

Animal timing: a synthetic approach

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Abstract Inspired by Spence’s seminal work on transposition, we propose a synthetic approach to understanding 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 article 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

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, such as 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 et al. 1994; Dews 1970; Gallistel 1990; Gibbon 1991; Gibbon et al. 1984; Killeen and Fetterman 1988; Lejeune et al. 2006; Lejeune and Wearden 2006; Machado 1997; Machado et al. 2009; Meck 1983; Meck and Church 1984; Platt 1979; Platt and Davis 1983; Roberts 1981, 1998; Staddon and Higa 1999; Zeiler and 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 article, we advance a synthetic approach to timing. That is, we take as primitives a set of well-known and reasonably consensual findings concerning temporal

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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. Generalization gradients volunteer as reasonable primitives for they are induced by simple and well-studied processes of reinforcement and extinction. By resorting to generalization gradients, it is needless to infer explanatory instances and structures that might differ across theoretical perspectives. In short, generalization gradients do not need to be translated from one theoretical approach to the other—they are *per se*.

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 1997; Machado et al. 2009), 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. 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.

The synthetic approach emerges from recent work from our laboratory wherein we explore generalization gradients as the ingredients from which complex timing performance derives (Carvalho et al. 2016; Vieira de Castro and Machado 2012; Vieira de Castro et al. 2013). Our proposal unifies our previous research and extends it to tasks we have not explored so far. Also, by importing to the time domain a Spencean approach transversal to the study of a variety of other stimulus dimensions, we reestablish a long-lost parallel between temporal stimulus control and other relevant stimulus dimensions (such as size, shape, brightness, and spatial location).

This paper 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 judgements is the temporal generalization task (Church and 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 and 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. The model's mathematical details are nonetheless presented in the ESM Appendix for the interested reader.

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 time judgements. 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 examining 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.

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 1 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 Fig. 1a), 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 Fig. 1b. 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 and Enquist 2003).

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 Fig. 2a). 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 trial begins. Because most reinforced responses occur shortly after T , the pigeon does not experience intervals much longer than T (shaded range).

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 2b 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 vs. scallop), or the running rate (e.g., Dews 1970, 1978; Guilhardi and Church 2004; Lejeune and Wearden 1991; Lowe and Harzem 1977; Lowe et al. 1979; Richelle and Lejeune 1980; Schneider 1969; Wynne and 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. Figure 2c exemplifies the gradient superimposition with the data reported by 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

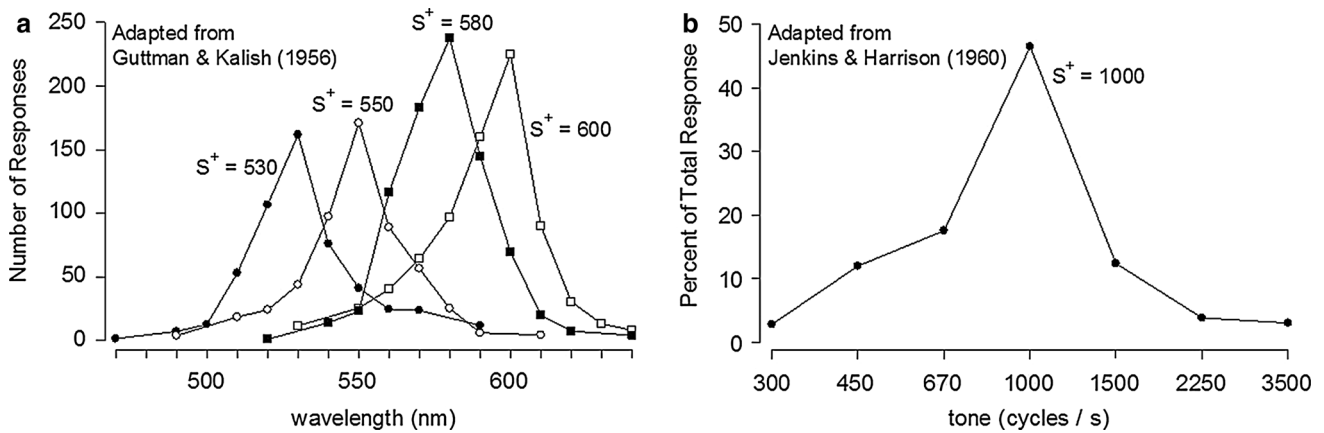
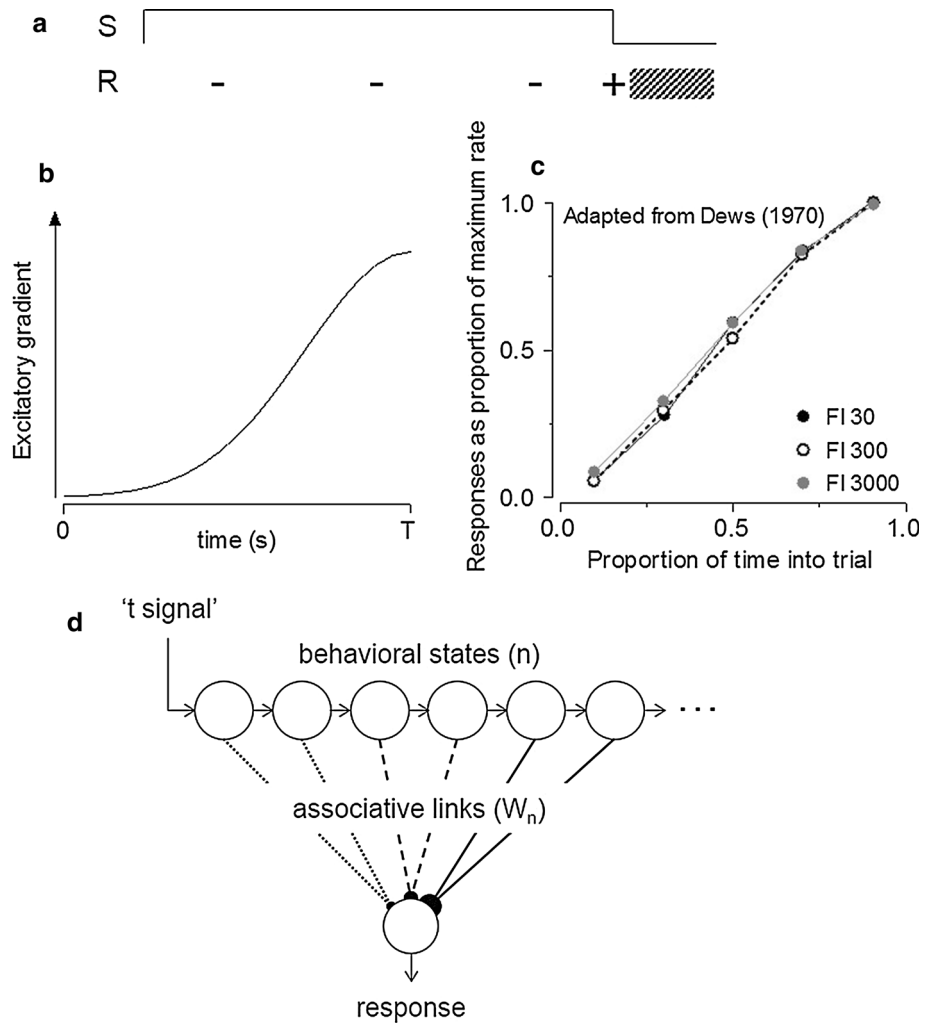


