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Though assisted by constructed clocks and calendars, our sense of time is actually deeply rooted in biological mechanisms we share with all other animal species (Lejeune & Wearden, 1991). Our understanding of these mechanisms has been much advanced by operant-conditioning experiments with humans and (infrahuman) animals. In these experiments, an operant response, such as key-pecking or button-pushing, is reinforced or not depending on the time elapsed since a specific stimulus (a so-called *time marker*¹).

In a fixed-interval (FI) schedule, for instance, a response is reinforced only after a certain, fixed amount of time has elapsed since the time marker (Skinner, 1938). The FI time marker, for the schedule and the organism, is usually reinforcement, but may also be the end of an intertrial interval. The peak procedure (Catania, 1970; Roberts, 1981) is very similar to FI, except that the subject is also exposed to unreinforced probe trials lasting much longer than the

reinforced FI trials, allowing us to look at behavior beyond the time of reinforcement. In the bisection procedure (Church & Deluty, 1977; Stubbs, 1968), the subject is reinforced for emitting a response $R1$ following a stimulus that lasts S units of time and for emitting a response $R2$ following a stimulus lasting L units of time ($S < L$). Temporal generalization is then tested on unreinforced probe trials where the duration of the stimulus is varied between S and L .

Various theoretical accounts of the results of these and similar experiments have been proposed over the years. All these accounts have three fundamental components (Staddon, 2001): (a) a short-term memory (STM) representation of the time elapsed since the onset of the time marker; (b) a long-term memory (LTM) representation of the time of reinforcement; and (c) a decision mechanism, which, through a comparison between the STM and LTM representations, generates behavior. This chapter will focus on the decision mechanism, or rule.

Models of timing use two types of decision rule: cognitive or associative. Cognitive rules guide behavior via a comparison between an STM scalar representation of time elapsed since the time marker and an LTM scalar representation of the time of reinforcement. Such a rule is used by *scalar expectancy theory* (SET; Gibbon, 1977; Gibbon, Church, & Meck, 1984), which was for many years the standard account for interval timing. Other models using

cognitive-type decision rules are the multiple-time-scale theory (MTS; Staddon & Higa, 1999) and the packet theory (Guilhardi, Yi, & Church, 2007b; Kirkpatrick, 2002), which both use the difference between, rather than the ratio of, the STM and LTM representations as their decision variable.

Models using associative decision rules are inspired by artificial neural-network modeling, in which a time marker triggers a series of time-dependent states. In these models, reinforcement strengthens, and nonreinforcement weakens, associations between currently active states and the reinforced response. The process can be modeled by the venerable Bush-Mosteller learning rule (Bush & Mosteller, 1955), but the details of the learning rule are probably not critical. Associative-type rules are used in the behavioral theory of timing (BET; Killeen and Fetterman 1988); the learning-to-time model (LeT; Machado, 1997; Machado, Malheiro, & Ernhagen, 2009); and the behavioral economic model (BEM; Jozefowicz, Staddon, & Cerutti, 2009). Associative rules are natural for any neutrally inspired model of timing (i.e., Church & Broadbent, 1990; Grossberg & Schmajuk, 1989; Ludvig, Sutton, & Kehoe, 2008).

In a model using an associative-response rule, temporal intervals are represented not as single numbers but by vectors: a vector of input activation for the STM representation, and a vector of associative weights connecting the input to the response for the LTM representation. In addition, contrary to what happens

in models using a cognitive rule, there is no clear separation between the LTM representation and the response rule: they are both implemented through the vector of associative strengths.

18.1 Reinforcement Effects on Timing

18.1.1 Reinforcement Effects in Choice Procedures

One basic prediction of associative decision rules is that in choice-based timing procedures, subjects should be biased toward the more-reinforced response. For instance, consider a bisection procedure where the subject learns a discrimination between two durations, S and L . There is a critical duration I (the *bisection point*) at which the subject is indifferent between $R1$, the response reinforced after a stimulus duration of S , and $R2$, the response reinforced after a stimulus duration of L . In an associative decision-rule framework, there is a post-time-marker state (or a series of states, depending on the model), x_I , which reaches its maximum level of activation at the time of the bisection point. By definition, the strength of that state's associative link with $R1$ is equal to its associative strength with $R2$. Now, if $R1$ is more reinforced than $R2$ —because reinforced trials with $R1$ are more frequent (trial-frequency manipulation), because $R1$ is more often reinforced (probability of reinforcement manipulation), or because $R1$ leads to a larger

reinforcer (reinforcement-magnitude manipulation)—the associative strength between x_I and $R1$ will be higher than the associative strength between x_I and $R2$, leading to a bias toward $R1$.

The most extensive studies of the effect of reinforcement on timing and choice have used the *free-operant psychophysical procedure* (FOPP; Bizo & White, 1994a, 1994b, 1995a, 1995b; Guilhardi, MacInnis, Church & Machado, 2007a; Machado & Guilhardi, 2000; Stubbs, 1980). In this procedure, a trial lasts T sec, during which the subject can freely choose between two responses, $R1$ and $R2$. Responding on $R1$ is reinforced with a probability $p1$ during the first half of a trial (from 0 to $T/2$ sec), while responding on $R2$ is reinforced with a probability $p2$ during the second half of a trial (from $T/2$ to T sec). The subject adapts to this temporal contingency by emitting mainly $R1$ during the first part of a trial before switching to $R2$. If $p1 = p2$, the subject is indifferent between the two responses roughly around $T/2$ sec in a trial. Otherwise, if $p1 > p2$, the subject switches later to $R2$ (earlier if $p1 < p2$), even though manipulations of the reinforcement rate leave the temporal contingency—which is the sole input to cognitive-rule models like SET—unaffected. But data like these are readily explained by an associative decision rule. Indeed, Machado and Guilhardi (2000) showed that the data from the procedure were very well fitted quantitatively by LeT, while Jozefowicz et al. (2009) showed the same thing for BEM.

