

## COMMENTARY

# Responses Compete and Collaborate, Shaping Each Others' Distributions: Commentary on Boakes, Patterson, Kendig, and Harris (2015)

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Boakes, Patterson, Kendig, and Harris (2015) showed that schedule-induced drinking (SID), typically concentrated in the first half of the interpellet interval, is not moved there exclusively by competition from magazine entries, and that not all arbitrary responses can be maintained by adventitious reinforcement. They attribute such inferences to Killeen and Pellón (2013) and Patterson and Boakes (2012), and on that basis reject their explanation for the excessive nature of many adjunctive responses as a result of reinforcement. It is a mistaken attribution, as Killeen and Pellón emphasized that reinforcers act on many competing interim and terminal responses. That attribution is a minor oversight on the authors' part; their return to a discredited motivational account is, however, a major blunder. It discards the seminal recent advances in understanding the nature of schedule-induced responses (e.g., those of Patterson and Boakes), and even the positive contributions of their own article: Their data show very strong correlations between magazine entries and drinking, providing much more evidence for response competition than their microanalysis provides against it.

*Keywords:* adjunctive behavior, response competition, schedule-induced behavior, schedule-induced drinking

Scientific progress is seldom monotonic. Critical scrutiny of hypotheses by the community, the heart of science, generates flows of opinion more like the response of an underdamped control system to a step-input: An over extension away from received opinion, an over reaction back, with slowly subsiding waves of correctives oscillating around the asymptotic newly received wisdom—*asymptotic*, at least, until the next paradigm shift. Our literature recently evidenced such a dynamic concerning the provenance and causal factors involved in the many vigorous behaviors that accompany the delivery of reinforcers and unconditioned stimuli (generically, *phylogenetically important events*, or PIEs; Baum, 2005, 2015). The final word for the 20th century was Staddon's (1977) characterization of such unexpected guests to schedules of reinforcement as instrumental responses to motivational states that are newly induced by Pavlovian conditioning. Thus, periodic delivery of PIEs would induce appetites for water, wood, feces, bugs, exercise, blood, and other PIEs. This motive-induction results in the instrumental responses of schedule-induced

polydipsia (SIP; aka schedule-induced drinking SID), schedule induced-wood-chewing, -pica, -scratching, -wheel-running, and -aggression.

Two recent articles challenged that perspective on similar grounds by showing how SID can be punished, reinforced, and marked, as well as come under dynamic stimulus control—all in the same manners as do other instrumental responses. Killeen and Pellón (2013) took pains deconstructing each of Staddon's arguments, and demonstrated that schedule-induced behaviors (SIBs) and operant (instrumental) behaviors share many formal and functional properties. For example, SID can be systematically reduced by imposing lick-contingent delays in food delivery, with the effect not attributable to changes in interfood interval length, but rather dependent on characteristics of the delay and on animal's degree of hunger (e.g., Lamas & Pellón, 1995b; Pellón & Blackman, 1987). Lick-food delays have also been shown to slow SID acquisition as a direct function of the length of the delays (e.g., Lamas & Pellón, 1995a; Moran & Rudolph, 1980). The prejudice against conceiving of such adjunctive behavior as being reinforced by the primary periodic reinforcer (e.g., food pellets) had been the 20th century assumption by many (including one of the present authors) that a few seconds of "protective contingency" prohibiting direct contiguity of SIBs and reinforcer would be adequate to rule out explanation in terms of "adventitious reinforcement." However, Killeen and Pellón echoed Patterson and Boakes (2012) in noting that arbitrary responses such as lever-pressing could be trained under delays up to 30 s. Making a response more memorable makes even longer delays possible. Different SIBs may be intrinsically more or less memorable, and thus, have longer or

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shorter delay of reinforcement gradients. If they compete with one another for expression, those with the longest memorial gradients have competitive advantage earlier in the interfood interval. A simple model of this competition, similar to one at the heart of Staddon's (1977) temporal discrimination model, accounted for many of the data reviewed, including the distribution in time of SIBs, and their bitonic relation to the period of reinforcement.

