconds is represented in associative links or in memory stores by a Gaussian density function with mean equal or close to T, which would seem to entail a bell-shaped response gradient centered at T. However, as we mentioned before, if reinforcement is omitted the response persists unabated for an interval much longer than T, which means that the Gaussian representation alone cannot explain the gradient.

At this juncture, the two models diverge. According to LeT, the response remains strong because the links from the states that become active only after T retained their initial, above threshold strength. But the account remains unsatisfactory not only because we lack direct evidence about the processes it assumes, but also because it does not specify any boundary conditions such as how long the response persists after T because of reinforcement at T.

According to SET, the response remains strong because the animal learned to start responding sometime between 0 and T, when the representation of elapsed time is sufficiently close to a sample extracted from the memory of reinforced times, but it did not learn to stop responding. A categorical decision rule carries the explanatory load. But the account also

remains unsatisfactory because SET has not explicated how such learning happens, or which circumstances determine when the start and stop rules are activated.

The shape of the gradient outside the trained range remains unclear also in retrospective tasks such as the temporal bisection procedure. As mentioned before, the empirical evidence is scarce and hard to interpret, but clearly responding outside the trained range is not random. In some cases, proportion ‘long’ returned to indifference, a result consistent with non-categorical decision rules similar to LeT, but in other cases proportion ‘long’ remained high for samples longer than the long trained sample, and low for samples shorter than the short trained sample, a result consistent with categorical decision rules similar to SET (see Carvalho et al., in press, for the pros and cons of categorical and non-categorical decision rules).

#### ***4.2. The ‘because’ of temporal generalization gradients***

What factors determine temporal generalization gradients? Do they remain the same throughout their range? Consider a bisection task with 1-s and 10-s training samples. We do not know whether the choice gradients for test samples shorter than 1 s and longer than 10 s are determined by the same factors. One such factor may be the intertrial interval that typically precedes all samples: If research shows that it influences choice following the shortest samples but not the very long test samples (see Pinto & Machado, 2011, 2015), we need to conclude that different factors affect different ranges of the generalization gradient and then proceed to define the boundary conditions of each factor.

Current timing models also may be overlooking some of the fundamental causal processes of temporal generalization, namely, inhibitory processes and their behavioral expression in terms of inhibitory temporal generalization gradients. Although such gradients remain speculative, some empirical findings seem to require them. Consider a situation in which the experimenter combines two peak procedures, each signaled by different cues,  $S_1$  and  $S_2$ , a tone and a light for example. In one peak procedure, the FI is T-seconds long; in the other, the FI is 2T-seconds long. Hence, the animal experiences four types of trials, two FI’s and two empty trials, in random order. After sufficient training, test trials with the compound cue  $S_1 + S_2$  (light + tone) are introduced under empty trial conditions. The outcome is that rats exhibit a response rate gradient that peaks between the two reinforced moments, T and 2T (other ratios have been used; Swanton, Gooch, & Matell, 2009; Swanton & Matell, 2011).

Although many effects obtained in these studies remain hard to interpret (e.g., the effects of reinforcement probability or signal modality), their authors have argued that the gradient on compound trials is due to some sort of averaging of the temporal memories formed during training (Matell & Henning, 2013; Matell & Kurti, 2014; Swanton et al., 2009; Swanton & Matell, 2011). From what we exposed earlier, the reader will not be surprised if we suggest an alternative, synthetic account grounded on three assumptions. First, during training, the states become coupled with the operant response by two sets of links, one controlled by  $S_1$  and changed during the  $S_1$  trials, and the other controlled by  $S_2$  and changed during the  $S_2$  trials. Second, the negative covariation between the activation of some states and reinforcement drives the link strengths,  $W(n)$ , to negative values, instead of zero. Third, on compound-cue trials, responding while state  $n$  is active depends on whether the sum of its two links, perhaps differentially weighted, exceeds a threshold. Our Spencean hypothesis is that the gradient on compound trials may result from the sum of the two gradients engendered by the distinctly cued, and separately trained, peak procedures, the gradient centered at  $T$  and the gradient centered at  $2T$ . Although the hypothesis remains to be elaborated mathematically, it makes a straightforward prediction: If the two reinforced moments are far apart, for example,  $T_1 = 30$  s and  $T_2 = 240$  s, and the empty trials eliminate response rate on the right wing of the gradients, then, on compound trials, no peak should occur in the interval from, say, 75 s to 150 s. A Gaussian-like gradient, with a clear peak within that interval, would refute the hypothesis.

The foregoing hypothesis tests inhibitory processes indirectly, by means of a peak of responding at a moment  $t$  clearly outside the generalization basins of reinforcement at  $T$  and  $2T$ , and on compound trials of a complex peak procedure. It would be desirable to test for inhibition also more directly – as Honig, Boneau, Berstein, and Pennypacker (1963) did for the dimension of line-tilt, for example –, and across different concurrent and retrospective procedures.

#### ***4.3. Generalization gradients and the structure of temporal memory***

The two preceding issues highlight the need for systematic studies of an analytical sort to better understand the primitives of the synthetic approach, the shape of the generalization gradients within and without the trained range and their causal factors and processes. A different set of issues comes to the forefront when we attempt to use these primitives to synthesize more complex temporal performances. One of them is the structure of

temporal memory, whether it is distributed across the links, as LeT assumes, or concentrated in distinct stores, as SET assumes.

The issue will impose itself whenever a single response is reinforced at two or more different moments since a time marker and no stimulus signals the trial duration. As mentioned above, this situation occurs in a mixed FI 10s-FI 120s schedule with a single response key illuminated with the same white light on both the short and long trials. Results show that on the majority of the long trials a pigeon will peck the key at a high rate during two periods, a period bracketing 10 s, and a period starting before 120 s and ending with food; the average rate gradient is bimodal.

To explain this result we may assume, following LeT, that temporal memory is distributed throughout the associative links,  $W(n)$ , and that each link exerts its effect only when its corresponding state becomes active. The two response periods observed on each trial as well as the bimodality of the average gradient stem directly from the distributed profile of link strengths. But we may also assume, following SET, that the animal forms two memory stores, one containing the subjective times at the end of the 10-s trials, and the other containing the subjective times at the end of the 120-s trials. This assumption of two concentrated memories would be represented by two Gaussian density functions, one for the 10-s FI and the other for the 120-s FI. The two response periods could be explained by assuming that the animal samples the two densities in the order “10-s” density first, “120-s” density second. The problem is that, as mentioned above, the reasoning is circular because it assumes the very discrimination it was intended to explain; it merges *explanans* with *explanandum*. First, to form the two stores, each with its own Gaussian density, the animal already needs to discriminate the two sets of reinforced times, for otherwise it would be unable to save in the correct store the subjective time reinforced at the end of each trial. And second, to access the stores in the right order also presupposes the discrimination of their contents. In other words, the circularity occurs twice, to form the temporal memories and thereby bootstrap the timing process, and to access the temporal memories and thereby generate the bimodal gradients (see also Machado & Silva, 2007a, 2007b; also Gallistel, 2007).

In addition to concurrent timing tasks, the problem of temporal memories occurs also in retrospective timing tasks. Singer, Klein, and Zentall (2006, Experiment 2) showed that pigeons can learn to map three samples onto two comparisons: ‘2s→green, 8s→red, 32s→green’. To explain successful learning in this many-to-one bisection task, LeT would

proceed in the same way as for any other bisection task. Because the associative links are distributed, the mapping of 2-s and 32-s samples onto the same ‘green’ comparison poses no problem. In contrast, models that posit concentrated memories, each indexed by a different comparison stimulus, have no principled way to explain how the ‘green’ key indexes the correct memory, the “2-s” store on the shortest, 2-s trials, and the “32-s” store on the longest, 32-s trials.

The same problem is illustrated in Figure 37 by the data from the Absolute group (bottom panels). Across the ABA'B' phases of Carvalho et al.'s (in press) study, this group was exposed alternately to the bisection tasks '2s→red, 6s→green' (A and A') and '18s→red, 6s→green' (B and B')<sup>10</sup>. The sample mapped to 'green' always equaled 6 s, but the sample mapped to 'red' was shorter than 6 s in one phase, and longer than 6 s in the subsequent phase. Hence, across phases, the pigeons effectively learned to map three samples onto two comparisons. Moreover, the association learned in one phase (e.g., '18s→red' in Phase B) was retained to a large degree while the pigeons learned another association ('2s→red' in Phase A').