Cognitive rules have difficulty with those data, because they assume that the subject's decision is based only on the representation of time intervals, which is not supposed to be affected by a manipulation of reinforcement rate. Still, a model using a cognitive rule could be made consistent with data from the FOPP by assuming that the reinforcement rate affects a response-bias parameter. Supporting this argument, Wearden and Grindrod (2003) studied the effect of reinforcement in a temporal-generalization task using human subjects and "points" reinforcement. Subjects were reinforced for emitting one response following a stimulus duration of 400 ms and again for any stimulus duration different from 400 ms. By manipulating the number of points associated with each response, Wearden and Grindrod (2003) were able to bias the performance of the subjects. They showed that SET could account for these effects by adjusting the bias parameter only: the parameters related to the representation of time did not change significantly across conditions.

The problem, of course, is that in the absence of any theory explaining how and why response bias is affected by reinforcement, tweaking the response-bias parameter is an unsatisfactorily ad hoc solution. It does not allow for a fair comparison with associative models such as BEM and LeT. To fit the data from the FOPP, Machado and Guilhardi (2000) and Jozefowicz et al. (2009) adjusted only one free parameter, controlling the level of noise in the STM representation

of time, to the control condition where $p1 = p2$. At this point, all the degrees of freedom in the models were exhausted, and the predictions for the conditions where $p1$ was different from $p2$ were automatically generated. By contrast, when a model like SET is applied to the FOPP, a two-stage process is required. Parameters controlling the representation of time would first be adjusted so the model can account for the data from the control condition. The response-bias parameter would then be adjusted so that the model can fit the other conditions. Under those circumstances, LeT and BEM would be lucky if they do as well as SET, but this is just because the principles governing the response bias in SET are undefined.

This limitation of SET-type models is perfectly illustrated by a study by Machado and Guilhardi (2000; also see Guilhardi et al., 2007a), where, as predicted by an associative-response rule, manipulations of the reinforcement rate did not lead to biased responding in the FOPP. In their procedure, response $R1$ was reinforced with a probability $p1$ from 0 to $T/4$ sec in a trial, and with a probability $p2$ from $T/4$ to $T/2$ sec in a trial. In the same way, response $R2$ was reinforced with a probability $p3$ from $T/2$ to $3T/4$ sec in a trial and with a probability $p4$. With this method, Machado and Guilhardi were able to manipulate the local probability of reinforcement for each response ($p1$, $p2$, $p3$, and $p4$) while keeping the overall reinforcement rate for each response the same ($p1 + p2 = p3$

+ p_4). The subjects were biased toward $R1$ (or $R2$) only when $p_2 > p_3$ (or $p_2 < p_3$). Performance in conditions where p_1 differed from p_4 was identical to performance in the control condition where all four probabilities were equal.

An associative account is as follows. The states sampled from 0 to $T/4$ sec and from $3T/4$ to T sec are already maximally associated with $R1$ in one case, and $R2$ in the other. Hence, any change in the reinforcement parameters for these two intervals is expected to have little effect. This is not the case for the states sampled around the point of indifference (from $T/4$ to $3T/4$ sec). Those states have similar associations to both responses, hence are strongly affected by manipulation of the reinforcement parameters that would favor one response over the other (see Jozefowicz et al., 2009 and Machado & Guilhardi, 2000 for more detailed explanations within the context of BEM and LeT). Both LeT (Machado & Guilhardi, 2000) and BEM (Jozefowicz et al., 2009) provide a good quantitative account of those data. By contrast, with no clear principle constraining the response bias, it is not clear how a cognitive model such as SET can account for these data, except in a purely ad hoc fashion. Even the vague “the subject will be biased toward the more reinforced response” principle used by Wearden and Grindrod (2003) fails here, because both responses were equally reinforced overall.²

Taken together, data from the FOPP favor an associative-response rule over a cognitive one. Outside of the FOPP, a few other studies have looked at the effect of reinforcement magnitude. We already mentioned Wearden and Grindrod (2003)'s study of temporal generalization in humans. By contrast, using rats as subjects, Galtress and Kirkpatrick (2010) found that reinforcing one response more than the other in a bisection study led to an overall flattening of the psychometric function, consistent with an overall decrease in temporal control. This is consistent with a human bisection study using points as reinforcers by Jozefowicz, Pollack, Machado & Miller (2013) found that manipulations of trial frequency lead to the type of biased performance predicted by associative models.

18.1.2 Reinforcement Effects in Simple Schedules

Timing manifests itself on an FI schedule by the fact that the subject pauses following the onset of the time marker before reinitiating a response. The duration of the pause (the so-called *wait time*) is roughly a linear function of the FI interval (Dews, 1970). In an associative decision rule framework, this is explained by the fact that states activated early in a trial are poorly associated with reinforcement (either because, as in LeT, they are weakly activated at the time of reinforcement, or because, as in BEM, they are rarely sampled at the time of reinforcement).

Hence, increasing the magnitude of reinforcement should decrease the wait time, because it would strengthen the associations of all the states with reinforcement.