Fig. 1 **a** Wavelength generalization gradients obtained by Guttman and Kalish (1956) with four groups of pigeons. **b** Example of a tone generalization gradient obtained by Jenkins and Harrison (1960) also with pigeons

Fig. 2 **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. **b** Hypothetical excitatory gradient for a FI task. **c** Response-rate generalization gradients obtained by Dews (1970) in three FI schedules. The curves that superimpose when plotted the axis are scaled. **d** 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



animal and human timing, SET (Gibbon 1977, 1991; Gibbon et al. 1984; but see Lejeune and Wearden 2006; Staddon and Cerutti 2003; Zeiler and Powell 1994 for discussions of its violations).

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, Θ . The LeT model formalizes this simple hypothesis.

Figure 2d 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 μ_λ and standard deviation σ_λ extracted at the time marker onset.

While a state is active, the strength of its link determines whether the subject responds: If that strength exceeds a threshold, Θ , 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 $W_0 > \Theta$.

When the reinforcer is delivered, the active state—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.¹ 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).

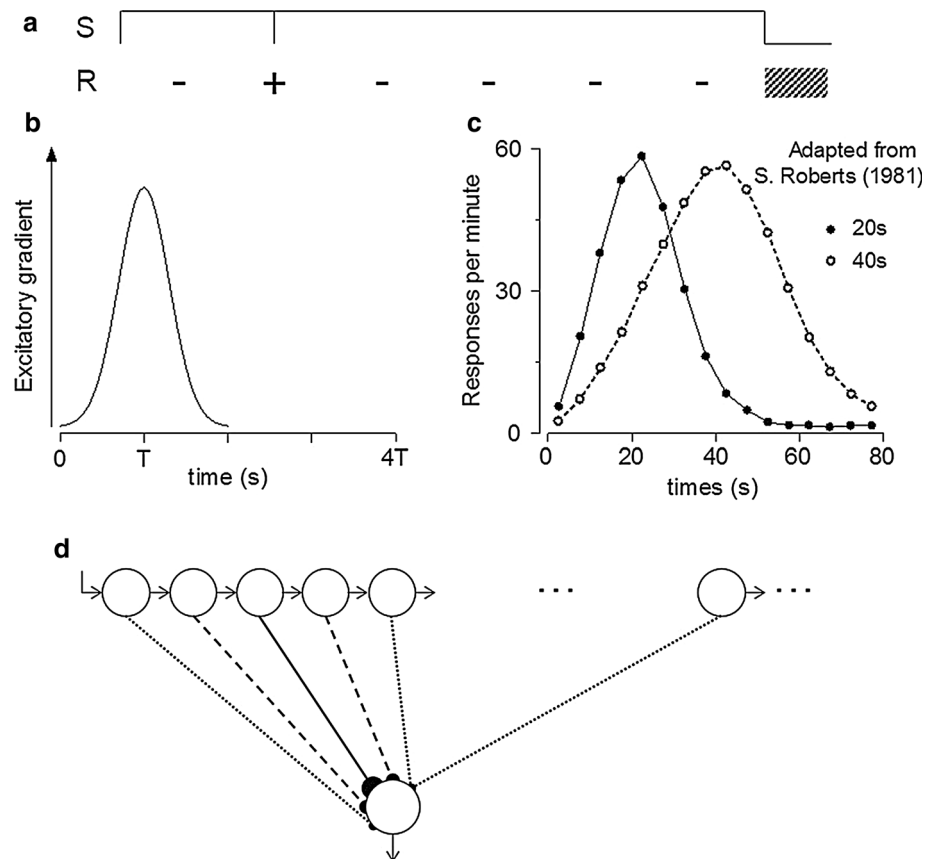
Reinforcement at T may have effects on intervals longer than T . To see them, the experimenter needs to omit the reinforcer and extend the trial. Surprisingly, these effects remain poorly understood. A few studies (Machado and Cevik 1998; Monteiro and Machado 2009) and non-systematic observations (Ferster and 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 and Baramidze 2006; Kirkpatrick-Steger et al. 1996; Machado and Cevik 1998; Monteiro and Machado 2009). For our present purposes, the important point is that the gradient after T seems to differ significantly from the gradient before T .

A high and sustained gradient after T does not follow from the simple excitatory gradient hypothesized above (Fig. 2b), 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 a 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 inter-trial 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 Fig. 3a 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 Fig. 3b for the hypothetical gradient, and Fig. 3c for empirical gradients obtained by Roberts 1981); sometimes response rate increases again as t approaches $4T$ (e.g., Roberts et al. 1989). The curves for different values of T also are scale invariant. At steady

¹ 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.

Fig. 3 **a** A Peak procedure trial and its reinforcement (at T) and extinction (at $t < T$ and $t > T$) contingencies. **b** Hypothetical Gaussian excitatory gradient for the peak task. **c** Response rates obtained by Roberts (1981) with rats in peak trials with FI 20-s and FI 40-s schedules. **d** 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



state, 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 and 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, 1998; Roberts et al. 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 et al. 1994; Kaiser et al. 2002). Recent studies have also shown that the decrease in the generalization gradients past T can occur abruptly (Balci et al. 2009) and develop slowly with higher proportions of empty trials (Kaiser 2008), even though this also entails less frequent FI trials and seems to rely on different neural substrates when compared to increasing limb of the generalization function (MacDonald et al. 2012). 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.

According to LeT (Fig. 3d), 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 Θ , responding stops.² 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 $t = T$ and 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

² A more complete model would assume different thresholds to start and stop responding, Θ_{start} and Θ_{stop} , both random variables possibly with different variances to account for the microstructure of responding on the individual trials of the peak procedure (e.g., the pattern of positive correlations between the start and stop times, and negative correlations between the start times and the duration of the response period—e.g., Cheng et al. 1993; Church et al. 1994; Gallistel et al. 2004; Gibbon and Church 1992; Killeen and Fetterman 1993; Machado and Keen 2003).