To see this result more clearly and appreciate its implications, Figure 37 shows a particularly striking case, the gradients produced by a single pigeon from the Absolute group and the curves fit by the LeT model. Consider the proportion of choices of the 'green' comparison following the 18-s sample. In Phase A (left panel, filled circles), after learning the mapping '2s→red, 6s→green', the pigeon chose 'green' on most 18-s trials. This result is consistent with SET's account for the bisection task (two memories stores, one for each sample durations, plus a categorical decision rule), but, as the solid line shows, it is inconsistent with LeT. In Phase B (left panel, empty circles), after learning the mapping '18s→red, 6s→green', the pigeon rarely chose 'green' on the 18-s trials, a result in line with the contingencies of reinforcement and consistent with both models. The critical issue is how the pigeon responds to the 18-s sample after relearning the mapping '2s→red, 6s→green' in Phase A'. According to SET's account for the bisection task, the pigeon should choose 'green' *on most trials* as it did in Phase A. According to LeT, the pigeon should choose 'green' on significantly *fewer trials* because the association '18s→red' learned in phase B should not be strongly affected during Phase A'. In fact, the only way to reduce the

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<sup>10</sup> Actually, the study included two Absolute groups (Upshift and Downshift) that differed in the order of the discriminations learned across phases. Because their average generalization gradients did not differ appreciably, we combined them and treat them as if they represented only one group. See Carvalho et al. (in press) for details.

‘18s→red’ association during Phase A’ is through generalization from the 6-s sample (associated with ‘green’); to the extent that reinforcement of ‘green’ following the 6-s sample does not generalize significantly to the 18-s sample, the ‘18s→red’ memory will be preserved. As the dotted line in the right panel shows, the data were more consistent with the LeT model.

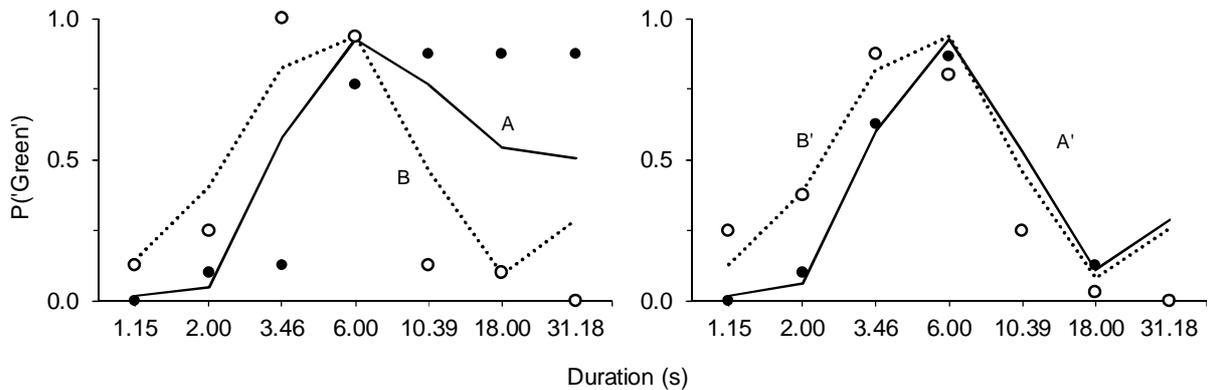


Figure 37. Generalization gradients produced by pigeon P751 (symbols) in Carvalho et al.’s (in press) study and the curves fitted by the LeT model. The pigeon learned the following bisection tasks (in each phase of the ABA’B’ design): ‘2s→red, 6s→green’ (A and A’), and ‘18s→red, 6s→green’ (B and B’).

The data from the 2-s sample revealed the same effect – having learned to associate 2 s with ‘red’ during Phase A (cf. left panel, filled circle at 2 s), the pigeon continued to choose ‘red’ during Phase B (left panel, empty circle at 2 s), whereas a SET-like account would predict that the mapping ‘6s→green, 18s→red’ learned during Phase B would engender a strong preference for ‘green’ at 2 s. Then same effect occurred during Phase B’.

These results challenge the two models, but in different ways. Concerning SET, the challenge is to explain how pigeons learn a many-to-one mapping in the temporal domain, either during a single task (Singer et al., 2006) or across tasks (Carvalho & Machado, 2012; Carvalho et al., in press), a challenge likely to require different assumptions concerning temporal memory. Concerning LeT, the challenge is to explain not memory formation but the categorical-like responding present during Phase A, a challenge likely to require a different decision rule.

#### 4.4. Temporal memory and sample context

A somewhat related issue deals with temporal memory and context. Consider the bisection task: Are the temporal memories associated with the two trained samples context-independent in the sense that each memory is unaffected by the other memory, or context-

dependent? If the latter, what is the specific form of the context-dependence? SET illustrates context-independence because all its features, including the memory representations of each sample, remain the same regardless of the alternative sample. Hence, without further assumptions, SET cannot explain the context effect observed in the double bisection studies. In contrast, by assuming that the distributed links change with both samples as the animal learns to choose one comparison *and* not to choose the other comparison, LeT naturally predicts the context effect.

The context-dependence of temporal learning and memory is also central to the relational versus absolute issue. Our approach based on LeT and the findings from our laboratory have supported the absolute, null hypothesis, but the picture is blurred by contrasting findings from other laboratories. If some form of relational temporal learning does take place, that is, if a sample is represented in terms of its absolute duration as well as its duration relative to the other sample, then we need to identify the processes underlying this form of relational learning, and integrate them with the processes of absolute temporal learning with generalization gradients. How to carry out this integration remains to be worked out (see also Maia & Machado, 2009).

While the four questions raised above await further research, we reaffirm our main message: The bulk of the evidence in the interval timing field seems to support the hypothesis that complex temporally regulated behavior may be synthesized from simple temporal generalization gradients. When properly operationalized (e.g., LeT), the hypothesis may play a role akin to a null hypothesis in conventional statistical testing. Like any null hypothesis, its ultimate fate is to be rejected by the data and replaced by a better hypothesis. When that happens we will have advanced significantly our understanding of timing.

**CHAPTER V – STUDY 3: CONTEXT EFFECTS IN TEMPORAL  
DIFFERENTIATION: SOME DATA AND A MODEL<sup>11</sup>**

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<sup>11</sup> This chapter is based on the publication

Carvalho, Machado, & Vasconcelos (in press). Context effects in temporal differentiation: Some data and a model. *International Journal of Comparative Psychology*. The Experiment 1 is not reported in the original publication and was added to the present Chapter. The introduction, the method, and the discussion reproduce the original publication.

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## **Abstract**

In two experiments, 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. Experiments 1 and 2 differed only in the position of the ‘start’ and ‘end’ keys. 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 s - 1.5 s] and [1.5 s - 4.5 s], respectively. During Phase 2, colors S2 and L2 signaled the ranges [1.5 s - 4.5 s] and [4.5 s - 13.5 s], respectively. We asked whether the intervals produced in the presence of L1 and S2, stimuli signaling the same range, varied with their temporal context, ‘short’ in Phase 1, ‘long’ in Phase 2. The results showed that a) in both experiments the intervals produced in the presence of the different keylight colors accorded with the main properties of temporal differentiation, including Weber’s law; b) in Experiment 1, the means of the L1 and S2 intervals did not differ, but in Experiment 2 the L1 intervals had slightly higher means than the S2 intervals, a weak contrast effect; c) in Experiment 2, 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 of Experiment 2 but left unanswered how context might change the model parameters.

*Keywords:* temporal differentiation, context effect, Learning-to-Time model, Weber’s law, pigeons



## 1. Introduction

Since the early 1900's, 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 '2s→left, 8s→right' or the relative mapping 'short→left, long→right' (see Carvalho & Machado, 2012, Chapter II here; Carvalho, Machado, & Tonneau, in press, Chapter III here; Church and Deluty, 1977, Hulse & Kline, 1993; Maia & Machado, 2008; Zentall, Weaver, & Clement, 2004; Carvalho, Machado, & Vasconcelos, submitted, Chapter IV here).

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 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; Lejeune & Jasselette, 1986; Lejeune & Richelle, 1982; Platt et al., 1973; Kuch, 1974; Zeiler, 1983; Zeiler et al., 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 (see, 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 ( $\approx 0.1$ ) 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’.

We report here two studies in which 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 studies differed only in the distance between the ‘start’ and ‘end’ keys, for in Experiment 1 they were far apart, whereas in Experiment 2 they were side-by-side. In approximating the response keys from Experiment 1 to Experiment 2 we expected to diminish motion delays that could mask any evidence of contextual timing on the produced intervals.

The color on the two keys signaled the range of produced intervals that would yield food. We created three ranges, a short range [0.5 s to 1.5 s], an intermediate range [1.5 s to 4.5 s], and a long range [4.5 s 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 + short) and a ‘long context’ (intermediate + 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?) 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 – are 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) 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” (Zeiler et al., 1987, p. 192). However, most theories and models of timing, including the Scalar Expectancy Theory (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<sup>12</sup>.

Hence, another goal of ours was to extend the LeT model to temporal differentiation tasks. In the final section of Experiment 2, 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 the present work 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 work, we propose a model of how animals might learn to respond according to temporal specifications.

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<sup>12</sup> 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., in press; Maia & Machado, 2008; Zentall et al., 2004). For a generalization-gradient based account of simple and double bisection tasks, see Carvalho et al., submitted.