Associative decision rules make similar predictions for the peak procedure. The average pattern of responding during an unreinforced probe trial follows a roughly Gaussian function, with a peak around the time of reinforcement (Catania, 1970; Roberts, 1981). While such a pattern would suggest an increasing rate of response as a function of time in a trial up to the peak time, followed by a decreasing one, it has been argued that on individual trials, the behavior actually goes from a phase of low-responding to a phase of high-responding before moving back to a phase of low-responding, reflecting the subject's changing reward expectation as a function of the time-to-reinforcement (Cheng & Westwood, 1993; Church, Meck, & Gibbon, 1994). Trial-to-trial variability in the start time (where the transition from the low-response phase to the high-response phase takes place) and in the stop time (where the transition from the high-response phase to the low-response phase takes place) would be responsible for the Gaussian pattern observed in the average data. The same reasoning that led us to infer that increasing reinforcement magnitude should decrease wait time on FI also predicts a decrease in wait time (and start time) in the peak procedure and an increase in stop time. If the stop and start times are equally affected, the peak time should remain unchanged.

Data in the literature appear at first glance to support those predictions only partially. Although any change in timing behavior as a function of reinforcement manipulation is beyond the reach of cognitive models, the changes that are observed appear to be inconsistent with existing associative models. For example, studies that have transiently changed reinforcement magnitude during a session have actually found longer wait times following a stronger reinforcer (Blomeley, Lowe, & Wearden, 2003; Hatten & Shull, 1983; Jensen & Fallon, 1973; Lowe, Davey, & Harzem, 1974; Staddon, 1970; see also Kello, 1972; Reid & Staddon, 1982). However, as Ludvig, Conover, and Shizgal (2007) have pointed out, reinforcement also acted as a time marker in all those studies due to the absence of an intertrial interval. Because it is a more salient stimulus, a stronger reinforcer will be a better time marker than a weaker one and will induce better temporal control, and hence longer wait time. This is illustrated by the so-called reinforcement omission effect (Staddon & Innis, 1969), where occasional omission of the reinforcer in an FI leads to dramatically shorter wait time on the next trial. Since this time-marker effect goes against the effect on temporal control a stronger reinforcer has, as far as reward expectation is concerned, it probably explains why studies that have chronically changed the reinforcement magnitude (keeping it constant over several sessions) but have still used reinforcement itself to mark the beginning and the end of a trial have failed to find

an effect of reinforcement magnitude on timing (i.e., Hatten and Shull 1983; see Ludvig et al., 2007 for more details).

Studies where the influence of the reinforcer as a time marker is weakened by the use of long intertrial intervals (which is always the case in the peak procedure) have, on the other hand, found a clear effect of chronic manipulations of the reinforcement magnitude, either through direct manipulation of its intensity (Galtress & Kirkpatrick, 2009; Grace & Nevin, 2000; Kacelnik & Brunner, 2002; Ludvig et al., 2007) or through an indirect manipulation of the reinforcer value through lithium chloride-induced food aversion or pre-feeding (Galtress & Kirkpatrick, 2009; Plowright, Church, Behnke, & Silverman, 2000; Roberts, 1981). Overall, it appears that, besides a change in overall response rate probably due to changes in arousal (Killeen, 1998), the most reliable effect of reinforcement on timing performance is, as predicted by associative rules, a shortening of the wait time and start time with stronger reinforcers (Galtress & Kirkpatrick, 2009; Ludvig et al., 2007; Plowright et al., 2000). The stop time, on the other hand, remains relatively unchanged (Galtress & Kirkpatrick, 2009; Ludvig et al., 2007). Most studies also report a leftward shift in the peak time with a stronger reinforcer (Galtress & Kirkpatrick, 2009; Grace & Nevin, 2000; Kacelnik & Brunner, 2002) and a rightward shift following a reinforcer devaluation procedure (Galtress & Kirkpatrick, 2009; Plowright et al., 2000;

Roberts, 1981), though this effect might depend on the methods used to assess the peak time. Ludvig et al. (2007) tested various methods and concluded that only the least sophisticated ones detected an effect of reinforcement on the peak time. Still, a leftward shift in the peak time with a stronger reinforcer as well as the rightward shift with a devaluated one is to be expected if the manipulation affects the start but not the stop time from the stop-start-stop view of performance on individual peak trials.

A procedure where an interaction between timing and reinforcement is well documented, even though poorly understood, is the mixed FI schedule (Catania & Reynolds, 1968; Leak & Gibbon, 1995; Whitaker, Lowe & Wearden, 2003, 2008). In this paradigm, the subject is trained simultaneously on two unsignaled FI schedules, so that there is no way to know which schedule is in place on a given trial. A proportion p of trials are reinforced according to the FI with the smallest interval, while the remaining $1-p$ trials are reinforced according to the other FI. For instance, in a mixed FI 10 s FI 30 s, the first response 10 s after trial onset would be reinforced for a proportion p of trials, while it would take 30 s since trial onset for reinforcement to occur in the remaining $1-p$ trials. The average response pattern in a mixed schedule can usually be fitted as the sum of two Gaussian functions, one peaking near the first time of reinforcement, the other near the second time of reinforcement (Catania & Reynolds, 1968; Whitaker

et al., 2003, 2008). The relative height of the first peak in responding relative to the other can be manipulated through variations of p (Catania & Reynolds, 1968; Whitaker et al., 2008). Although this changes the height of the peaks, this does not change their timing (Whitaker et al., 2008). This is somehow reminiscent of the manipulation of the number of probe trials in the peak procedure, which also affects response rate without changing the start, peak, or stop times (Galtres & Kirkpatrick, 2009; Roberts, 1981). Yet this simple fact remains unsatisfactorily explained by contemporary theories of timing, no matter if they use a cognitive or an associative-response rule.