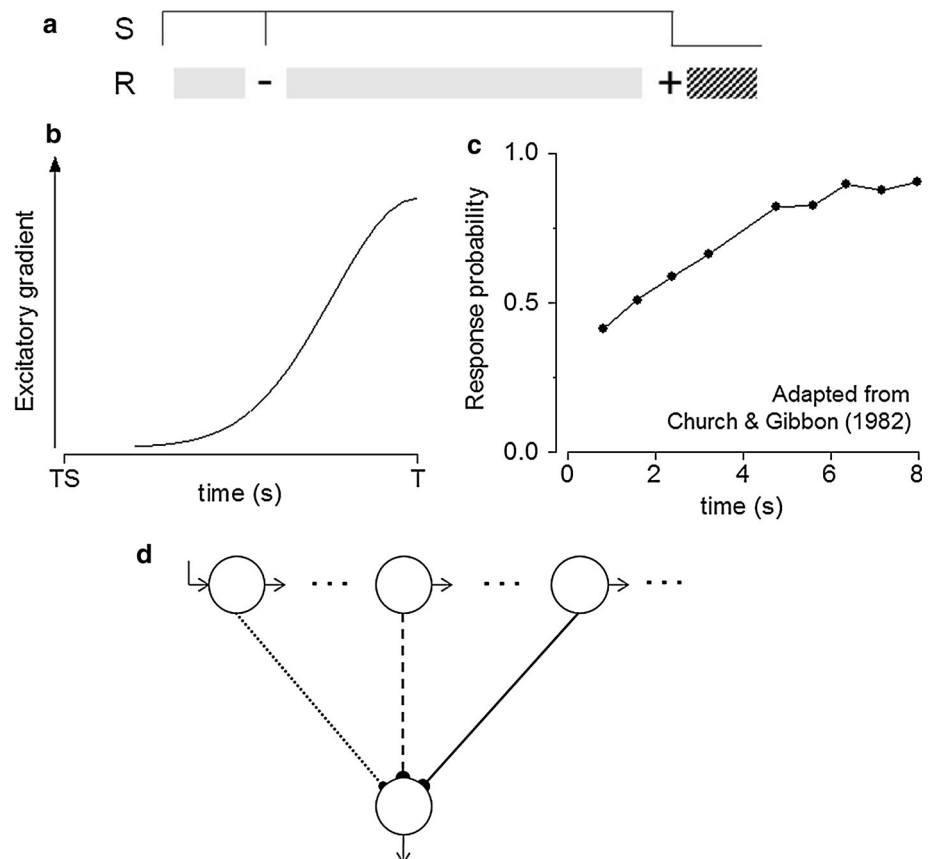
response rate *will* increase if the experimenter extends the empty trials significantly beyond the value used during training, $4T$ in the foregoing example (see Monteiro and Machado 2009). This prediction, which remains to be tested systematically, shows that we need to explore the shape of the temporal 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 .

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 judgement 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., Elmsore 1971; Spetch and 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 time judgement tasks, and the correct analog of the FI schedule, is the temporal generalization procedure. In its simplest form (see Fig. 4a), 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 and Gibbon 1982; Reynolds and Catania 1962). In this conditional discrimination task, the duration of the sample signals whether a response will be reinforced. In the terminology of Switalski et al. (1966), the procedure is an instance of intra-dimensional discrimination training.

Fig. 4 **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 gray areas stand for the periods when responding is not allowed; the shaded area stands for intervals the subjects do not experience. **b** Hypothetical excitatory gradient for a temporal generalization task. **c** Temporal generalization gradient obtained by Church and Gibbon (1982) with 8 s as the $S+$ and shorter durations as the $S-$. **d** Profile of link strengths predicted by LeT



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 $4T$.

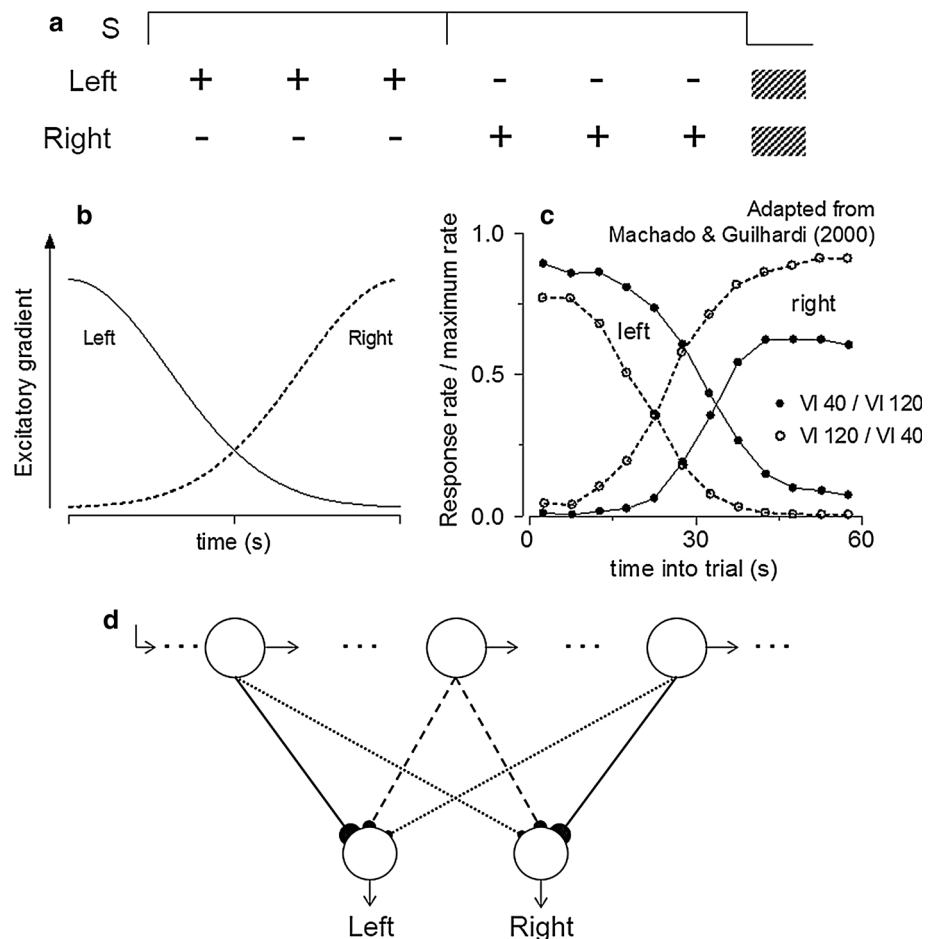
Mixed FI–FI schedules are important in the study of timing because they show how generalization gradients may combine to produce new forms of temporally regulated behavior. Moreover, they also challenge timing models that concentrate the effects of reinforcement in distinct memory stores (e.g., SET). 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).

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 7a 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

Fig. 7 **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. **b** Hypothetical excitatory gradients for Left and Right responses. **c** Response rates on the left and right keys as a function of time elapsed in the trial; data adapted from Machado and Guilhardi (2000) in a task with a VI 40 s on the left key and a VI 120 s on the right key (black circles), and with a VI 120 s on the left and a VI 40 s on the right (empty circles). **d** 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



responses cease to be reinforceable, and responses become reinforceable.

Typically, at the steady state, two response-rate generalization gradients are obtained, one for each operant (Fig. 7b, c shows the hypothetical gradients and the empirical gradients obtained by Machado and Guilhardi 2000, respectively). 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 0.5, 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 and White 1995; Machado and Guilhardi 2000).