## 2. EXPERIMENT 1 – DISTANT RESPONSE KEYS

### 2.1 Method

#### 2.1.1. Subjects

Six pigeons participated in the experiment. They had previous training with a similar production task that served as a pilot experiment 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 am.

#### 2.1.2. 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 center key was not used in the present experiment. The left 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.

#### 2.1.3. Procedure

Throughout the experiment, the pigeons learned to produce interval durations that fell within one of three ranges, 0.5 s to 1.5 s (short), 1.5 s to 4.5 s (intermediate), and 4.5 s 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 left 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. 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 left 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 s to 6 s. After reinforcement, a 10-s 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 the relatively short and long ranges in the ‘short context’ as S1 and L1, respectively, and to the relatively short and long ranges in the ‘long context’ as S2 and L2, respectively, yielding  $S1 < L1 = S2 < L2$ .

The four keylight colors signaled the four ranges as follows (see Table 3). 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. Table 1 summarizes the design.

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 3). 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 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.

Table 3. 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
	Condition 2	Green: 0.5-1.5	Green: 4.5-13.5
	Condition 3	Red: 1.5-4.5 and Green: 0.5-1.5	Red: 1.5-4.5 and Green: 4.5-13.5
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

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 left 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 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 3) there were four additional immediate-reinforcement trials 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.

## 2.2. Results

We focus the analysis on the last three sessions of each phase, when two ranges occurred in the same session. During these sessions, the pigeons 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 38 shows three statistics of these intervals, the means ( $\mu$ ), standard deviations ( $\sigma$ ), and coefficients of variation ( $\gamma = \sigma/\mu$ ). The top panel plots the means against the lower limit of each range. For five pigeons, the mean interval increased linearly with the range (all  $r^2 \geq .92$ ), and the least-squares regression line had a slope close to 1 (average slope = 0.95, range: 0.77 – 1.04). For the five pigeons, the slope did not differ significantly from 1 ( $p$ 's > .05 based on t-test), and the intercepts were greater than 0 (average = 0.66 s; range: 0.43 s – 1.25 s). The values for the slope agree with the results from previous studies, but the intercepts are considerably greater than previously reported. For one pigeon (P948), the mean interval did not increase linearly with the range, mainly because several of the intervals produced for the 0.5-1.5 s range were much greater than 1.5 s (range: 4.70 s – 21.01 s, on 34% of the 172 trials considered). We consider later the effect of intervals inadequate for the ranges on the proportion of reinforcement.

The middle panel in Figure 38 shows that the standard deviations increased linearly with the mean for four of the pigeons ( $r^2 \geq .81$ ), with regression lines with slopes averaging 0.15 (range: 0.11 – 0.20) and intercepts averaging 0.07 s (range: 0.00 s – 0.13 s). The slopes of three pigeons differed significantly from 0 ( $p$ 's < .05; exception for P536). Once more, these values are consistent with the results from other studies. The standard deviations of subjects P665 and P948 clearly deviated from a linear trend because the values observed for the short range were much bigger than we would expect (2.63 s and 3.31 s, respectively). Such a great variability is mainly due to trials in which the subjects stopped responding after the initial peck on the 'start' key and, hence, produced too long intervals when resumed pecking on the 'end' key.

The bottom panel in Figure 38 shows that the coefficients of variation remained constant across the three ranges for four of the pigeons, with regression lines with slopes close to 0 (average = -0.06; range: -0.004 – 0.001; all  $p$ 's > .05), and intercepts averaging 0.20 (range: 0.19 – 0.21). Taken together, the results show that the statistical properties of the

intervals produced accorded with the key properties of temporal differentiation for most of the pigeons.

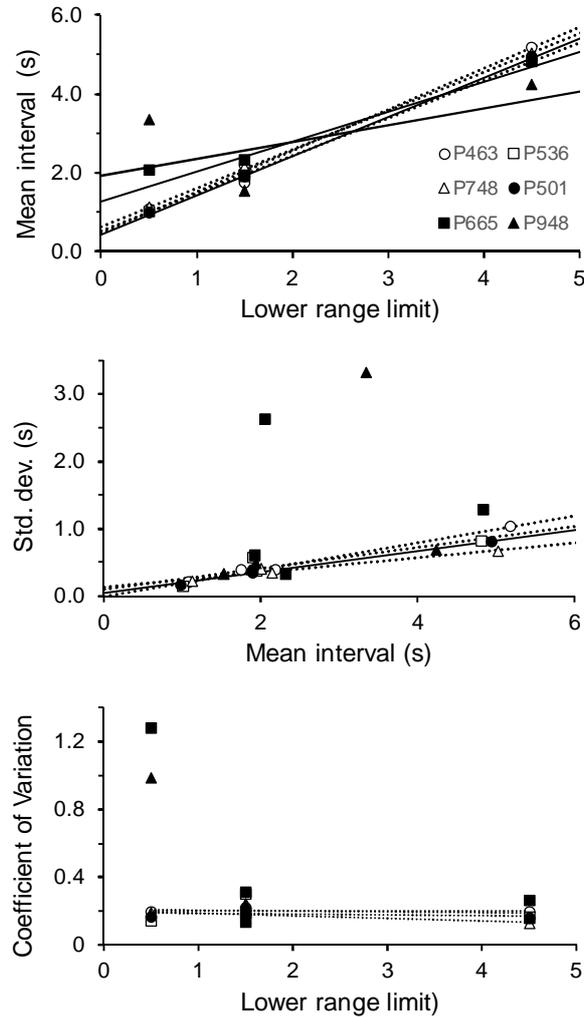


Figure 38. The symbols show the mean of the produced intervals for each range as a function of the lower limit of the range (top), the standard deviation of the produced intervals as a function of the mean (middle), and the coefficient of variation of the produced intervals for each range as a function of the lower limit of the range (bottom). The lines show the best-fitting regression lines.

A visual inspection of the results for the intermediate range in Figure 38 does not suggest any effect of context. To make the evidence clearer, Figure 39 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 range in the ‘short’ and ‘long’ contexts, respectively. Three

distinct patterns are evident: for P501 and P748 the curves almost perfectly superimpose; for P948 the L1 curve is to right of S2; for P463, P536 and P665 the curve for L1 is to the left and have a greater spread than the curve for S2. As would be expected, the between-subjects variability yielded non-significant statistical results. Even though the means for L1 ('short context',  $\bar{x} = 1.90$  s) were slightly smaller than the means for S2 ('long context',  $\bar{x} = 2.00$  s), a paired t-test revealed no significant differences ( $t(5) = .83$ ,  $p = .44$ ). Also, the standard deviations for L1 ('short context',  $\bar{x} = 0.47$  s) tended to be larger than for S2 ('long context',  $\bar{x} = 0.36$  s), but again the difference was not significant (paired t-test,  $t(5) = 2.19$ ,  $p = .08$ ).