Models using cognitive rules, such as SET, do not anticipate the effect of manipulating p and have a problem assimilating it, notably because they lack any principle explaining how response rate is generated (Whitaker et al., 2008).

Moreover, Machado and Silva (2007) have identified a fundamental conceptual flaw in SET's account of mixed schedule (as developed, for instance, by Leak & Gibbon, 1995), which is probably also true of most models using a cognitive rule.

This account relies on the idea that the subject stores separately a LTM representation of the time of reinforcement for each FI composing the mixed schedule. However, as Machado and Silva (2007) point out (see also Machado et al. 2009), *there was no way for the subject to know from which FI a specific reinforcement was coming*. Probably for all these reasons, while SET has been

successfully applied to the quantitative modeling of FI, the peak procedure, and the bisection procedure, there is no equivalent account of mixed schedule performance.

On the other hand, models with associative rules at least anticipate the effect of p on performance, and Machado (1997) showed that LeT provides a satisfactory quantitative account of the data on mixed schedules from Catania and Reynolds (1968). But the model cannot account for data sets where the first response peak is higher than the second, as it is often the case when the ratio between the FI intervals is high, especially in rats (see Whitaker et al., 2003 for instance). Hence, although they might seem at first glance a simple variation of the FI procedure, mixed schedules provide an interesting challenge for models of timing. Very little is known about them since this procedure has been somehow neglected by researchers. Further research on it should be encouraged, as it might provide an interesting testing ground for theories of timing as well as a fertile source of new ideas.

18.2 Contextual Effects on Time Perception

18.2.1 Relative Temporal Coding in the Double Bisection

Procedure

Machado and Keen (1999) trained pigeons in two bisection procedures simultaneously. In the first task, response *R1* was reinforced after a 1-s stimulus, while response *R2* was reinforced after a 4-s stimulus. In the second task, response *R3* was reinforced after a 4-s stimulus while response *R4* was reinforced after a 16-s stimulus. On unreinforced probe trials, the pigeons were presented with stimulus duration ranging from 1 to 16 s and had to choose between *R2* and *R3*. Despite the fact that both responses were reinforced following a 4-s stimulus, the pigeons were not indifferent between them: preference for *R2* increased with the stimulus duration, the indifference point between *R2* and *R3* being reached around 4 s.

This paradoxical effect is quite robust as it is observed despite several modifications of the original double bisection procedure. For example, the increasing preference for *R2* as the sample duration increased held up when probe trials were nondifferentially reinforced (Machado & Pata, 2005); when the two bisection tasks were trained independently and never mixed together during the same session (Arantes & Machado, 2008); when, during the training of a bisection

task, the two responses were never shown together but were instead differentially reinforced as a function of the stimulus duration (Arantes, 2008); and when each bisection task was signaled by a stimulus (Oliveira & Machado, 2009).

Hence, it seems that the LTM representation of the time associated with a response in a bisection procedure is context-dependent, since it is affected by the time associated with the other response trained in the bisection. This is a critical challenge to cognitive timing models, as context independency of the LTM representation is essential to cognitive decision rules (Machado et al., 2009). On the other hand, context dependency comes naturally to models using associative rules (Jozefowicz et al., 2009; Machado et al., 2009). To see how this works in the Machado et al. experiments, let's parse the input states into three categories: early, middle, and late. Early states are strongly activated/sampled after a 1-s stimulus, mildly activated/sampled after a 4-s stimulus, and weakly activated/sampled after a 16-s stimulus. Late states present the reverse pattern. Middle states are strongly activated/sampled following a 4-s stimulus and mildly activated/sampled following a 1-s or 16-s stimulus. During the course of the 1-s vs. 4-s discrimination, differential reinforcement will lead the early states to be strongly associated with *R1* and weakly associated with *R2*, while the reverse will be true for the middle states. If we assume that every state has an initial weak connection with the responses (Machado & Plata, 2003, connections between the

late states and both *R1* and *R2* will remain weak, as those states will rarely be activated during the 1-s vs. 4-s task. In the same way, during the 4-s vs. 16-s discrimination, the middle states will develop strong connections with *R3* and weak connections with *R4*, while the reverse will be true for the late states. Connections between the early states and both *R3* and *R4* will remain weak. Hence, when *R2* is pitted against *R3*, the subjects will prefer *R3* for durations around 1 s (stronger associations between the early states and *R3*), will be indifferent between the two around 4 s (equivalent association strength between the middle states and both responses), and will prefer *R2* around 16 s (stronger associations between the late states and *R2*).

This analysis also correctly predicts the outcome of further probe trials where the pigeons were given the choice between *R1* and *R3* on one hand, and *R2* and *R4* on other. In the first case, the preference for *R3* increased up to a duration of 4 s before the subjects switched back to *R1*. In the second case, preference for *R4* increased up to a duration of 4 s (even though *R2* has been reinforced after a 4-s stimulus duration) before the subjects switched back to *R2*. In all these cases, a model using a cognitive rule predicts that the preference for the response associated with 4-s stimulus, no matter if it has been trained in a 1-s vs. 4-s discrimination or a 4-s vs. 16-s discrimination, will increase with the stimulus duration.

The associative interpretation of the double bisection procedure was further strengthened by a study by Machado and Arantes (2006). After training pigeons in a 1-s vs. 4-s discrimination and 4-s vs. 16-s one, they used *R2* and *R3* (the two responses associated with a 4-s stimulus duration) in a new bisection task pitting a 1-s stimulus against a 16-s one. In group 1, *R3* was now reinforced following a 1-s stimulus, while *R4* was now reinforced following a 16-s stimulus. The contingencies were reversed in group 2. In the former group, the pattern of associative strength induced by the double bisection task is consistent with the pattern of associative strength required by the new task, while this is not the case for the later group. Hence, Machado and Arantes (2006) predicted that the new task would be much easier to learn for group 1 than group 2. This was indeed the case, as group 1 learned the new task almost without mistakes while performance in group 2 was initially poor. This difference between the two groups cannot be explained by a cognitive rule.