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 (Fig. 7d). 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 Fig. 7d). Hence, when the VI's are equal the relative rate on the Right key at time t is ogival and crosses 0.5 close to the middle of the trial. However, when the VI's differ, the reinforcement contingencies bias the links of the 'intermediate' states toward the richer operant and, as a consequence, the two response-rate gradients and the ogival relative gradients shift in the expected direction (Fig. 7c, Machado and Guilhardi 2000; see also Bizo and White 1995; Guilhardi et al. 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 and Guilhardi 2000; Machado et al. 2009).

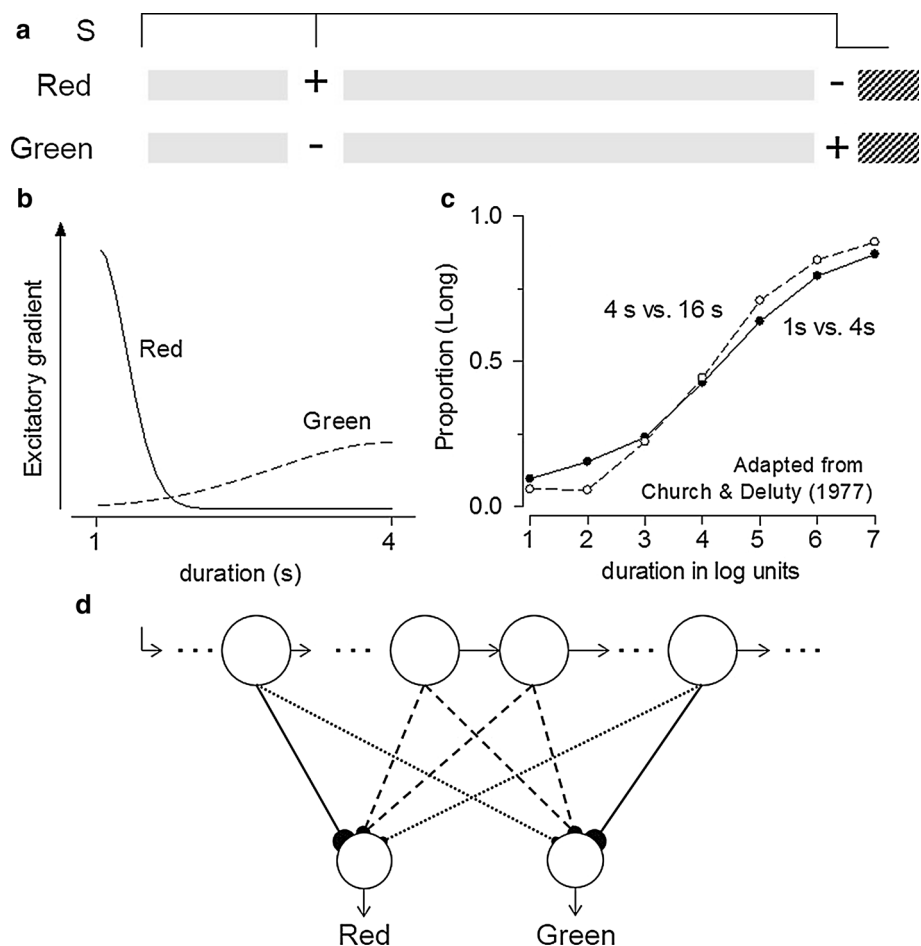
Somewhat analogous to the FOPP is the midsession reversal task, which can be conceived of as a session-wide or single-trial FOPP. Typically, in a simultaneous discrimination procedure, the animal faces two options, S_1 versus S_2 ; responses to S_1 are reinforced in the first half of the session and responses to S_2 are reinforced in the second half (for an extension to a 3-stimuli/2-reversals procedure, see McMillan and 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 perseverate 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 mid-session reversal effect, a flurry of studies ensued (e.g., Laude et al. 2014; McMillan et al. 2014; McMillan and Roberts 2012, 2015; Rayburn-Reeves et al. 2011, 2013; Rayburn-Reeves and Zentall 2013; Stagner et al. 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 and Rosen 2010; McMillan and 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 ITIs, 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.

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 Fig. 8a), 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 that of R_2 following TL are reinforced. After the animal learns the mappings "TS $\rightarrow R_1$,

Fig. 8 **a** A simple bisection trial and its contingencies. Responses on Red and Green keys are reinforced after the short and long samples, respectively. **b** Hypothetical excitatory gradients for Red and Green responses. **c** Temporal generalization gradients obtained by Church and Deluty (1977) with rats in two simple bisection tasks, one with 1-versus 4-s samples, and the other with 4- versus 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. **d** 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



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 $t = TS$ and ending close to 1 at $t = TL$. Moreover, in animals, the duration t^* following which the subject is indifferent between R_1 and R_2 [i.e., $P(R_2|t^*) = P(R_1|t^*) = 0.5$], called the point of subjective equality (PSE) or the bisection point, tends to be at the geometric mean of the trained durations [$GM = \sqrt{(TS \times TL)}$] (Catania 1970; Church and Deluty 1977; Stubbs 1976). It is also the case that the gradients obtained with TS–TL pairs with the same ratio (e.g., $TS_1 = 1$ vs. $TL_1 = 4$, and $TS_2 = 4$ vs. $TL_2 = 16$) superimpose when t is scaled with respect to TS_i , another instance of scale invariance. Figure 8c from Church and Deluty (1977) shows an example.

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 and Deluty 1977), sample modality (e.g., Wearden et al. 1998, 2007), drugs (e.g., Meck 1983; Odum et al. 2002), and neurological conditions (e.g., Brown et al. 2011; Carroll et al. 2008; Caselli et al. 2009; Merchant et al. 2008).

The measured gradient may result from two excitatory gradients (Fig. 8b), 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 and Pata 2005; Vieira de Castro and Machado 2012; Vieira de Castro et al. 2013).

LeT instantiates the preceding hypothesis (Fig. 8d). 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

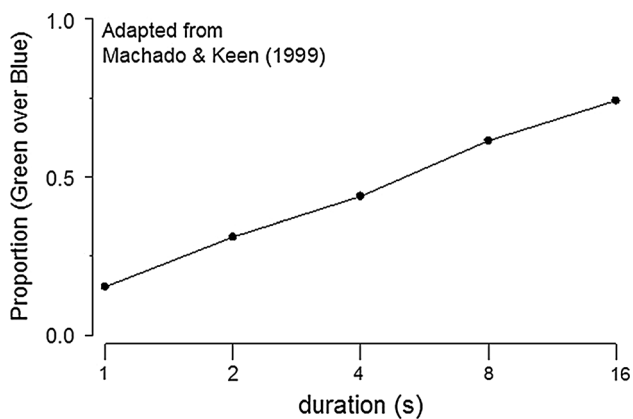


Fig. 10 The context effect obtained by Machado and Keen (1999) after training pigeons in a double bisection task. Given a choice between Green and Blue, the keys associated with 4-s samples but in different sample contexts, preference for Green increases with sample duration

bisection, pecking a Blue key is correct following a 4-s sample, and pecking a Yellow key is correct following a 16-s sample (Fig. 9a, right panel); the subject learns the mapping “4 s → Blue; 16 s → Yellow.” Figure 9b 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 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 and Machado 2008; Machado and Arantes 2006; Machado and Keen 1999; Machado and Oliveira 2009; Machado and Pata 2005; Oliveira and Machado 2008, 2009). Figure 10 shows this finding.