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

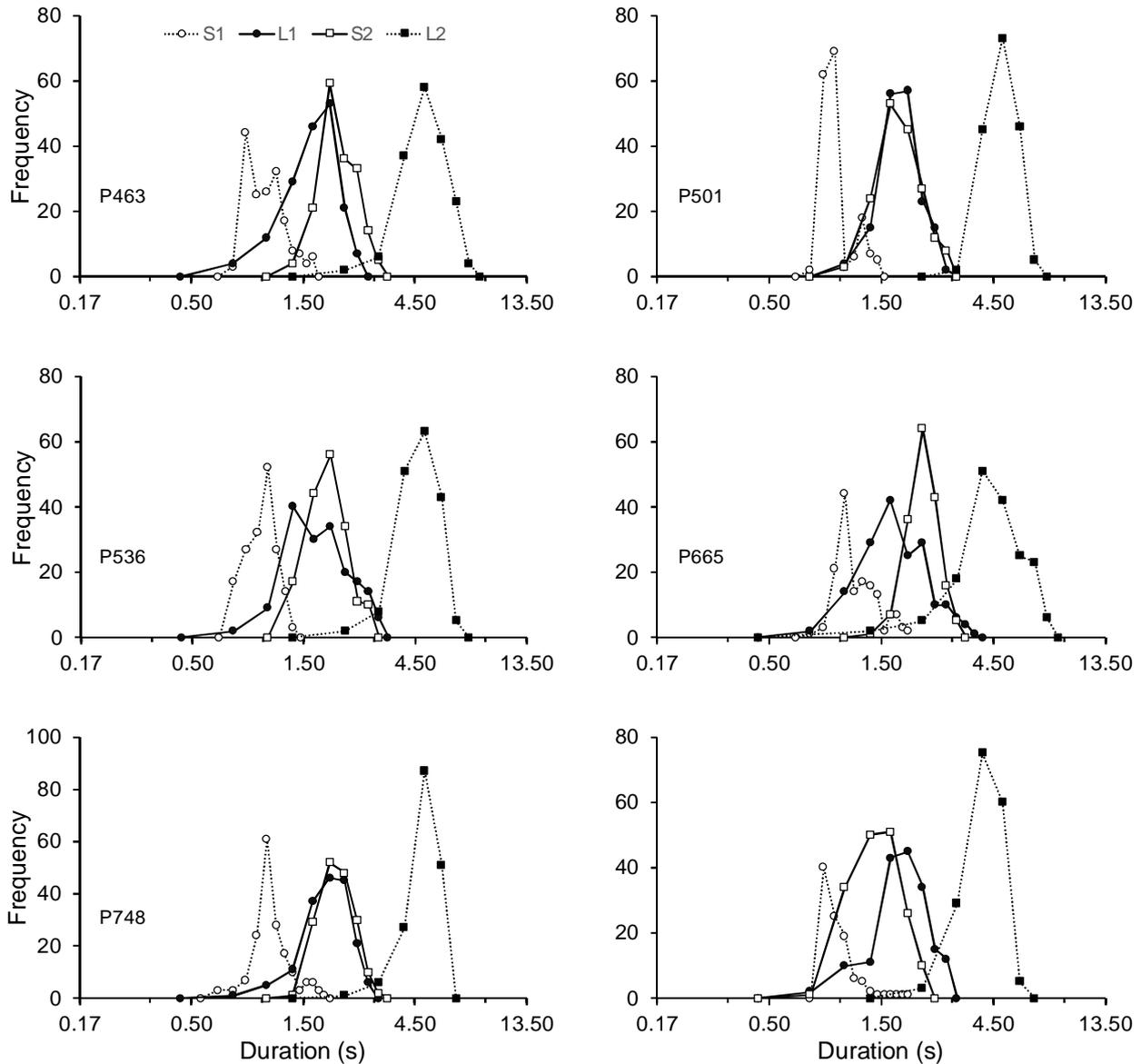


Figure 39. Frequency distributions of the intervals produced in the presence of the four discriminative stimuli. S1 and L1 define the ‘short context’, and S2 and L2 define the ‘long context’. The stimuli signal the following reinforced ranges: S1 = [0.5-1.5], L1 = [1.5-4.5] = S2, and L2 = [4.5-13.5].

Figure 40 shows how the well Gaussian density function fit the data. We divided each set of absolute frequency values displayed in Figure 39 by the total number of trials, 172, to change them into proportions and then divided the proportions by the bin size (.1 for S1, .3 for L1 and S2, or .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.

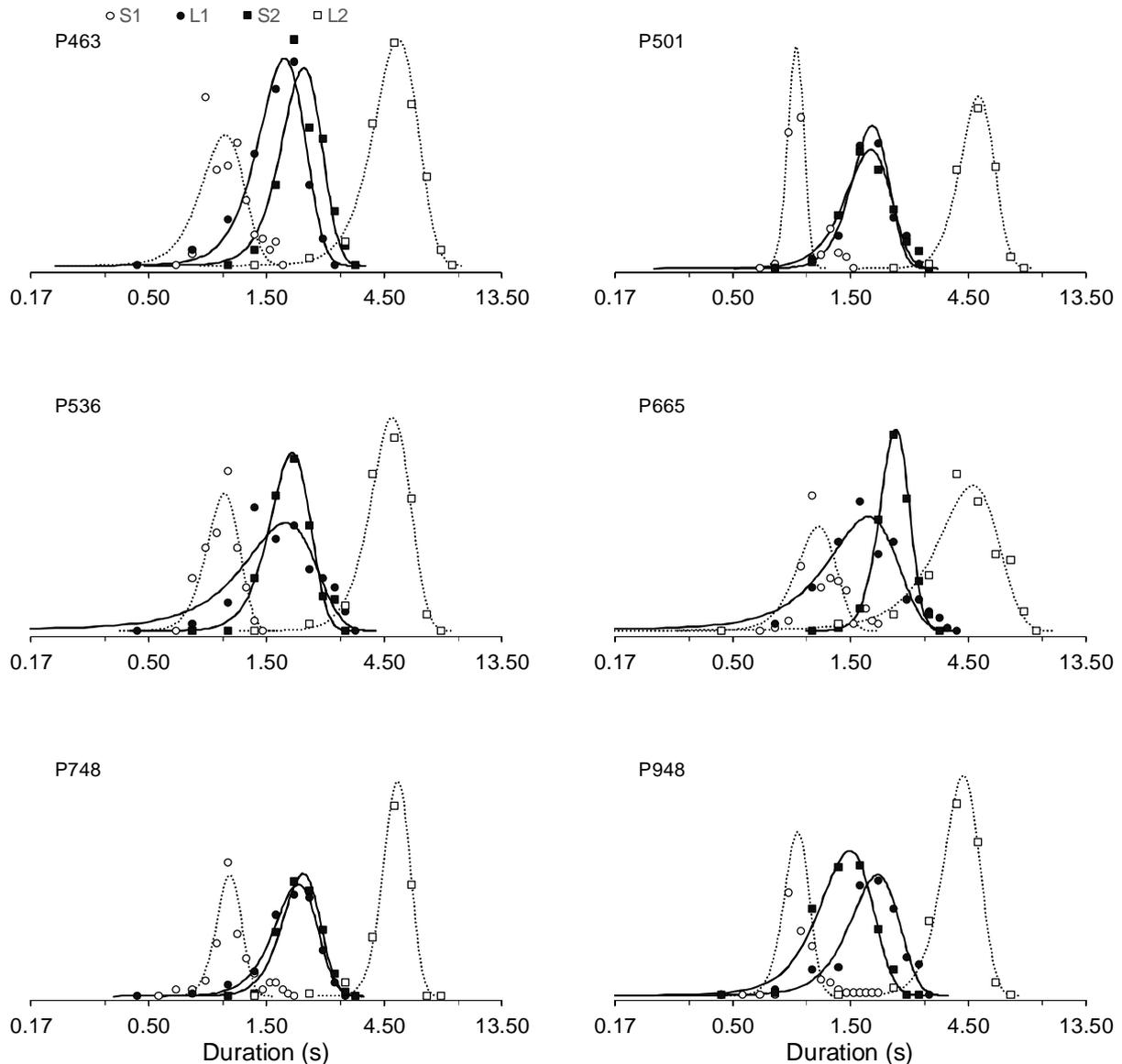


Figure 40. Obtained densities (symbols) and best-fitting Gaussian functions (lines) of the intervals produced in the presence of the four discriminative stimuli. S1 and L1 define the ‘short context’, and S2 and L2 define the ‘long context’. The stimuli signal the following reinforced ranges: S1 = [0.5-1.5], L1 = [1.5-4.5] = S2, and L2 = [4.5-13.5]. Logarithmic x-axis.

The Gaussian curves fit reasonably well the data of the short (average  $\omega^2 = .83$ ) and long ranges (average  $\omega^2 = .98$ ). The quality of the fit in the short range was smaller because the distributions of this range exhibited right tails and/or two modes for most of the subjects (cf. Figure 39). The Gaussian curves also fit well the data of the intermediate ranges in both contexts, with average  $\omega^2 = .94$  for L1 and  $.97$  for S2. The statistical analysis of the best-

fitting means and standard deviations showed that the difference in means (L1: 1.85 s; S2: 1.95 s) was not significant,  $t(5) = .75$ ,  $p = .49$ ; nor was the difference in the standard deviations (L1: 0.45 s; S2: 0.36 s),  $t(5) = 1.58$ ,  $p = .17$ . Hence, the results did not reveal context effects in the temporal differentiation task, for the means of the intermediate distributions did not differ. The context manipulation also did not induce differences in other relevant properties of temporal responding, such as the standard deviations of the produced intervals.

The differently located distributions suggested that the pigeons were efficient in obtaining reinforcers. Figure 41 (left panel) shows the proportion of reinforced trials for each range, and confirms that the subjects collected most of the reinforcers available, even though their efficiency decreased with the range. Obtained reinforcers decreased with the range, from  $\bar{x} = .86$  at S1,  $.81$  at L1,  $.87$  at S2, and  $.64$  at L2. A paired  $t$ -test for the intermediate range was not significant,  $t(5) = .67$ ,  $p = .53$ , 95% CI for the mean difference =  $[-0.31, 0.17]$ . Figure 41 also suggests that the proportion of reinforced trials in the ‘long context’ (S2 + L2,  $\bar{x} = 0.76$ ) was smaller than in the ‘short context’ (S1 + L1,  $\bar{x} = 0.83$ ), but a paired  $t$ -test for the difference was not significant,  $t(5) = 1.62$ ,  $p = .17$ , 95% CI =  $[-0.05 - 0.20]$ .

The right panel of Figure 41 compares the obtained proportions of reinforced trials with the corresponding values computed from the best-fitting Gaussian curves (.i.e., the area under the curve and between the range limits). The predicted values and the obtained values are roughly close, and most deviations regarded the short range, mainly due to the performance of P948 and P665.