Working along similar lines, Patterson and Boakes (2012) showed that SID was acquired more quickly at short interpellet intervals where accidental proximity to reinforcement was greatest, supporting the hypothesis of adventitious reinforcement. Conclusive evidence came from Patterson and Boakes's demonstration that two iconic effects of instrumental conditioning, blocking and marking, affect SID just as they do lever-pressing and key-pecking. All of the earmarks of an SIB being reinforced by proximity to primary reinforcers were present. All four authors agreed as well to the provenance of SIBs: Responses that the situation makes likely are apt to be strengthened by that reinforcer. For instance, rats normally drink after eating dry pellets, but not after consuming milk or wet mash, and SID is much more likely in the first case than in the latter two. Patterson and Boakes further asked why drinking did not occur most often near the expected time of food, and suggested that exploratory magazine entry ("focal search") competed effectively with it, to leave it regnant only during the early part of the period. They concluded "SID develops as a result of adventitious reinforcement by the next pellet of the licking that was initially evoked by the previous pellet" (p. 312). This was essentially Killeen and Pellón's (2013) model of elicitation and reinforcement as prime causal factors, with competition by a panoply of behaviors, each reinforced through different delay gradients by the primary schedule reinforcer, affecting its distribution in time. This hypothesis subsequently was supported by Pellón and Perez-Padilla's (2013) demonstration that SID and lever pressing showed differential sensitivity to delays in food imposed between the last response of either category and food delivery, with lever pressing reduced at much shorter delays than licking. In terms of the Killeen-Pellón theory, drinking manifests a much shallower but longer gradient than lever pressing.

### Analyses of Boakes et al. (2015)

The recent article by Boakes and associates (2015) is a reaction—an oscillation back to the status quo ante—from the above paragraphs. Their experiments were triggered by re-examination of an article (Shurtleff, Delamater, & Riley, 1983) that showed virtually identical distributions of SIP under periodic (a Fixed-Time, or FT 60-s), random (Random Interval, or RI-60 s), and irregular (Variable-Time, or VT-60) schedule of pellet delivery (see Figure 1). This presented "a challenge to Patterson and Boakes' (2012) proposal that the distribution of licking produced by fixed interpellet intervals is a result of competition from the development of magazine entries at the end of an interval" (Boakes et al., 2015, p. 53), because if that were true, licks should be concentrated in the first half of the period under the FT schedule, and "spread fairly evenly" in the case of the VT schedule—and they were not.

Comparison of Shurtleff and associates' (1983) Figure 3 with Figure 3 of the target article, panels from which are reproduced in Figure 1, shows a marked failure to replicate. The former showed the same peak licking of 5 licks/s (Lps) at 25% of the way into the average interpellet interval on all schedules; indeed, their three distributions lay atop one another at almost every point through training. In contrast, the FT distributions in the target article were strongly peaked, and by the end of training the VT distribution fell smoothly from about 0.3 licks/s to 0 at 60 s. The distributions of licks evolved with training sessions, but at no point resembled those of Shurtleff et al., and generally involved only about 1/10th as many licks.

Rather than consider this a failure to replicate what were in any case atypical findings, protecting Patterson and Boakes (2012) from that threat, they interpreted their data as a refutation of Patterson and Boakes's competition hypothesis—that is, that magazine entries (ME) were a causal factor in giving shape to the SID distributions. This is because, despite substantial correlations between licking and ME, the correlations were less than perfect: "the most important finding from this [first] experiment was that within 11 to 15 sessions, the VT-water rats began to concentrate their licking early in an interval, even though the distribution of their magazine entries—ignoring the first 5 s—remained flat for 15 sessions." p. 56. They view this as inconsistent with

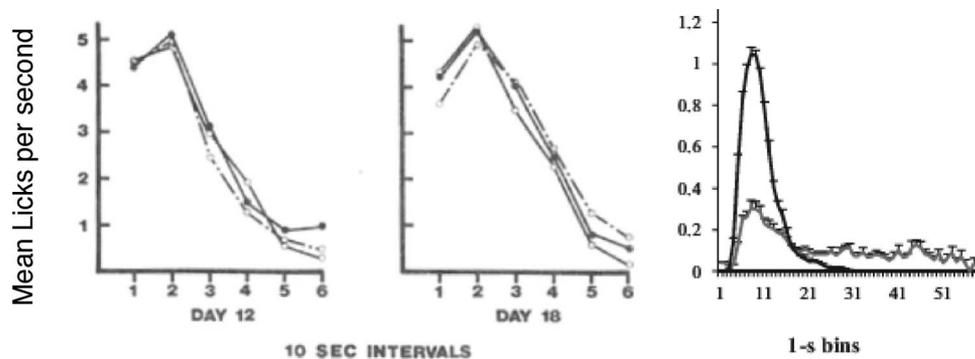


Figure 1. Left and center: Panels from Shurtleff and associates' (1983) Figure 3 showing the distribution of licking on FT 60, RT 60, and VT 60 schedules (responses for the RT and VT intervals beyond 60 s are plotted in the 6th bin). Right panel: Data from Experiment 1 of Boakes and associates over Sessions 16–20 on FT and VT 30 schedules. Note the different range for the ordinates. Figure 1 reprinted with kind permission from Springer Science and Business Media.