A possible alternative interpretation of the double-bisection result can be found in a study by Zentall, Weaver, and Clement (2004). They trained pigeons in a 2-s vs. 8-s bisection task as well as in a 4-s vs. 16-s one. Note that the long-duration stimulus in the first bisection is located at the geometric mean of the two durations used in the second bisection task, while the short-duration stimulus in the second bisection task is located at the geometric mean of the durations used in

the first bisection task. In a bisection study with nonhuman animals, the time at which the subject is indifferent between the two responses (the so-called bisection point) is located at the geometric mean between the two training durations (Church & Delutty, 1977; Stubbs, 1968). Hence, the pigeons should be indifferent between the two response alternatives if they are presented with a 4-s stimulus in the first bisection task and with an 8-s stimulus in the second bisection task. Instead of that, Zentall et al. (2004) observed that responding following a 4-s stimulus was biased toward the 2-s response in the first bisection, while responding following an 8-s stimulus was biased toward the 16-s response in the second bisection task.

Zentall et al. (2004) proposed that the subjects were encoding not only the absolute duration of the stimulus, but also its category, as relatively “long” or “short.” In other words, Zentall et al. added a kind of cognitive encoding to the purely temporal one. When exposed to a 4-s stimulus in the first bisection task, the categorical code would overrun the absolute duration code, since the latter could not be used to decide which response to choose. Hence, since the 4-s duration would have been tagged as “short” because of the training in the second bisection task, while, in the first bisection task, the response reinforced after a stimulus categorized as “short” is the 2-s answer, the pigeon would be biased

toward that response. The same reasoning explains the bias toward the 16-s response following an 8-s stimulus in the second bisection task.

Zentall et al.'s scheme might explain the results from Machado and collaborators, albeit at some cost in terms of parsimony. When given the choice between two responses, both reinforced following a 4-s duration, the absolute duration code would be useless to decide which response to choose, and it would be overridden by the categorical code. Durations around 1-s would be categorized as "short," and hence, the subject would tend to associate them with the 4-s response reinforced following "short" durations, that is to say *R3*. On the other hand, durations around 16 s would be categorized as "long," and hence, the subjects would associate with them the 4-s response reinforced following "long" durations, that is to say *R2*. The categorical coding for durations around 4 s would be ambiguous (they were categorized as "long" in the 1-s vs. 4-s discrimination, but as "short" in the 4-s vs. 16-s discrimination), and hence the pigeons would be indifferent between the two responses at 4 s.

Unfortunately, without a proper quantitative formulation to define the category-formation process, it is difficult to know if categorical encoding provides a better account of the double bisection data than associative models such as LeT. Further research is necessary to establish the generality of Zentall et al.'s (2004) result. While Molet and Zentall (2008) were able to replicate their

results with humans (using the arithmetic mean instead of the geometric one), Maia and Machado (2009) failed to find the predicted switch in the psychometric curves of pigeons submitted to Zentall et al.'s (2004) double bisection procedure.

18.2.2 Other Instances of Relative Encoding

One of the most interesting conclusions that can be drawn from the double-bisection procedure is that, much like other forms of perception such as brightness or color, the perception of time is not absolute but depends on the context. There are a few other examples of this in the literature outside of the double-bisection procedure.

For instance, Jazayeri and Shadlen (2010) presented human subjects with stimuli lasting x ms and asked them to reproduce those durations. Depending on the condition, x was drawn from three possible stimulus distributions: one ranging from 494 to 847 ms in condition 1, one ranging from 847 to 1200 ms in condition 2, and finally, one ranging from 671 to 1023 ms in condition 3. They found, that in all conditions, shorter durations were overestimated while longer ones were underestimated. The effect was stronger the further a specific duration was from the mean of the stimulus distribution from which it was drawn and the higher the mean of that distribution. As a consequence, estimates for a specific interval

varied as a function of the distribution from which it was drawn. For instance, an estimate of a 847-ms stimulus lasted about 847 ms in condition 2 (where 847 ms corresponded to the mean of the stimulus distribution), while it lasted less than 847 ms in condition 1 (where 847 ms was above the mean of the distribution) but more than 847 ms in condition 3 (where 847 ms was below the mean of the distribution).

Another example of context dependency can be found in a study on choice in starlings by Shapiro, Siller, and Kacelnik (2008). The starlings were trained to choose between stimuli leading to different delays and amounts of food. They were exposed to both choice trials, in which two stimuli were presented concurrently and the animal had to decide which one to choose, and no-choice trials in which only one stimulus was presented. On those trials, the wait time was not only a function of the delay of reinforcement signaled by the stimulus but depended also of the delay of reinforcement signaled by the stimulus against which the target stimulus was pitted in the choice trials.

It would be interesting to see if other examples of relative temporal coding could be demonstrated and whether they can be explained by the same mechanisms, or if different explanations are required for each of them. For instance, it is hard to see how Machado and collaborators' explanations for the context effect in the double bisection procedure could apply to Jozaveri and

Shadlen's (2010) results. On the other hand, it seems that they could be very simply explained within the context of a cognitive decision rule. A stimulus lasting x ms would lead to a LTM representation $f(x)$, which would itself lead to a LTM representation $f^*(x)$. When asked to reproduce the interval, the subject would compare the value of its current STM representation $f(t)$ with $f^*(x)$. The effects observed by Jazayeri and Shadlen (2010) would be the consequence of, on one hand, proactive interference, which would lead $f^*(x)$ to regress toward the mean of the stimulus distribution, and, on the other, Weber's law (see below), which would increase the degree of proactive interference as the stimulus durations are increased³.