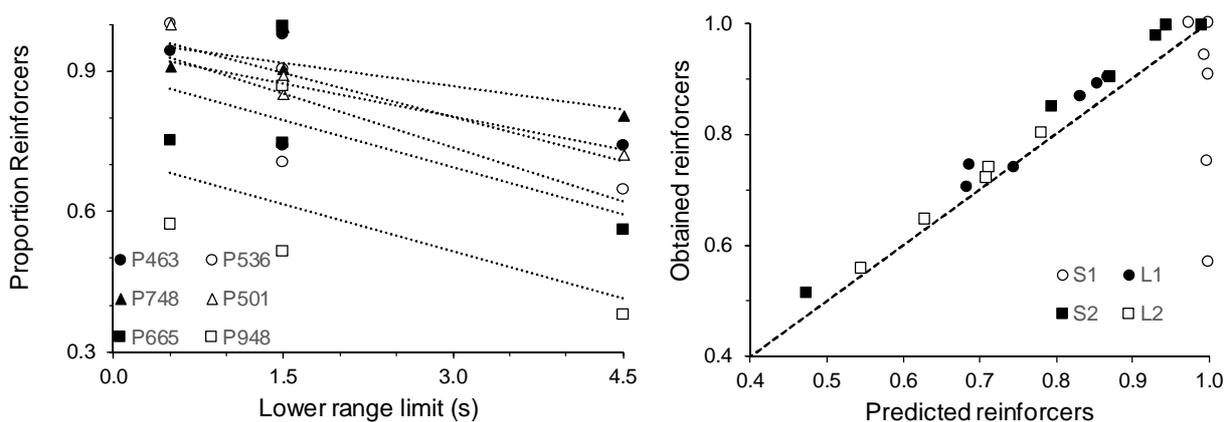


Figure 41. Left: Proportion of obtained reinforcers as a function of the lower limit of each range and best-fitting regression lines. Right: Proportion of obtained reinforcers as a function of the proportion predicted from the Gaussian fits.

### **3. EXPERIMENT 2 – CLOSE RESPONSE KEYS**

We hypothesized that the lack of either assimilation or contrast effects in Experiment 1 could be due not to the absence of contextual timing in pigeons, but to the demanding characteristics of the task: The delay taken to move from the ‘start’ to the ‘end’ key could mask any context effects by increasing the produced intervals. We illustrate the argument with the intermediate range (1.5-4.5 s). An increase in the produced intervals would make them depart from the mean of the ‘short context’, but approach the mean of the ‘long context’. In the former case, the result is consistent with contrast and inconsistent with assimilation, but in the latter case, it is consistent with assimilation and inconsistent with contrast. Under both scenarios, the magnitude of putative context effects would be diminished and, arguably, harder to detect. In order to prevent the interference of motion delays on the produced intervals, in Experiment 2 we made the ‘start’ and ‘end’ keys closer and replicated the procedure used in Experiment 1.

#### **3.1. Method**

##### *3.1.1. Subjects*

The same six pigeons that participated in Experiment 1.

##### *3.1.2. Apparatus*

Idem as Experiment 1. The one exception was that the center key could be illuminated with red, green, yellow and blue hues, and replaced the left key. The left key was not used in the present experiment.

##### *3.1.3. Procedure*

Idem as Experiment 1, with the exception that in Experiment 2, the ‘right’ key was the ‘start key’ and the ‘center’ key was the ‘end’ key.

#### **3.2. Results**

For each range, we filtered the data as in Experiment 1 by removing the largest eight produced intervals (< 5%) and based all analysis on the remaining 172 trials. The top panel of Figure 42 plots the means against the lower limit of each range. For all pigeons, the mean interval increased linearly with the range (all  $r^2 \geq .99$ ), and the least-squares regression line had a slope close to 1 (average slope = 1.1; range: 0.98 – 1.25). For four pigeons, the slope did not differ significantly from 1 ( $p$ 's > .05 based on  $t$ -test); for the other two pigeons, the

slope (1.13 and 1.25) was significantly greater than 1 ( $p$ 's  $< .05$ ). The intercepts were slightly greater than 0 (average = 0.33 s; range: 0.02 s – 0.76 s). These values agree with the results from previous studies.

The middle panel in Figure 42 shows that the standard deviations increased linearly with the mean ( $r^2 \geq .90$ ). The regression lines had slopes ranging from 0.15 to 0.26 (average = 0.21) and intercepts ranging from -0.02 s to 0.17 s (average = 0.09 s). All slopes differed significantly from 0 ( $p$ 's  $< .05$ ). Again, these values are consistent with the results from other studies.

The bottom panel in Figure 42 shows that the coefficients of variation remained roughly constant across the three ranges. The regression lines had slopes close to 0 (average = -0.01; range: -0.025 – 0.007; all  $p$ 's  $> .05$ ). The intercepts ranged from 0.17 to 0.30 and averaged 0.22, both sets of values consistent with previous studies. 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.

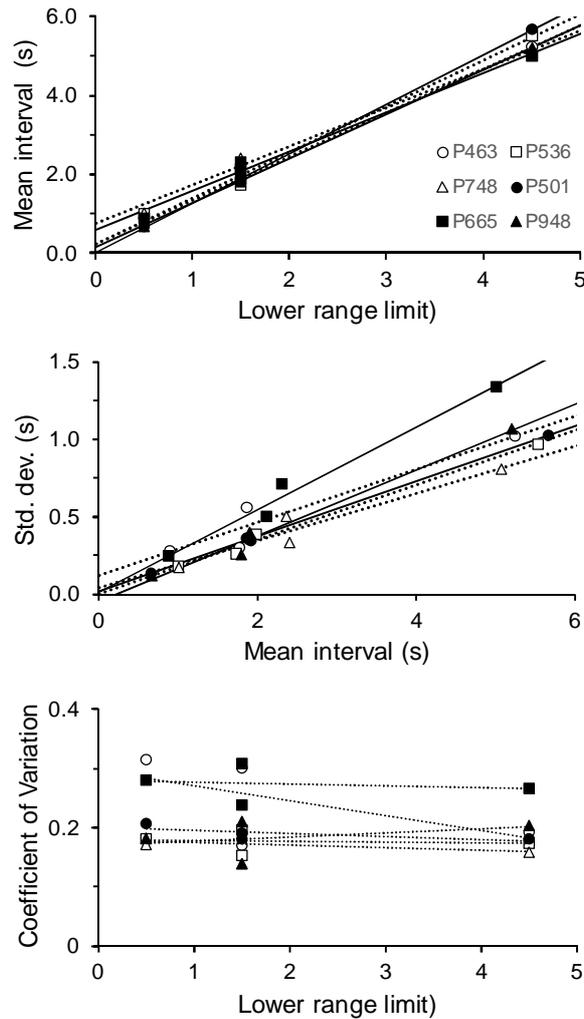


Figure 42. The symbols show the mean of the produced intervals for each range as a function of the lower limit of the range (top), the standard deviation of the produced intervals as a function of the mean (middle), and the coefficient of variation of the produced intervals for each range as a function of the lower limit of the range (bottom). The lines show the best-fitting regression lines.

The statistics for the intermediate range displayed in Figure 42 suggest that any effect of context, if present at all, was small. Figure 43 shows the frequency distributions of the intervals produced in the presence of each discriminative stimulus. 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 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’,  $\bar{x} = 2.06$  s) tended to be slightly greater than the means for S2

(‘long context’,  $\bar{x} = 1.95$  s): paired  $t$ -test  $t(5) = 2.72$ ,  $p = .04$ . Although the effect size was large (Cohen’s  $d = 1.1$ ), its 95% confidence interval [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’,  $\bar{x} = 0.49$  s) tended to be larger than for S2 (‘long context’,  $\bar{x} = 0.34$  s): paired  $t$ -test  $t(5) = 3.99$ ,  $p = .01$ ,  $d = 1.6$ , 95% CI = [0.34, 2.86]. Third, the coefficients of variation for L1 (‘short context’,  $\bar{x} = 0.24$  s) tended to be larger than for S2 (‘long context’,  $\bar{x} = 0.17$  s): paired  $t$ -test  $t(5) = 3.33$ ,  $p < .05$ ,  $d = 1.36$ , 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).