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 samples; Fig. 9c, left panel), whereas the choice of Blue is extinguished when the late states are active (the effect of 16-s samples; Fig. 9c, 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.

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 versus Green test, they obtained two generalization gradients. After the “2 s → Red, 6 s → Green” training, they obtained the gradient for Green over Red with samples ranging from 0.7 to 51.4 s (Fig. 11a). Similarly, after the “6 s → Blue, 18 s → Yellow” training, they obtained the gradient for Blue over Yellow with samples also ranging from 0.7 to 51.4 s (Fig. 11a). Finally, they used these two gradients to predict the gradient of Green over Blue. Although the magnitude of the context effect was smaller than in previous studies, the predicted gradient matched qualitatively the obtained gradient (Fig. 11b).

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- 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 samples, but not after the 1-s samples; 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 to 16 s and measured response rate on Green (see Fig. 11c).

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 Fig. 11c).

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 11d 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; Machado and 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.

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 duration of the samples. In each bisection task, one sample is short and the

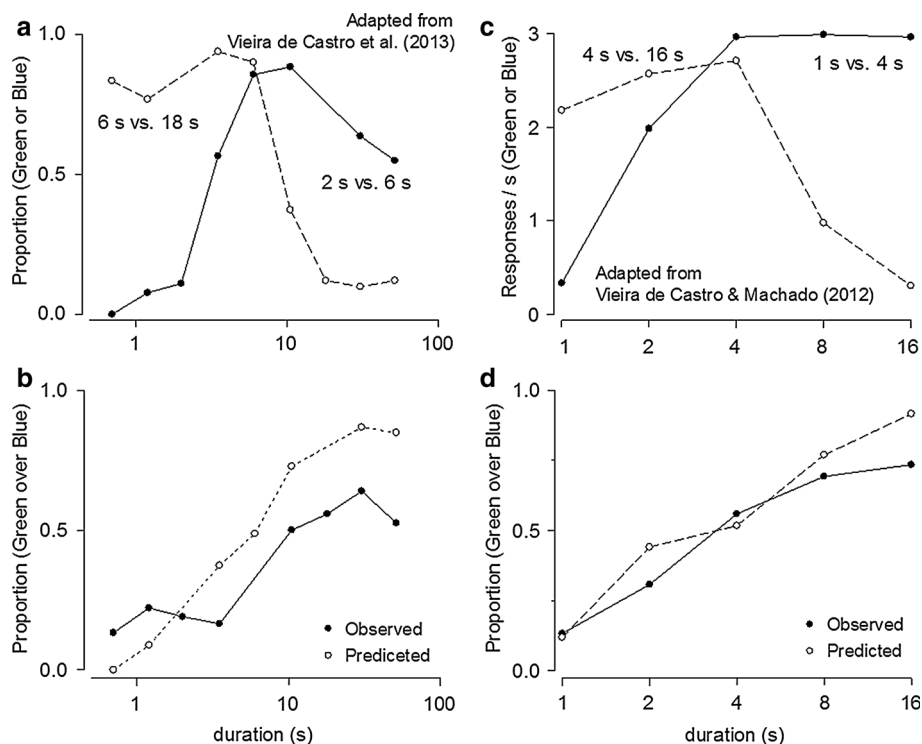


Fig. 11 **a** Generalization gradients obtained by Vieira de Castro et al. (2013) after training pigeons in a double bisection tasks with 2- versus 6-s samples in one task and 6- versus 18-s samples in the other. Green and Blue were reinforced after 6-s samples, but Green was extinguished after 2-s samples and Blue after 18-s samples. **b** Obtained gradient for Green over Blue (the context effect), and the gradient predicted from the two gradients in **a**. **c** Generalization

gradients obtained by Vieira de Castro and Machado (2012) in a double bisection, go/no-go task, with 1- versus 4-s samples in the first task, and 4- versus 16-s samples in the second task. Green and Blue were reinforced after 4-s samples, but Green was extinguished after 1-s samples and Blue after 16-s samples. **d** Obtained gradient for Green over Blue (the context effect), and the gradient predicted from the two gradients in **c**

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 versus 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 and Deluty 1977), starlings (Hulse and Kline 1993), pigeons (Zentall et al.

2004), and humans (Molet and 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 12 shows the first, introduced by Church and Deluty (1977). In Phase A, one group of four rats learned the mapping “1 s → Left, 4 s → Right” (Fig. 12a, left panel). Then, in Phase B, half of the rats, the relative group learned the new mapping “4 s → Left, 16 s → Right,” which preserves the relative assignments “short → Left, long → Right” (Fig. 12a, middle panel). The other half, the absolute group, learned the new mapping “16 s → Left, 4 s → Right,” which preserves the absolute assignment “4 s → Right” (Fig. 12a, right panel). A second group of four rats learned the same discriminations but in the opposite order, initially the “4 s → Left, 16 s → Right” mapping (Phase A), and then, after the group was divided into two, half learned the relational-preserving mapping “1 s → Left, 4 s → Right,” whereas the other half learned the absolute-preserving mapping “4 s → Left, 1 s → Right” (Phase B). The preserved mapping, relative or absolute, and the training order, upshift (from 1 vs. 4 to 4 vs. 16 s) or downshift (from 4 vs.