a competition explanation of the distributions. However, abstracting those key data from the top right panels of Figures 1 and 3 (Sessions 11–15), we find that the slope for licking is  $-0.00113$  Lps, and that for ME was  $+0.00120$  entries per second (Eps). They are almost exact mirror images.

How did the authors of the target article come to their asymmetric conclusion despite these very symmetric data? They did so by normalizing the slopes over seconds 6–29 by the mean Lps or Eps over those ranges (using their “See-Saw Ratio,” or SSR). This differentially decreased the slope of the more vigorous ME, making it seem flatter than it was. However, if responses are competing for expression, it throws away key data: What is relevant is *how much* of one or the other is present, not relativized changes in their rates.

The “second important finding” of Experiment 1 was that licking started to depart from a uniform distribution in the FT group before ME did. We fit learning curves to their SSR and confirm their analysis: Those curves exceeded 0.5 (level for their SSR) by the end of the first session for L, but not until the third session for ME. In those sessions ME was occurring at five times the rate of L; therefore, a 10% shift in the slope for ME that brought it up to a SSR of 0.5 would leave sufficient uncontested time for a fivefold change in licking, bringing it well beyond 0.5. The SSR handicaps most vigorous response and seriously misleads the key inference of the authors. It is a matter of indifference to us, however, who did win this race to disequilibrium, as we have no stake in it. That reality will be discussed below in conjunction with the last figure in this article, after further reviewing of the Boakes and associates’ article.

Boakes and associates (2015) conclude their discussion of Experiment 1 with: “the results of this experiment do not support the proposal that competition from the development of magazine entries toward the end of an interval causes licking to be concentrated early in an interval” (p. 57). The authors, however, offered no other explanation for the correlations carried by their Figure 2 that ranged from 0.64 to 0.86, and look to us to be good evidence for competition. The authors went on “On the other hand, under VT conditions, SID early in an interval may effectively compete with magazine entries.” Well it takes at least two to compete. Perhaps the authors meant “suppress.” However, that is belied by their own data, as all panels of their Figure 1 show that ME for VT-Water lay everywhere *above* those for VT-Dry; along with competing with ME, SID is apparently cooperating with it, enhancing the reinforcing effectiveness of dry pellets, and thus exerting in turn a positive incentive motivational effect on ME.

In Experiment 2, Boakes and associates (2015) compared licking on the protruded tube used in their first experiment with licking on one made less salient by recessing it into the wall of the chamber. The manipulation failed its intent, as the authors recorded twice as many licks to the recessed spout as to the protruding one (such recession typically reduces drinking; Weijnen, 1998). The experiment constituted nonetheless a useful manipulation of one of two competing responses. The authors main conclusions were that “there was no support for the response competition account [using the SSR], whereby ME distributions were expected to sharpen prior to those of the L distributions.” This race of SSRs was reported won between Sessions 5 and 9 over the region of interest from 6 to 29 s. The correlation between L and ME rates (top center panels of their Figures 4 and 6) over that range was  $-0.87$  for the recessed spout, and  $-0.91$  for the protruding spout. Those relations constitute, in our eyes, very strong

support for a hypothesis that these responses compete. If they do not, then a third factor must be adduced that influences both in coordinated, reciprocal, and precise fashion. We prefer the simpler explanation that rats cannot be in two places at the same time.

In their Experiment 3, Boakes and associates pretrained a lever-pressing response, and their “first important finding” was that lever-pressing was not maintained when reinforcement was not contingent on it. This shows that not all responses can be sustained by adventitious reinforcement. Although this is not news (Catania, 2005), it is a helpful reminder in the context of this discussion that arbitrary responses will not be sustained without a contingency between them and reinforcement, especially when other competing responses such as ME enjoy that contingency. Which responses can and which cannot be sustained by noncontingent reinforcement? Seligman (1970) named the dimension of differential susceptibility to reinforcement “preparedness.” What makes a response prepared is presumably its natural location in the behavioral system (Timberlake & Lucas, 1989) induced by the deprivation and reinforcement context. There is a large body of experiments and anecdotes of prepared responses that are not required for reinforcement displacing arbitrary responses such as operating a lever (Boakes, Poli, Lockwood, & Goodall, 1978; Breland & Breland, 1961). Some examples of responses that may be sustained and often amplified by noncontingent reinforcement are given in Figure 2.