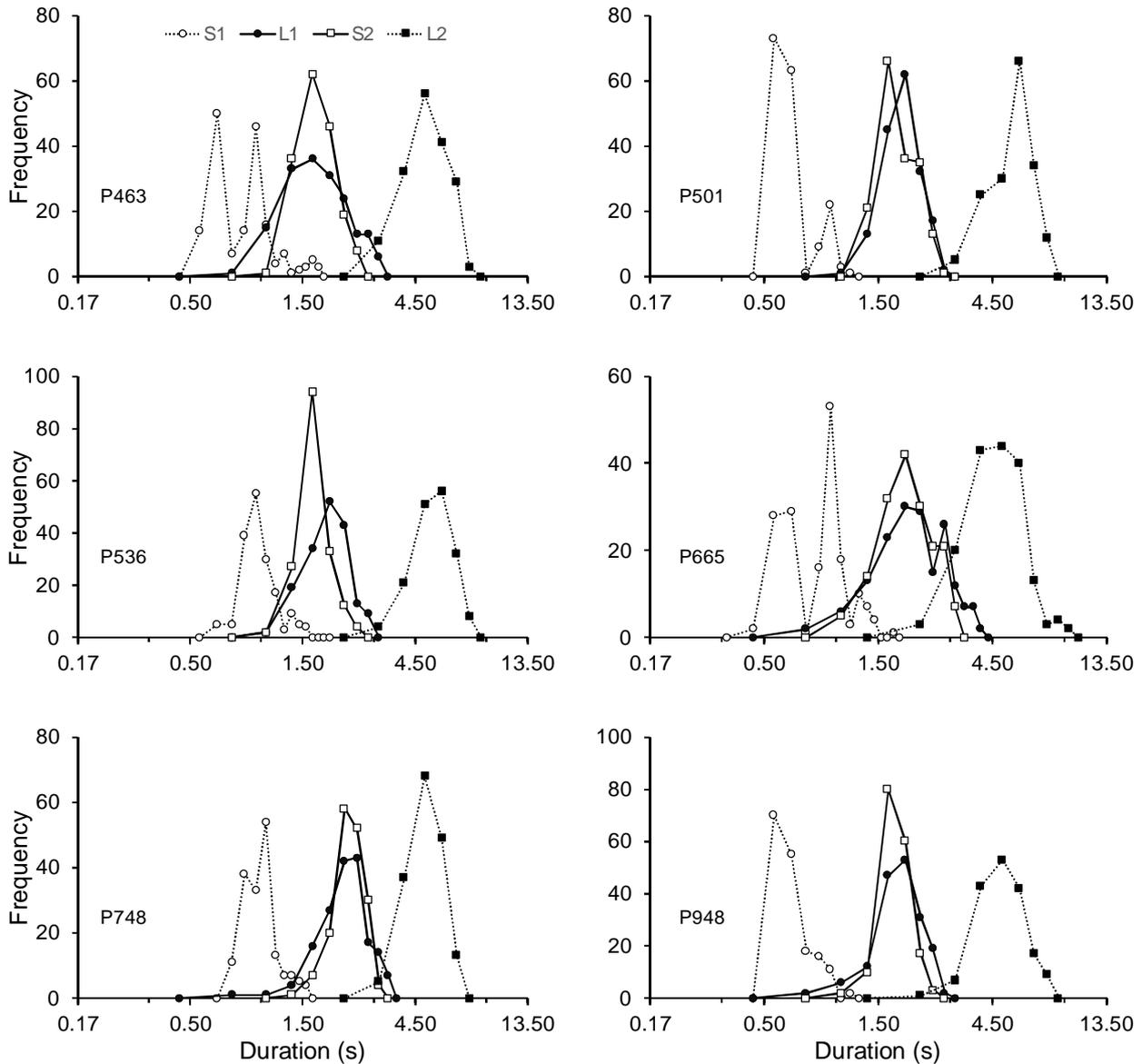


Figure 43. Frequency distributions of the intervals produced in the presence of the four discriminative stimuli. S1 and L1 define the ‘short context’, and S2 and L2 define the ‘long context’. The stimuli signal the following reinforced ranges: S1 = [0.5-1.5], L1 = [1.5-4.5] = S2, and L2 = [4.5-13.5].

Figure 44 shows how well the Gaussian density function fit the data. The curves fit well the data from the two intermediate ranges, with  $\omega^2$  averaging .95 for L1 (‘short context’) and .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 = 2.0 s vs. S2 = 1.9 s) was almost significant,  $t(5) = 2.39$ ,  $p = .06$ , and the difference in standard

deviations (L1 = 0.48 s vs. S2 = 0.32 s) was significant,  $t(5) = 3.8$ ,  $p = .01$ ;  $d = 1.55$ , 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  $\omega^2$  averaging .98. In contrast, they did not fit well all data sets from the short range (average  $\omega^2 = .75$ ). We return to this finding below.

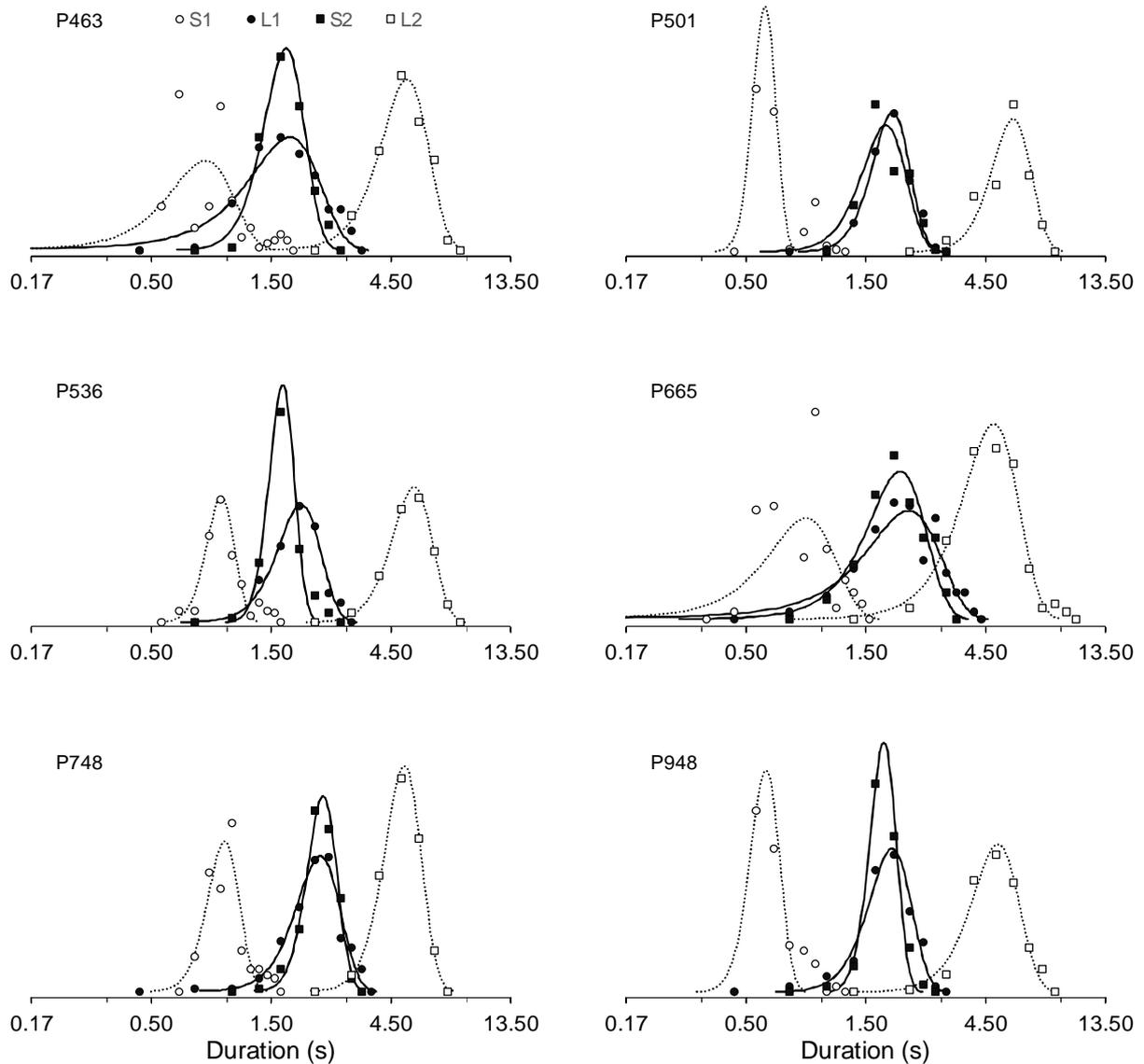


Figure 44. Obtained densities (symbols) and best-fitting Gaussian functions (lines) of the intervals produced in the presence of the four discriminative stimuli. S1 and L1 define the ‘short context’, and S2 and L2 define the ‘long context’. The stimuli signal the following reinforced ranges: S1 = [0.5-1.5], L1 = [1.5-4.5] = S2, and L2 = [4.5-13.5]. Logarithmic x-axis.