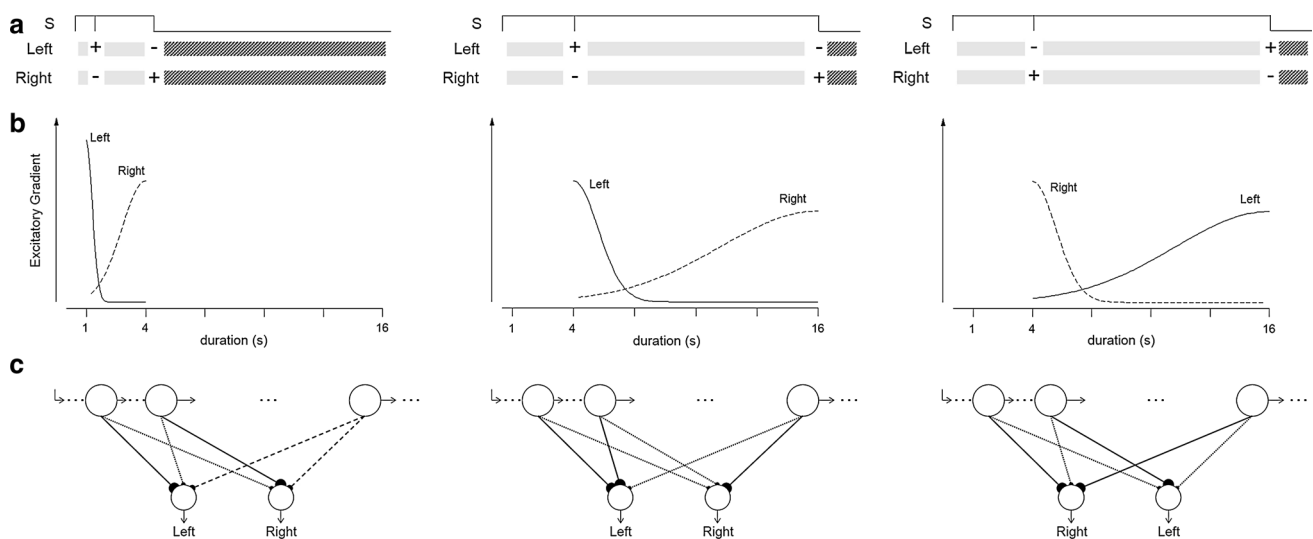


Fig. 12 **a** The two types of bisection trials used in some studies about relational temporal control. In the first bisection task (*left*), Left and Right responses are reinforced after 1- and 4-s samples, respectively. In the second bisection task, for the Relative Group (*middle*) Left and Right responses are reinforced after 4- and 16-s samples, respectively; for the Absolute Group (*right*), Left and Right responses are

reinforced after 16- and 4-s samples, respectively. **b** Hypothetical excitatory gradients for each response in each task. **c** Profile of link strengths predicted by LeT. In the second task, Group Relative reverses the link strengths from the modal state at 4 s (cf. *middle circle* in *middle panel*)

16 to 1 vs. 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.

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 ten sessions (see Fig. 13a, b). The authors did not report performance on the 1- or 16-s samples.

Carvalho and Machado (2012) 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- and 16-s samples, and (d) comparing the data with the predictions of the LeT model. Figure 14 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 (Fig. 14a); similar results were obtained in Phase A'

(Fig. 14b). 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- and 16-s samples (Fig. 14c–f).

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” (Fig. 12c). After the “1 s → Left, 4 s → 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 (Fig. 12c, left panel). Consider the relative group with the new mapping “4 s → Left, 16 s → 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 (Fig. 12c, 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 “4 s → Right, 16 s → 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

Fig. 13 Acquisition curves for Groups Relative (*full circles*) and Absolute (*empty circles*) in the second bisection task. **a** Results obtained by Church and Deluty (1977) with rats. **b** Results obtained by Hulse and Kline (1993) with starlings

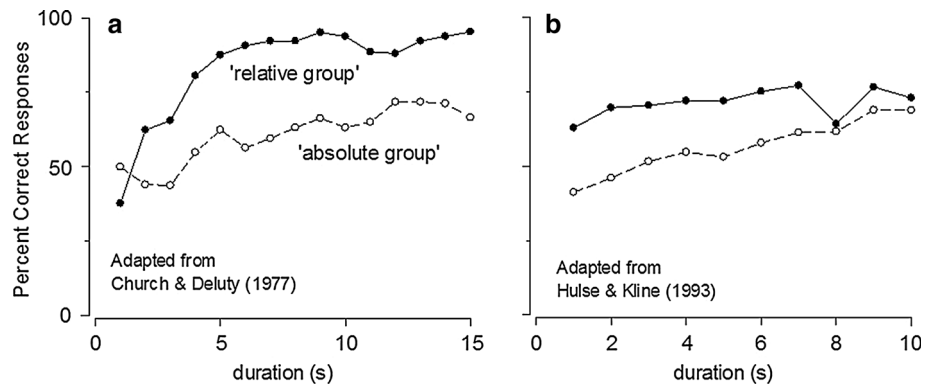
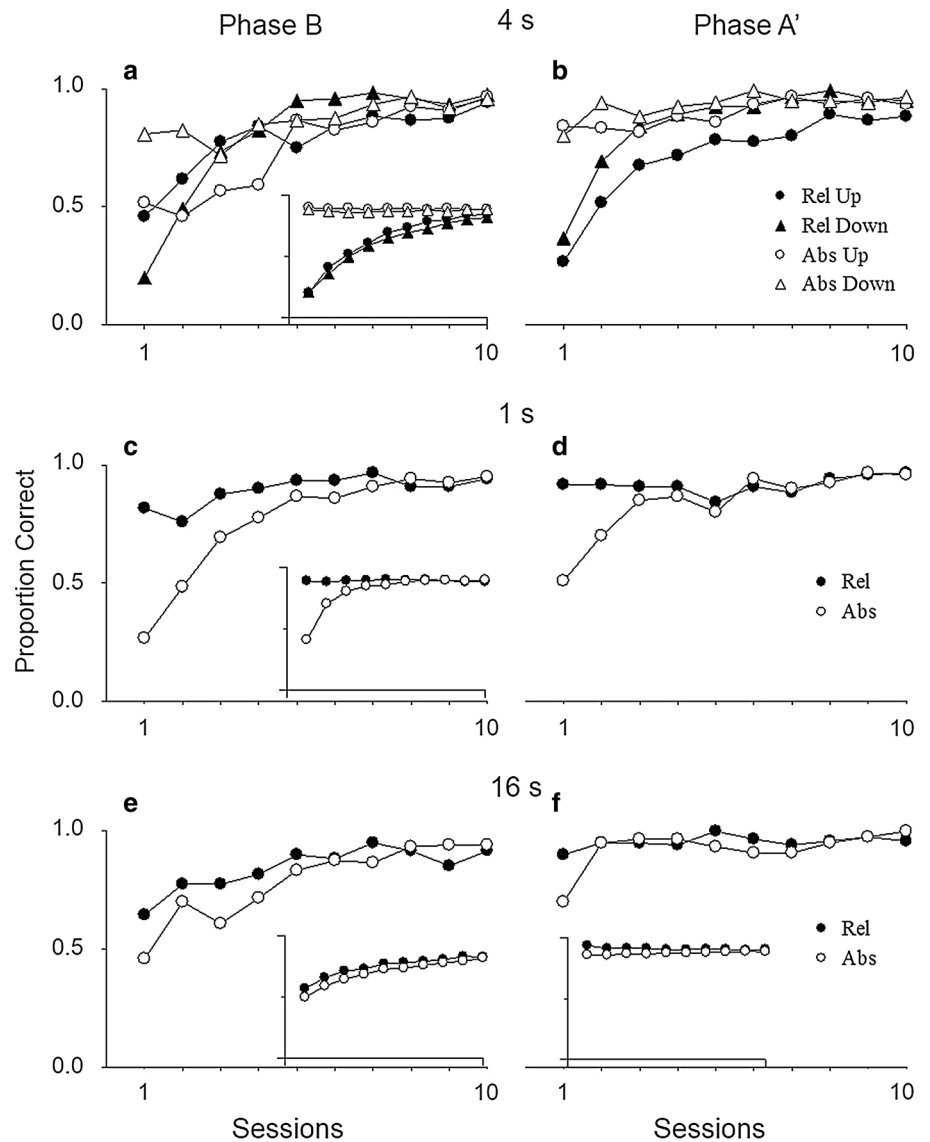