18.3 The Coding of Subjective Time

18.3.1 Implications of the Decision Rule for the Representation of Time

One important constraint on timing models is the fact that time perception follows Weber's law: the ability for a subject to perceive changes in a stimulus increases linearly with its intensity, in this case its duration (see the reviews, for instance, in Gibbon, 1977, Lejeune & Wearden, 2006 and Wearden & Lejeune, 2007).

Various representation schemes consistent with Weber's law have been proposed

in the literature. In SET (Gibbon, 1977; Gibbon et al., 1984), a time marker triggers an internal pacemaker whose pulses start to accumulate in STM. The rate of pulses emitted by the pacemaker is supposed to vary on a trial-to-trial basis according to a Gaussian law with mean a and standard deviation k . Hence, the number of pulses accumulated in STM t units of time since the time-marker onset is also a random variable, following a Gaussian law with mean at and standard deviation kat . A popular alternative to this “scalar” encoding scheme is the logarithmic encoding scheme, according to which the LTM representation $f(t)$ of an interval t is a random variable drawn from a Gaussian distribution with $\ln t$ and standard deviation k . It is used, notably, by BEM (Jozefowicz et al., 2009) and somehow by MTS (Staddon & Higa, 1999). BET (Killeen & Fetterman, 1988) assumes that a time marker triggers a series of ordered behavioral states. Transition from one state to the other is controlled by a Poisson process. In order to account for Weber’s law, the theory needs to postulate that the rate of the Poisson process is proportional to the reinforcement rate. LeT (Machado, 1997) uses a mathematically equivalent scheme.

While the issue of the LTM representation of time and the one of the decision process might appear to be separate questions, they are not, because Weber’s law is respected only for specific combinations of STM representation scheme and decision rule (Jozefowicz & Machado, 2013). In the case of cognitive

rules, for instance, it is well known that the Weber's law properties of timed behavior can be explained either by combining a logarithmic representation with a difference rule (a rule where the decision variable is a function of the difference between the STM representation of the time elapsed since the time-marker onset and the LTM representation of the time of reinforcement) or a scalar representation with a ratio rule (a rule where the decision variable is a function of the difference between the STM representation of the time elapsed since the time-marker onset and the LTM representation of the time of reinforcement). Combining a scalar representation with a difference rule or a logarithmic representation with a ratio rule does not work (Gibbon, 1981).

Although a full formal treatment is still lacking (see Jozefowicz & Machado, 2013 for further step in that direction), it seems that similar incompatibilities exist with associative decision rules. Obviously, a logarithmic representation scheme as well as Poisson timing process works, since they are used by BEM, BET, and LeT, which are all using associative decision rules. On the other hand, it seems that a scalar representation scheme does not work well when combined with an associative decision rule. Jozefowicz et al. (2009) showed that, if a scalar representation is substituted for a logarithmic one in BEM, the model fails to accurately predict psychometric functions in the bisection procedure, notably because Weber's law is violated. Similarly, Machado et al.

(2009) showed that a modified version of LeT, using a scalar representation instead of the original Poisson timing process, fares much more poorly than the original model when applied to data from the peak procedure and the bisection one.

Roberts (2006) trained pigeons to emit one response when presented with a stimulus whose duration ranged from 1 to 8 s (respectively, 2 to 16 s) and another one when presented with a stimulus ranging from 8 to 16 s (respectively, 16 and 32 s). The closer the stimulus duration was to the category boundary (8 s in one condition, 16 s in the other), the worse the performance of the pigeons. The psychometric curves also displayed some systematic asymmetries. Roberts (2006) fitted those data with various models using associative rules and concluded that in all cases, a model using a logarithmic representation better accounted for the data, especially the asymmetries, than one using a scalar representation.

Yi (2009) used signal-detection theory to analyze the performance of rats submitted to a variant of the bisection procedure: a correct response was reinforced only after a random interval drawn from an exponential distribution (a so-called random-interval schedule of reinforcement). This allowed Yi (2009) to compute not only the probability of a correct response following a specific stimulus but also the rate at which the rats were responding. She postulated that different levels of response rate were akin to different thresholds in a signal-

detection model, which allowed her to plot ROC curves for her subjects. She showed that those curves were compatible with a signal-detection model assuming a logarithmic representation of time with constant variance and incompatible with a signal-detection model assuming a linear representation with a standard deviation proportional to the mean. Since models using associative rules are often formally equivalent to signal-detection theory as far as simple discriminations are concerned (models using a cognitive rule share the same relation with another psychophysical model: Thurstone's law of comparison; see Falmagne, 1985 for a review of that theory), Yi's data provide additional evidence that an associative decision rule is incompatible with scalar time representation.

18.3.2 Associative and Cognitive Accounts of the Time-Left Procedure

Hence, any argument in favor of an associative-response rule is an argument against a scalar representation of time, and so against the idea that interval timing relies on an internal pacemaker. On the other hand, any argument for a scalar representation is an argument against an associative-response rule (Jozefowicz & Machado, 2013).