The pigeons were relatively efficient at collecting the available reinforcers, but their efficiency varied with the range. Figure 45 (left panel) shows the proportion of reinforced trials for each range. Obtained reinforcers decreased with the range, from  $\bar{x} = .98$  at S1, .87 at L1, .89 at S2, and .75 at L2. A paired t-test for the intermediate ranges was not significant,  $t(5) = .64$ ,  $p = .55$ , 95% CI for the mean difference = [-0.06, 0.04]. However, the overall proportion of reinforced trials in the ‘short context’ (L1 + S1,  $\bar{x} = .93$ ) was greater than in the ‘long context’ (S2 + L2;  $\bar{x} = .82$ ),  $t(5) = 6.36$ ,  $p < .01$ ,  $d = 2.1$ , 95% CI = [0.83, 4.3]. We conclude that the pigeons were more efficient in the ‘short’ than the ‘long context’, not because their efficiency varied between the two intermediate ranges, but because they were more efficient in the short (S1) than the long (L2) range.

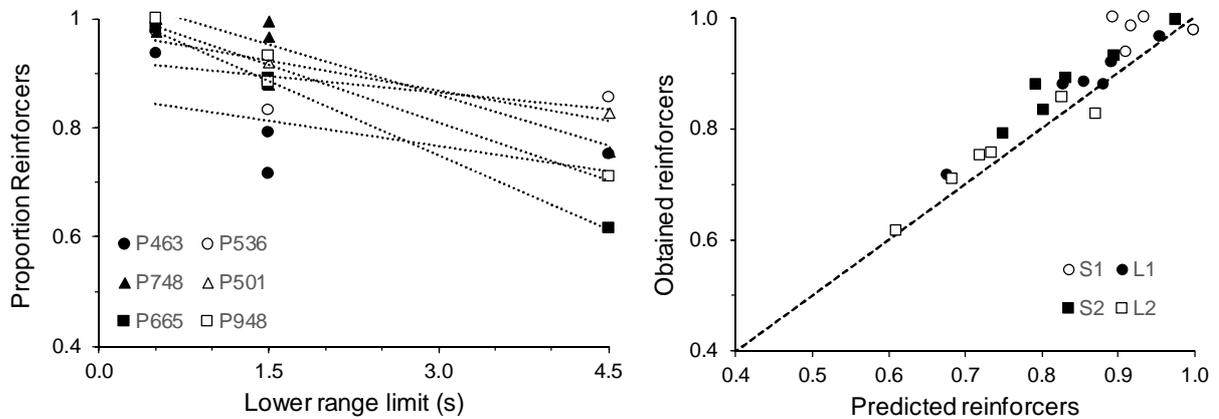


Figure 45. Left: Proportion of obtained reinforcers as a function of the lower limit of each range and best-fitting regression lines. Right: Proportion of obtained reinforcers as a function of the proportion predicted from the Gaussian fits.

The right panel of Figure 45 compares the obtained proportions of reinforced trials with the corresponding values computed from the best-fitting Gaussian functions. Although reasonably close, the predicted values underestimated slightly the obtained values; the pigeons were more efficient than predicted by the Gaussian fits.

#### 4. General discussion

In two experiments, 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 s to 4.5 s. The

other member of each pair signaled a shorter range (S1, from 0.5 s to 1.5 s) or a longer range (L2, from 4.5 s 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 data of Experiment 2.

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., 1998; Lejeune et al., 2000; Lejeune & Jasselette, 1986; Platt, 1979; Zeiler, 1985; Zeiler & Hoyert, 1989). Our studies add to previous findings on temporal differentiation the fact that pigeons can learn two temporal differentiations simultaneously.

In Experiment 1, we had the ‘start’ and ‘end’ keys far apart, and found that the distribution of the intervals produced in the presence of L1 and S2 did not differ neither in location, nor in spread. We also identified a great variability between pigeons, expressed in three different patterns of distributions. The between subjects variability seemed to support our hypothesis that the motion from the ‘start’ to the ‘end’ key was affecting the produced intervals: If different pigeons vary in the way they reach the ‘end’ key (and, as a consequence, in the time taken to), the distribution of the produced intervals would presumably vary considerably between subjects. The between-subjects variability in Experiment 1 yielded no significant effects of the context manipulation on the produced intervals. In Experiment 2, we had the ‘start’ and ‘end’ keys side-by-side, and 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 in Experiment 2 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 the effects observed in Experiment 2? 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’). Additionally, our Experiment 1 seem to corroborate the hypothesis, since the reinforcement proportions in the presence of S1 and L1 combined (‘short context’) and of S2 and L2 combined (‘long context’) did not differ, and in this case we did not find differences in the means and standard deviations of the intermediate distributions. According to some timing models and studies (e.g., Killeen & Fetterman’s (1988) Behavioral Theory of Timing), 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 Experiment 2, 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 in Experiment 2, 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 (2007) observed 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 – run length – corresponds to the produced interval in the present studies. 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 studies, 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, 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 in Experiment 2. We return to this hypothesis below.

In both studies, the Gaussian density function described the shape of the intermediate- and long-range distributions, and of some 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 3). 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 39 and 43 showed, the second mode did not fall inside the L1 distribution. Perhaps different topographies of moving from the ‘start’ to the ‘end’ key, or even of pecking the ‘end’ key, each with a different speed, could underlie the mixture. We suggest yet another hypothesis below, a hypothesis suggested by the LeT model.

#### ***4.1. The Learning-to-Time (LeT) model***

As Figure 46 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 ‘start’ key (the time marker) activates the first state in the series. This state remains active for a random interval,  $\tau$ , at the end of which the animal pecks the ‘end’ 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  $\tau$  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  $\tau$  seconds.

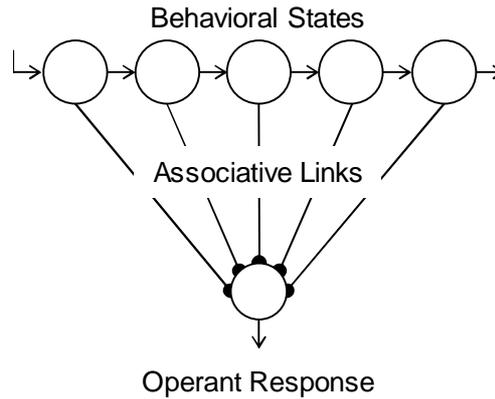


Figure 46. Structure of the Learning-to-Time (LeT) model. The response that initiates the interval activates a set of behavioral states serially. Each state is linked with the operant response that ends the interval, and the strength of the link equals the probability of emitting that response while the corresponding state is active. When a response is emitted, the link from the active state changes with the outcome, reinforcement or extinction.

The model assumes that the residence time in each state,  $\tau$ , is a Gaussian random variable (mean  $\mu_\tau$  and standard deviation  $\sigma_\tau$ ) 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  $\tau$  but its reciprocal, the speed of activation of the behavioral states, usually denoted by  $\lambda$  (Machado et al., 2009). We changed the random variable because initial simulations with  $\lambda$  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 44 or reported in previous temporal differentiation studies (e.g., Mechner & Latranyi, 1963, Figure 15; Nevin & Berryman, 1963, Figure 2). Hence, temporal differentiation and discrimination tasks entail different random variables for the same state dynamics, state residence time and speed of activation, respectively.

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 experiments, 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 47 shows two sets of results, each obtained with a slightly different set of parameters. With  $\mu_\tau = 0.5$  s,  $\sigma_\tau = 0.075$  s,  $\beta = 0.02$ , and  $\alpha = 0.16$  (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 (.95, .91, and .78). With  $\mu_\tau = 0.3$  s,  $\sigma_\tau = 0.03$  s,  $\beta = 0.04$ , and  $\alpha = 0.2$  (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 (.96, .88, and .71).

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.

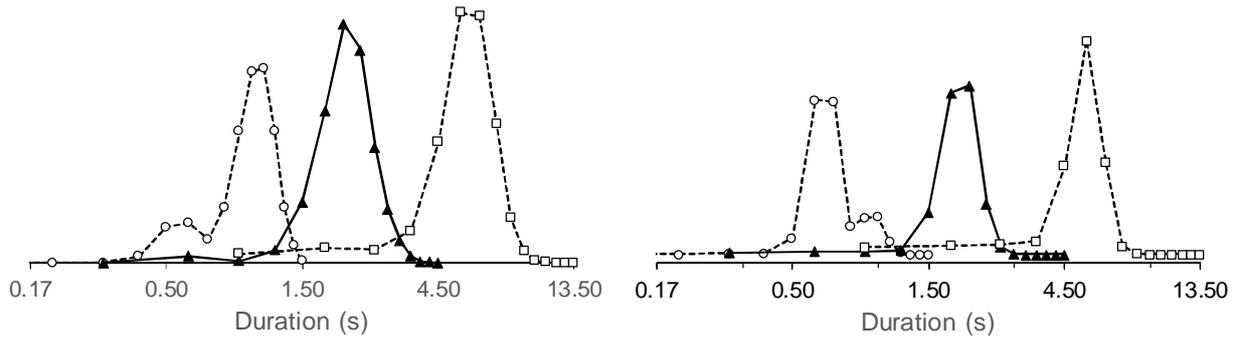


Figure 47. Simulation results of the LeT model. In each panel, the left, middle, and right curves show the density function of the intervals produced when the reinforced ranges were [0.5-1.5], [1.5-4.5], and [4.5-13.5], respectively. Left:  $\mu_\tau = 0.5$  s,  $\sigma_\tau = 0.075$  s,  $\beta = 0.02$ , and  $\alpha = 0.16$ . Right:  $\mu_\tau = 0.3$  s,  $\sigma_\tau = 0.03$  s,  $\beta = 0.04$ , and  $\alpha = 0.2$ .