The second important result of Experiment 3 was that the VT-lever group peaked “in the same 5–15 s postpellet interval at which licking peaked in the previous experiments . . . they were unlikely to have been produced by competition from magazine entries because distributions of magazine entries remained fairly flat for at least eight sessions.” Inspection of Figure 7 shows that the largest peak of VT lever-pressing occurred at the end of training; analysis of that epoch shows the correlation between VT lever-pressing and ME to be  $-0.90$ . Looks like competition to us.

Why was VT responding not flat? Because the progression that the authors used was arithmetic, it contrived an increase in probability of reinforcement with time. The probability of reinforcement was 0 for the first few seconds postpellet, and increased as a staircase to 60 s where it became 1.0 (because that was the longest interval, when rats made it that far reinforcement was guaranteed

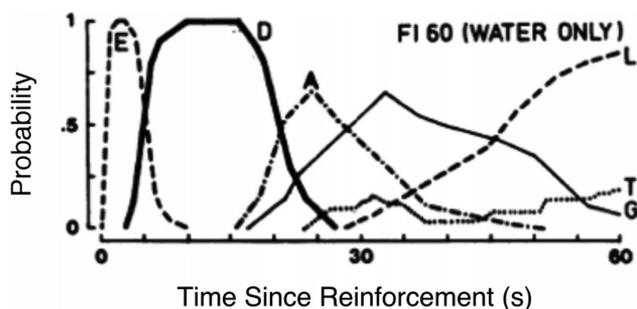


Figure 2. Relative frequency of occurrence in each 1-s bin of various activities for one rat on a FI 60 s reinforcement schedule (from Roper’s, 1978 Figure 6). The symbols initial Eat, Drink, Activity (general), Groom, Tray visit, and Lever press. A prior condition also offered a wheel, which for this animal led to the complete suppression of drinking by running. Figure 2 reprinted with permission from John Wiley & Sons, Inc.

in the next second.) Conversely, the probability of nonreinforcement decreased from 1.0 after a pellet to 0 after 1 min: The probability of drinking largely followed suit.

### The Temporal Discrimination/Motivation Hypothesis

Staddon (1977) suggested that during periods of low reinforcer availability other motivations would be induced, such as thirst, leading to SID. A variant of this hypothesis was advocated in the target article, whose discussion contrasts it with the reinforcement account, and concludes with: “as Staddon (1977) implied, learning that a pellet is unlikely to be delivered shortly after the previous pellet converts postprandial drinking into a motivational state akin to thirst produced by water deprivation.” However, Staddon associated the hypothetical induced states with temporal epochs; not, as we read him in this case, conversion of “post-prandial drinking” itself “into a motivational state akin to thirst.” Because the authors of the target article labeled theirs a temporal discrimination account, we proceed under the assumption that they intended it to be the temporal conditional stimulus (CS) epoch that induced thirst, not the drinking associated with it that made drinking a motivational state that induced drinking; for SID may be generated when no postprandial drinking is allowed (see below).

If the temporal discrimination/motivation (TDM) hypothesis were true, SID should be greatest at the very longest interpellet intervals, where the discrimination is most powerful. It is not (Flory, 1971), nor is it in islands of low probability (e.g., Corfield-Sumner, Blackman, & Stainer, 1977; Minor, 1987). The operant model of Killeen and Pellón (2013, Figures 5, 6, and 7) accommodates the observed bitonic function between period and consumption, whereas the TDM has not. SID does not appreciably vary as a function of water deprivation (e.g., Roper & Posadas-Andrews, 1981) or pre-experimental water preloads (e.g., Porter, Young, & Moeschl, 1978). It varies strongly with food deprivation, as increasing deprivation makes the forthcoming pellet a more potent reinforcer. This speaks against the motivational account.