The most convincing case for a scalar representation is usually considered to come from the time-left procedure, a complex paradigm invented by Gibbon and Church (1981). The basic idea is to compare the preference of the subject for an elapsing time-to-reinforcement $C-t$ on the so-called time-left side over a constant time-to-reinforcement S on the so-called standard side for various time t in a trial. If the subject always chooses the side associated with the shorter delay of reinforcement, it should prefer the standard side early in a trial, before switching to the time-left side. Moreover, if the subjects encode time linearly and use a ratio decision rule, they should be indifferent between the two responses when $(aC-at)/aS = 1$; that is to say, when $t = C-S$. On the other hand, if the subjects encode time logarithmically and use a difference decision rule, they should be indifferent between the two responses when $(\ln C - \ln t) - \ln S = 0$; that is to say, when $t = C/S$. Moreover, we can imply from this analysis that, if the absolute values of C and S are changed but their ratio is held constant, the location of the point of subjective equality should change only if the representation is linear (Gibbon & Church, 1981).

Gibbon and Church (1981) used two versions of the time-left task to test these predictions. In the first version, rats were first trained on two fixed-interval (FI) schedules: the time-left schedule, reinforcing responses C sec after trial onset, and the standard schedule, reinforcing responses S sec after trial onset. Then, as

the subject is already responding on the time-left side for t sec, it is given the opportunity to respond on the standard side. Using rats as subjects and with $C = 2S = 60$ sec, Gibbon and Church (1981) were able to show that the rats preferred the standard side for $t = 15$ sec, the time-left side for $t = 45$ sec, while they were indifferent between them for $t = 30$ sec (see Machado & Vasconcelos, 2006 for a replication in pigeons and Wearden, 2002 for an adaptation of the procedure with similar results in humans).

In the second version of the procedure (which used pigeons as subjects), the subject has continuously available the choice between the time-left and the standard side. At a random time t , a response on either commits it to that schedule. The reward is then delivered $C-t$ seconds later if the subject is committed to the time-left side, S seconds later if the subject is committed to the standard side. If preference for the standard side decreased as time in a trial increased, the point of indifference was located well before $C-S$ seconds. This result was also observed by Gibbon and Fairhurst (1994) and Cerutti and Staddon (2004) in pigeons and by Preston (1994) in rats; a similar bias was found by Brannon et al. (2001) in a time-left procedure in pigeons using number instead of time as the relevant dimension to solve the discrimination. Still, holding the C/S ratio constant, the switchover point changed linearly with C , allowing Gibbon and Church (1981) to conclude in favor of a linear representation of time.

Despite its methodological complexity, which may affect interpretations of performance in ways still little understood (see, for instance, the analysis by Cerutti & Staddon, 2004; Preston, 1994; Machado & Vasconcelos, 2006 and Vieira do Castro & Machado, 2010), the time-left procedure seems to offer a plausible way to compare linear and logarithmic representation, given that the subject uses a cognitive decision rule. But how would a model using an associative decision rule fare in the time-left procedure? Jozefowicz et al. (2009) looked at it in the case of BEM (see also Dehaene, 2001). In BEM, the STM representation⁴ x of an interval t is a random variable drawn from a Gaussian distribution with mean $\ln t$ and standard deviation k . The subject then retrieves $V_{TL}(x)$ and $V_S(x)$ —the payoff for picking, respectively, the time-left side and the standard side when the representation takes the value x , that it could have learned through a simple associative learning rule such as Bush-Mosteller. The subject simply chooses the side associated with the higher payoff. Overall, at the asymptote, we have

$$V_{TL}(x) = \sum_{i=0}^n P(x | t_i) I(C - t_i) \quad (18.1)$$

and

$$V_S(x) = I(S), \quad (18.2)$$

where $I(x)$ is the value of a reinforcer delayed by x units of time and $t_0, t_1, \dots, t_i, \dots, t_n$ are times in a trial where the subject had to choose between the time-left and the standard side. In the first version of the time-left procedure, where there are only three times like this, including one at $C-S$ and where $2S=C$, we have

$$V_{TL}(x) = P(x | t_1)I(C - t_1) + P(x | t_2 = C - S)I(S) + P(x | t_3)I(C - t_3). \quad (18.3)$$

If t_1 , $C-S$, and t_3 are far enough apart, the states x sampled at each of these three intervals will negligibly overlap. Hence, the value of the time-left side will roughly be equal to $I(C - t_1)$ at t_1 , $I(S)$ at $C-S$, and $I(C - t_3)$ at t_3 . In other words, the subject will prefer the standard side at t_1 , the time-left side at t_3 , and will be indifferent between the two at $C-S$. Interestingly, as shown by the simulations of Jozefowicz et al. (2009), as the number of times where the subject has the opportunity to choose between the time-left and the standard side increases (as is the case in the second version of the time-left procedure), the point of indifference shifts to display a strong bias toward the time-left side, a result found in all replications of the time-left procedure—but not predicted by SET. This bias is a consequence of the logarithmic representation used by the model. Yet, the point of indifference remains a linear function of C . Indeed, the predictions of the model concerning the location of the indifference point are very close to the data reported by Gibbon and Church (1981; see Jozefowicz et al., 2009).

Hence, the results for the time-left experiment are compatible with a model combining a logarithmic representation with an associative-response rule like BEM, but incompatible with a model combining a linear representation with a ratio cognitive rule like SET.