Two-mode distributions occur when the mean residence time (e.g.,  $\mu_\tau = 0.5$  s or  $\mu_\tau = 0.3$  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  $\mu_\tau$ -s apart; hence the two distinct modes. For the intermediate and longest ranges,  $\mu_\tau$  is significantly lower than the range's 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 in Experiment 2, provided the 'long context' has a higher relative effect of extinction over reinforcement ( $\alpha/\beta$ ) and a lower coefficient of variation of residence times ( $\sigma_\tau/\mu_\tau$ ) 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 in Experiment 2.

Figure 48 illustrates these effects with model fits to two data sets of Experiment 2. 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.

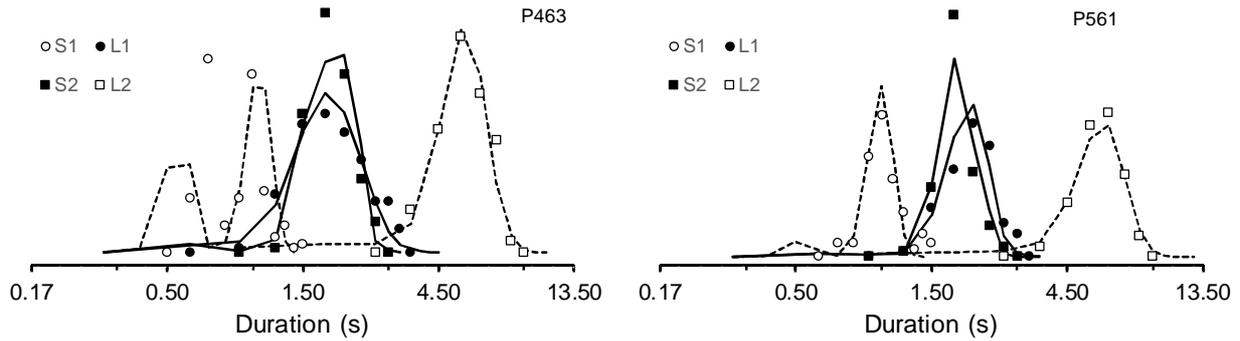


Figure 48. The symbols show the relative frequencies of the produced intervals for two pigeons, and the curves show the simulation results of the LeT model with the following parameter values ( $\mu_\tau$ ,  $\sigma_\tau$ ,  $\alpha$ ,  $\beta$ ): Left, S1 = (0.5, 0.05, .1, .04), L1 = (0.5, 0.1, .1, .08), S2 = (0.5, 0.05, .1, .08), and L2 = (0.5, 0.075, .2, .05). Right: S1 = (0.475, 0.0475, .2, .04), L1 = (0.4, 0.048, .2, .04), S2 = (0.4, 0.032, .053, .04), and L2 = (0.45, 0.0675, .22, .02).

The two panels show that with smaller coefficients of variation (see figure caption for the parameters values) the model produces S2 distributions narrower than L1 distributions. Because the moments a state becomes active varies less with smaller coefficients of variation ( $\sigma_\tau/\mu_\tau$ ), 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’.

On the other hand, the right panel shows that a smaller ratio of  $\alpha/\beta$  produces S2 distributions to the left of L1 distributions. The reason for the effect is that, all else being equal, the ratio  $\alpha/\beta$  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 48 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 experiments show that pigeons can learn to produce two temporal intervals simultaneously, and that these intervals accord with Weber's law. By making the response keys closer from Experiment 1 to Experiment 2, we were able to 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.

**CHAPTER VI – CONCLUSIONS**



## 1. The temporal bisection and the temporal production procedures

### *1.1. Relational bisection task*

Our replications with pigeons of Church and Deluty's (1977) original procedure did not produce results similar to theirs, for we did not find a prevalence of relational-based learning in the bisection task. In both of our studies, Relative and Absolute groups learned the successive discrimination tasks, although with different acquisition patterns. Moreover, performance in the first training session with a new discrimination was generally better in the Absolute than in the Relative groups. The Absolute groups, however, also showed consistent and unexpected tradeoffs in acquisition marked by a decrease in correct responses to one interval as correct responses to the other interval increased. At this moment, we can only speculate that these tradeoffs, which occur also with other stimulus dimensions (Vyazovska, Teng, & Wasserman, 2014), seem to be an extinction effect. We do not know why they occurred mostly in the Absolute groups.

One of our studies (Chapter III) showed that the empirical generalization gradient of one discrimination explained the acquisition in the first session of a new discrimination for both the Relative and the Absolute groups, and, hence, endorsed the absolute hypothesis of stimulus control in the temporal bisection task.

In both studies, LeT predicted the general shape of the acquisition curves of both the Relative and the Absolute groups. In Chapter III, the model also predicted reasonably well the shape of the generalization gradients of both groups. Because LeT derives temporal regulated behavior from absolute stimulus control, the similarity between the model's simulations and the pigeons' data indicate that, regardless of a relative or an absolute mapping, the absolute value of the sample durations controlled choice. We conclude that, in the bisection task, pigeons respond absolutely.

### *1.2. Context effects in temporal differentiation*

Our time production study showed for the first time that pigeons can learn to produce two different intervals in the same session, each signaled by a distinctive cue. Further evidence of the effectiveness of the procedure was that the distributions of the produced intervals had different locations and spreads and accorded with Weber's law.

In the first study in Chapter V, we did not find differences in the distributions of the target duration contingent on the different contexts, and hence did not conclude in favor of contrast or assimilation effects. These results also did not corroborate a previous study by Jazayeri and Shadlen (2010) in which humans showed an assimilation effect on reproduced

durations. In the second study, group data revealed a small contrast effect, but the confidence interval of the effect size was large which suggests caution in asserting the presence of temporal context-effects in pigeons.

We simulated with LeT the performance in the production task. Generally, the model correctly duplicated important features of the produced intervals under the different contexts, such as their distributions, means and spreads. By replacing the speed of activation of the states, as used in temporal discrimination tasks, with the residence time in these same states and making the mean of the residence time close to the lower limit of the required intervals, LeT could also reproduce the bimodal distributions of the short duration required.

Since our studies were the first to investigate the effect of context on timing, replications with other non-human subjects, and probably with different experimental protocols, are needed before concluding for the effect or ruling it out.

## **2. The Spencean approach to timing**

Our Spencean approach to temporal regulated behavior proved successful and fruitful. Successful because, as we showed in Chapters II and III, we were able to predict the acquisition of relative and absolute tasks in the bisection procedure from the generalization gradients. In Chapter IV we also showed that our Spencean-like model, LeT, covered a wide scope of results obtained in a variety of complex timing tasks (such as the mixed FI-FI schedule, the FOPP procedure, and the double bisection task) by simply describing one way in which generalization gradients may interact and combine. The approach was fruitful too because it helped identifying shortcomings of two prominent timing models, LeT and SET and suggested new experimental protocols to further test how generalization gradients modulate timing behavior.

## **3. Implications for the Learning-to-Time model**

From our point of view, one of the strongest features of LeT is its account of generalization gradients. Because the passage of time correlates with states activation, and because the links between the states and the responses change with reinforcement and extinction, the profile of the associative links mirror the temporally controlled generalization

gradients. As described earlier the model dynamics accounted for a variety of typical timing findings, under a panoply of procedures.

Our findings, however, also revealed important shortcomings of the model. In the bisection task, LeT struggled with the acquisition tradeoffs (Chapters II and III) and with the high tails of ogival psychometrical functions (Chapter III). In Chapter V, LeT only reproduced our empirical duration distributions when we changed one of its key parameters, the speed of transition across states by its reciprocal, the residence time in each state. The implications of this change remain to be further investigated.

Another shortcoming of LeT relates to its inability to deal in a principled way with context-effects in the production task. As we described in Chapter V, LeT could only account for a small context effect when key parameter values were allowed to change across contexts. Had we observed more pronounced shifts in the intermediate distributions, LeT would have been unable to explain them. Nonetheless, it does not follow that another generalization-based account could not derive the context-effect. Still, it is not clear whether generalization gradients would suffice as *explanans*. Another unclear issue is whether a temporal contrast effect would be similar to the brightness contrast effect, that is, whether it would constitute a perceptual illusion (Robinson, 1972) in which the same stimulus would induce different percepts.



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