With regard to Lashley and Rosellini’s (1980) Pavlovian CS-variant of the temporal discrimination hypothesis, favored by Boakes and associates (2015), we are unaware of any experiment that has shown elicitation of licking by placing an inhibitory CS on top of a feeding schedule. We doubt that such a result could be found, apart from the postfood period itself. Quite the contrary, some results have shown that the introduction of excitatory CS+ stimuli on a feeding baseline can enhance drinking (Plonsky & Rosellini, 1986). A number of experiments have shown that drinking can be moved to portions of the interfood interval closer to next food delivery by simply impeding the possibility of drinking in the postfood period (Avila & Bruner, 1994; Gilbert, 1974; López-Crespo, Rodríguez, Pellón, & Flores, 2004). These latter epochs are associated with a greater proximity to food. Finally, SID is not reliably obtained after conditioned reinforcers (in comparison to primary reinforcers), even though both might be equally informative about the improbability of food delivery (Corfield-Sumner et al., 1977).

There is recent evidence that ME during a CS has Pavlovian aspects (Harris, Andrew, & Kwok, 2013) analogous to those shown to share control over pigeons’ key pecking during a CS (Killeen, Sanabria, & Dolgov, 2009). There are also Skinnerian

aspects, as ME in the current studies is on an FI schedule with reinforcement contingent on the last such response in a trial. Its distribution late in the trials of the target article looks much like the distribution of lever-pressing when that is the contingent response. However, the argument in the target article concerns the nature, causes, and distribution of SID, not ME. SID most certainly originates as an unconditioned response (UR) to the dry food pellet, just as the “area-restricted search” of ME during the several seconds after pellet delivery is also a UR. It is our argument that both are amplified by the delivery of the ensuing pellet, and that SID has the advantage at longer delays over arbitrary responses such as lever presses, and over ME whatever its blend of Pavlovian and Skinnerian causal factors.

No hypotheses exist in a vacuum; they are evaluated with respect to other hypotheses that attempt to cover the same data. Therefore, it is not enough to raise our concerns with the TDM hypothesis, but need must also restate why we think the reinforcement model provides a better way to think about these rich data sets.

### The Competition/Reinforcement Model

We do not believe that the authors make a strong case against competition between goal-tracking and SID; on the contrary, we believe that their data speak *for* such competition. However, we also do not think that that is the whole story. It was against the hypothesis of Patterson and Boakes (2012) that their conclusions are aimed; yet they generalized it to all kindred accounts of reinforcement and competition. Contra Patterson and Boakes, in fact, magazine entry is not the only behavior that might compete with SID. Shettleworth (1975) found different action patterns emerging and receding over the course of conditioning. As Killeen and Pellón (2013, p. 14) noted, “. . . chance and history play an important role in which members of a class prevail. Once fate smiles on one action pattern, its emission, followed (even remotely) by reinforcement, will increase its frequency. Moore (1973) calls this a ‘Pavlovian trapping mechanism, which leads to instrumental learning’ (p. 175), a process also proposed by Bindra (1972).” Reid, Bacha, and Morán (1993) showed how the distributions of these behaviors reflected an averaging over trials where some were much more dominant, and in others the same behaviors subservient: In other words these distributions are averages over dynamically changing fields of dominance. The “same” instrumental response may consist of different forms, or styles, each with a different time course of associability. Gallo and associates (Gallo, Duchatelle, Elkhessaimi, Le Pape, & Desportes, 1995) found that on schedules of continuous reinforcement, rats emitted 14 actions around a lever, with the lever pressing comprising three of those disparate actions. Powell and Curley (1976) showed that adjunctive behavior such as scratching and biting would displace lever pressing by gerbils as fixed-ratio requirements were increased. An additional score of articles were cited attesting to the wide range of adjunctive behaviors found on reinforcement schedules, many noting the competition among them for expression (e.g., Boakes et al., 1978), with some of those responses overshadowing a Pavlovian CS (Shettleworth, 1981). Whenever people have looked, they have seen invigoration of responses that were not required for reinforcement; Figure 2 provides one example among many possible.

Not only can SIBs block control by a CS and be blocked by a CS (Patterson & Boakes, 2012), they can play a functional role in instrumental performance. Fetterman, Killeen, and Hall (1998) showed that adjunctive responses may come to serve as discriminative stimuli in timing a 6 s versus a 12 s interval. Mouthing the dispenser (analogous to Boakes and associates “magazine entries”) and sniffing at the *short* lever were associated with pressing the short lever when the interval ended; moving to the long lever and sniffing it were associated with a judgment of *long*. Prediction of their performance was much more accurate when based on their SIBs than when based on clock time. This protean nature of behavior—invoked by a prior PIE, species-typical, shaped by proximity to a subsequent PIE, with strong predilections to sign and goal tracking (Boakes, 1977; Burns & Domjan, 1996), and usable as a discriminative stimulus in its own right, explain some of the creativity of behavior and at the same time the difficulty of subjecting it to monothetic explanatory schemes (Killeen, 2014).