Moreover, the associative account predicts that the subject will need some experience with the choice procedure in order to learn the delay to reinforcement on both schedules at the various choice points. Previous training on the time-left and standard side outside of the context of a choice paradigm will not be sufficient. On the contrary, SET predicts that such a training will be sufficient, as it allows the subject to learn the various intervals on which its choice performance is assumed to rely. Machado and Vasconcelos (2006) tested those two accounts in a replication of the first version of the time-left procedure, using pigeons as subjects (see also Vieira de Castro & Machado, 2010). Overall, their results are not consistent with SET, as they showed that extensive experience with the choice paradigm is necessary for the pigeons to reach stable-state performance in the time-left procedure. On the other hand, after as few as nine choice trials (three for each value of t_i), the pigeons already preferred the time-left side more at t_3 than at t_1 , even though their preference for the standard side was more extreme than what it would be at asymptote. This seems to indicate some carry-over effect of the training of the time-left and standard schedules outside of the choice paradigm, an

effect not predicted by the associative rule. The transfer effect between choice and nonchoice procedures are overall poorly understood. At any rate, it would be interesting to see how an associative model (i.e., BET or LeT) using an alternative representation of time would fare in the time-left procedure.

Note that, except when explicitly mentioned, all the data discussed in this chapter have been collected on nonhuman animals, mainly rats and pigeons. Although human timing is thought to rely on the same mechanisms as timing in nonhumans (Allan, 1998), a critical difference between the two can be observed as far as the location of the bisection point in a bisection procedure is concerned. While it is usually located near the geometric mean of the two trained durations in animals (i.e., Church and Deluty 1977), it is usually observed near the arithmetic mean of the two trained durations in animals, although a few experiments have also reported a bisection point at the geometric mean (see Allan, 1998 for a review). These differences are still poorly understood, but they have one major implication. A bisection point at the geometric mean is highly suggestive of logarithmic encoding, just as a bisection point at the arithmetic mean is highly suggestive of a linear encoding. But if it is possible to reconcile a bisection point at the geometric mean with a linear encoding scheme (Gibbon, 1981), it is on the other hand impossible to reconcile a bisection point at the arithmetic mean with a logarithmic encoding. Hence, it strongly suggests that in some situations, at least,

humans encode time linearly. If arguments favoring an associative-response rule argue against a scalar representation of time, do arguments favoring a linear encoding of time argue against an associative decision rule? Not necessarily. One encoding scheme assuming a linear representation of time and compatible with an associative decision rule is one where the representation $f(t)$ of an interval t is a random variable drawn from a Gaussian distribution with mean at and constant standard deviation k . In order to get Weber's law, this scheme has to postulate, a little like in BET and LeT, that k is proportional to the rate of reinforcement⁵. The issue of whether the representation of time is affected by the reinforcement rate has been investigated in the animal literature and so far has received mixed support (see, for instance, Fetterman & Killen, 1995 and Oliveira & Machado, 2009 for positive evidence and MacEwen & Killeen, 1991 and Leak & Gibbon, 1995 for negative), but has received comparatively little attention in the human literature. Given the potential importance of this issue regarding the decision rule most appropriate to accounting for human timing, more research should perhaps be conducted on this topic.

18.4 Conclusion

All in all, the data reviewed in this chapter favor associative rules over cognitive rules, mainly because the latter are able to account neither for the effects of

reinforcement on timing nor for the contextual effects evidenced in the double-bisection procedure. Further theoretical additions would be necessary before cognitive rules could cope successfully with those two classes of phenomena. To deal with reinforcement effects, a rigorous theory of how response bias is affected by reinforcement needs to be developed. The double bisection effect is more challenging, as it will necessitate a profound revision of the mechanisms underlying the formation of the LTM representation of the time of reinforcement so as to include the possibility for context dependence. On their side, associative models need to improve their account of reinforcement effects on timing, notably by tackling the challenge of mixed FI schedules. Overall, we believe more research should be devoted to the study of reinforcement and contextual effects on timing. Few studies have yet been conducted on those two issues, and we hope to have shown in this paper that they provide a fertile ground to contrast opposing theories of interval timing.

Acknowledgments

J. Jozefowicz, laboratoire URÊCA, Université Lille Nord de France, Campus de Lille3, Villeneuve d'Ascq, France and Escola de Psicologia, Universidade do Minho, Braga, Portugal; A. Machado, Escola de Psicologia, Universidade do Minho, Braga, Portugal; J. E. R. Staddon, Department of Psychology and

Neurosciences, Duke University, Durham, North Carolina, and Department of Psychology, The University of York, York, United Kingdom. J. Jozefowicz and A. Machado were both supported by the Fundação para a Ciência e a Tecnologia as well as from the European project COST ISCH Action TD0904 "Time in Mental activity" (www.timely-cost.eu), J. E. R. Staddon by grants from Duke University. Correspondence concerning this article should be addressed to Jeremie Jozefowicz, laboratoire URÊCA, Université Lille Nord de France, Campus de Lille3, Villeneuve d'Ascq, email: jeremie.jozefowicz@univ-lille3.fr

{Notes_begin}

Notes

1. Note a time marker is defined behaviorally: tests may reveal that the time marker used by the controlling reinforcement schedule is not always the one used by the subject.
2. Machado et al. (2009) have suggested that SET could account for these results by combining a threshold biased by the difference in absolute reinforcement rate with memory stores that represent relative reinforcement rates, but careful quantitative analysis is needed in order to see if this explanation is adequate.

3. This explanation is actually much simpler than the convoluted Bayesian model provided by Jazayeri and Shadlen (2010). Moreover, this Bayesian account might actually be flawed, as shown by ???. These authors also provide an alternative explanation of the results by Jazayeri and Shadlen (2010), which is very much in line with the one proposed here.

4. The STM representation is discretized, so that $P(x/t)$ is different from 0.

5. Including rate of reinforcement in a timing model is tricky from a theoretical point of view, because the model must then define the averaging process—linear or exponentially weighted, over what window, etc.

{Notes_end}

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