Fig. 14 Average acquisition curves obtained by each of the four groups of pigeons in Carvalho and Machado (2012) study. The groups learned distinct bisection tasks across the three phases of an ABA' design. The tasks (phases) were: Group Relative Upshift: '1 s → Left, 4 s → Right' (A and A'), and '4 s → Left, 16 s → Right' (B); Group Relative Downshift: '4 s → Left, 16 s → Right' (A and A'), and '1 s → Left, 4 s → Right' (B); Group Absolute Upshift: '1 s → Left, 4 s → Right' (A and A'), and '16 s → Left, 4 s → Right' (B); Group Absolute Downshift: '4 s → Left, 16 s → Right' (A and A'), and '4 s → Left, 1 s → Right' (B). The *top*, *middle* and *bottom* panels show the proportion correct following the 4-, 1-, and 16-s samples, respectively. The inset graphs show the predictions of the LeT model. From Carvalho and Machado (2012)



(Fig. 12c, 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- and 16-s samples (see Carvalho and Machado 2012, for an extended discussion).

In a follow-up study, Carvalho et al. (2016) 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 15 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: “2 s → Red, 8 s → Green” and “4 s → Vertical, 16 s → Horizontal.” Then, on test trials, they chose between Red and Green following the 4-s sample and between Vertical and Horizontal following the 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 Fig. 16 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.

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- and 8-s samples. The generalization gradients obtained with each pair of comparisons almost superimposed (Fig. 16).

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 and 8 s. The causal account runs as follows. The sets of states active after the 2- and 4-s samples have more common elements than the sets active after the 4- and

8-s samples and these common elements bias choice toward the Red comparison. Similarly, the sets of states active after the 4- and 8-s samples have more common elements than the sets active after the 8- 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.

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 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, and 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), and 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, and 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. LeT also encompasses a relatively small number of free parameters as compared to other influential timing models (e.g., SET), and hence it is *parsimonious* and easily falsifiable. 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 generalize responses to stimuli) and their derivatives (how the generalization 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

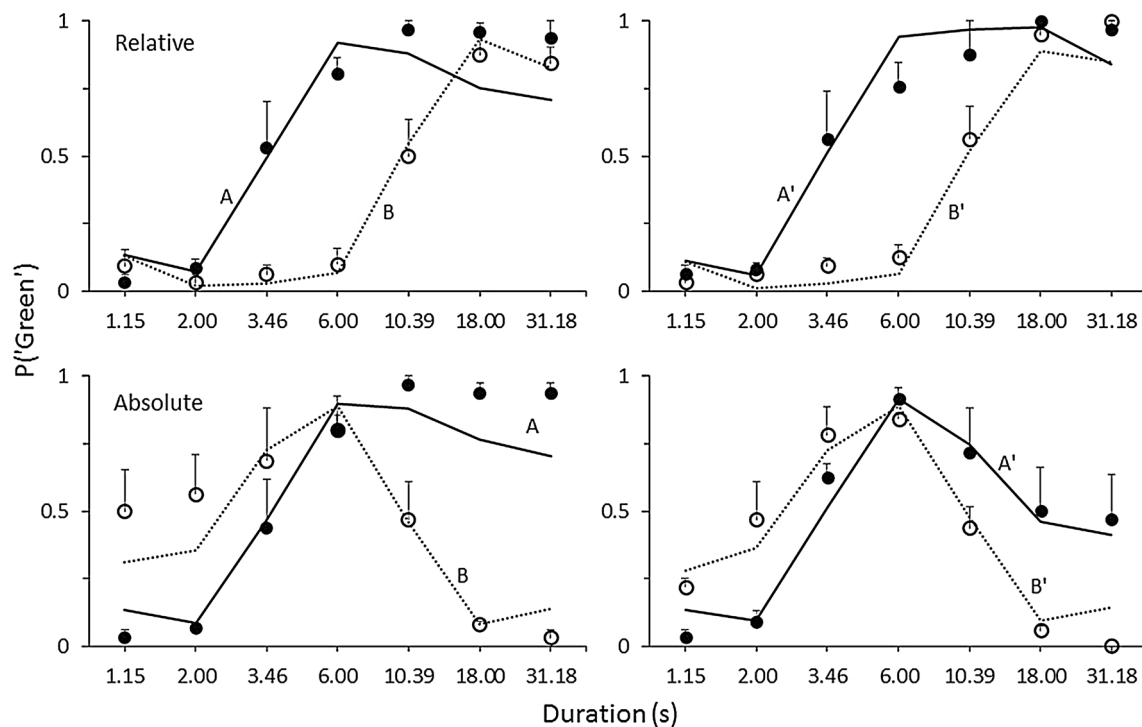


Fig. 15 Generalization gradients produced by pigeons (*symbols*) in Carvalho et al.’s (2016) study and the curves fitted by the LeT model. The pigeons learned distinct bisection tasks across the four phases of an ABA’B’ design. The tasks (phases) were: Group Relative Upshift: ‘2 s → Red, 6 s → Green’ (A and A’), and ‘6 s → Red, 18 s → Green’ (B and B’); Group Relative Downshift: ‘6 s → Red, 18 s → Green’ (A and A’), and ‘2 s → Red, 18 s → Green’ (B and B’); Group Absolute Upshift: ‘2 s → Red, 6 s → Green’ (A and A’),

and ‘18 s → Red, 6 s → Green’ (B and B’); Group Absolute Downshift: ‘6 s → Red, 18 s → Green’ (A and A’), and ‘6 s → Red, 2 s → Green’ (B and B’). The *top* and *bottom* panels show the average gradients for the Relative and Absolute groups, respectively. The data from the Downshift groups were reflected around the 6-s vertical line before averaging them with the data from the Upshift groups. Adapted from Carvalho et al. (2016)

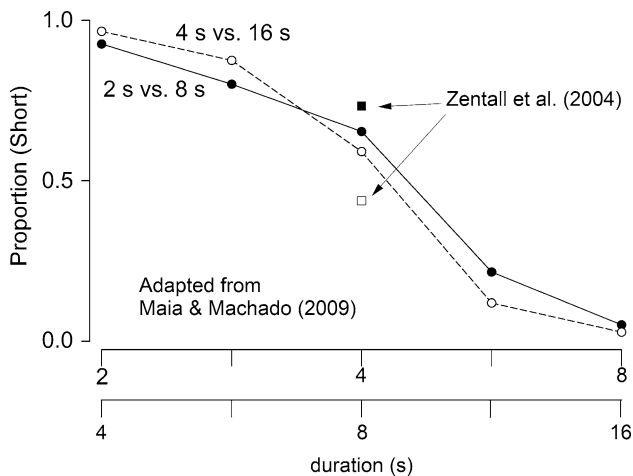


Fig. 16 Pigeons learned two bisection tasks, one with a ‘2 s → Red, 8 s → Green’ mapping, and the other with a ‘4 s → Horizontal, 16 s → Vertical’ mapping. Next they were exposed to new test samples but with the same comparisons. Zentall et al.’s (2004) data show the preference for Red over Green following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

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, as both *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.

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. 2016, for the pros and cons of categorical and non-categorical decision rules).

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- 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 and 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 FIs 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 et al. 2009; Swanton and 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 and Henning 2013; Matell and Kurti 2014; Swanton et al. 2009; Swanton and 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, 75–150 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 et al. (1963) did for the dimension of line-tilt, for example—and across different concurrent and retrospective procedures.

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 10-s–FI 120-s 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 FT. 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 therefore

bootstrap the timing process, and to access the temporal memories and thereby generate the bimodal gradients (see also Machado and Silva 2007a, b; also Gallistel 2007).

In addition to concurrent timing tasks, the problem of temporal memories occurs also in retrospective time judgements tasks. Singer et al. (2006, Experiment 2) showed that pigeons can learn to map three samples onto two comparisons: “2 s → Green, 8 s → Red, 32 s → 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- 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 Fig. 15 by the data from the absolute group (bottom panels). Across the ABA'B' phases of Carvalho et al.'s (2016) study, this group was exposed alternately to the bisection tasks “2 s → Red, 6 s → Green” (A and A') and “18 s → Red, 6 s → Green” (B and B'). 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., “18 s → Red” in Phase B) was retained to a large degree while the pigeons learned another association (“2 s → Red” in Phase A').

To see this result more clearly and appreciate its implications, Fig. 17 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 “2 s → Red, 6 s → 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 “18 s → Red, 6 s → 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 “2 s → Red, 6 s → 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

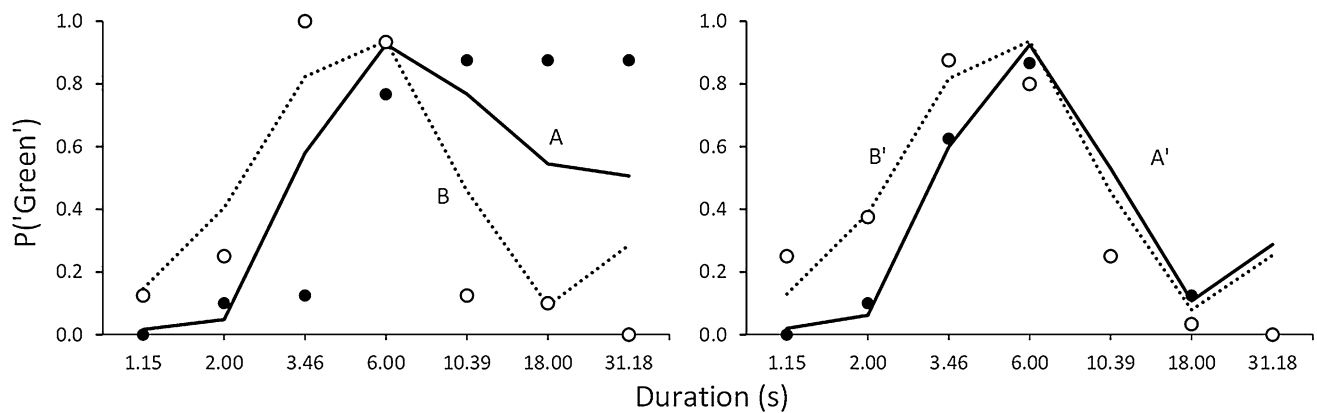


Fig. 17 Generalization gradients produced by pigeon P751 (symbols) in Carvalho et al.'s (2016) study and the curves fitted by the LeT model. The pigeon learned the following bisection tasks (in each

phase of the ABA'B' design): '2 s → Red, 6 s → Green' (A and A'), and '18 s → Red, 6 s → Green' (B and B')

Green on significantly *fewer trials* because the association "18 s → Red" learned in phase B should not be strongly affected during Phase A'. In fact, the only way to reduce the "18 s → 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 "18 s → Red" memory will be preserved. As the dotted line in the right panel shows, the data were more consistent with the LeT model.

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 "6 s → Green, 18 s → 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 and Machado 2012; Carvalho et al. 2016), 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.

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 and 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.

Even though the study of timing was originally embedded on the general field of stimulus control of responding, in the last decades it has grown as an independent research field. The synthetic approach to temporally regulated behavior can potentially reestablish the link between timing and other stimulus dimensions. One promising extension of our reasoning involves spatial cognition. An obvious connection is Weber's law: Pigeons

accustomed to search for hidden food in an arena show clustered search patterns around the goal location when food is absent. Similarly, when pigeons have to estimate the perpendicular distance from a surface, their search accuracy follows Weber's law (Cheng 1990, 1992).

In an extension of Guttman and Kalish (1956) and Jenkins and Harrison's (1960) classic studies on stimulus generalization, Cheng et al. (1997) explored the applicability of the stimulus generalization concept to the spatial realm. In their Experiment 2, for example, pigeons learned a spatial discrimination with pecks to a touchscreen reinforced in the presence of a $S+$ and extinguished in the presence of a horizontally displaced $S-$. The subsequent generalization tests involved presenting the discriminative stimulus at different horizontal locations. They found clear evidence for an area shift in the direction away from the $S-$, and when the $S+$ and the $S-$ were closer together (Experiment 3) a peak shift was also observed. Although the modeling efforts were by no means exhaustive, the authors themselves implemented a Spencean approach using spatial generalization gradients to explain their results (for a broad revision of small-scale spatial cognition, see Cheng et al. 2006).

Transformation tests implemented to understand how information from multiple landmarks is combined provided another tests to our approach. Suppose that animals are trained to search for food between two landmarks. Suppose further that after learning the task, the two landmarks are moved further apart. Where should animals search for food? Gerbils (*Meriones unguiculatus*) concentrate their search in the two spots each at the correct distance and location for one of the landmarks (Collett et al. 1986). In contrast, pigeons search for food at intermediate locations as if they were averaging information from the different landmarks (e.g., Cheng 1989). Despite these differences across species, the results suggest that once the animal learns that food is at a given distance from a landmark, it distributes its responses according to this distance, and the more a location differs from the learned distance, the less the subject responds to that location. Such spatial differentiation describes a spatial gradient of responding (our spatial primitive), and we could conceive of it as one of the ingredients to take into account in a synthetic approach to spatial cognition. How the gradients interact to generate a single search location or a larger search area is still unclear but the landmarks themselves could, under certain circumstances, distort the primitive generalization gradients.

To sum up, when properly operationalized, the synthetic hypothesis (e.g., LeT) 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.

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