### The Competing Traces Model

The authors of the target article held the most important finding from Experiment 1 to be that “within 11 to 15 sessions, the VT-water rats began to concentrate their licking early in an interval, even though the distribution of their magazine entries—ignoring the first 5 s—remained flat for 15 sessions.” Figure 3 shows the data they reported from those sessions, with the licking of the VT water rats drawn as inverted triangles, and their ME shown as squares. Also shown for comparison are the FT licking data (circles). The model of Killeen and Pellón (2013, Equation 4) drew all three curves using all the same parameters but for one: The scale factor for ME was 0.67, reduced from the value of 1.0 for the other curves. The details of this model, which assumes that responses classes have delay of reinforcement gradients differing in slope and intercept, are given in the Appendix. Parsimonious and

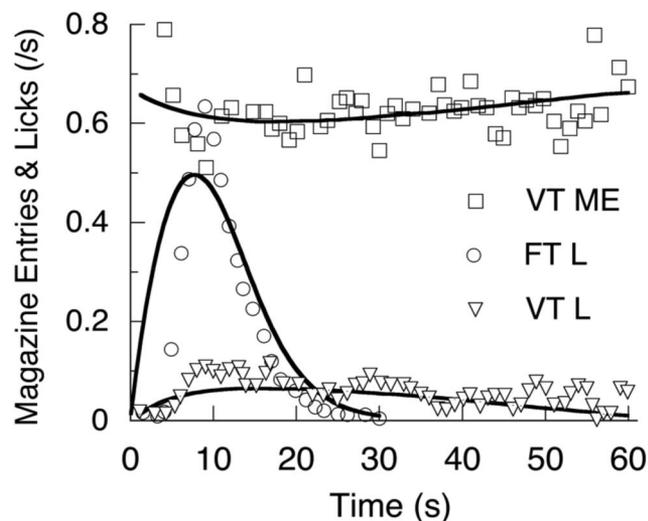


Figure 3. Data from Sessions 11–15 of Boakes and associates (2014) Figures 1 and 3. Curves are from the competing traces model of Killeen and Pellón (2013), using all the same parameter values (except for the scale of ME), under the assumption that there are no other competing responses. See Appendix for the model.

providing a good description of the data, the fit of model to data is nonetheless imperfect: Around 10 s into the trial the VT L data lie systematically above the model, and the VT ME data lie below the model. The latter deviation, however, is not so sustained as the former, causing the SSR to deviate from 0.5 more for VT L than for VT ME. This figure cannot show the predictions of the temporal discrimination/motivation model, and what deviations, if any, they incur.

Why should the licking data deviate above the trace of the model around 10 s into the trial (and do so to a greater extent in the subsequent sessions)? The model describes data under the assumption that all key competitors are entered into the equations. The authors of these data did not record other behaviors; if they had, we suspect that they would have measured activities that competed with drinking around 20 s into the interval, as the A trace in Figure 2 seems to, and as the affordance of a wheel for running did for that rat in another condition.

### Conclusion

We believe that the implications drawn by Boakes and associates (2015) were an overreaction. Instead of simply recognizing once again that water complements dry pellets, and it is reasonable for rats once in a consummatory mode to take a sip after a chew before going back to focal search, they changed opinion back to the motivational hypothesis, concluding that: “learning that a pellet is unlikely to be delivered shortly after the previous pellet converts postprandial drinking into a motivational state akin to thirst produced by water deprivation.” We think this unlikely for many reasons, noted by Patterson and Boakes (2012), reviewed in the section on motivation in Killeen and Pellón (2013), and mentioned above.

Boakes and associates (2015) were not the only researchers to find a negative correlation between magazine entries and SID. That there is such competition, and that it can be powerful, is evidenced both by their data and by the astonishingly high correlation between rats’ head-in-hopper time and amount of water consumed from one interval of FT 60 to the next ( $r = -.95$ ) reported by Reid and Dale (1983). Boakes and associates did not monitor any of the other SIBs that were undoubtedly occurring during these schedules, which the literature has shown can compete effectively among themselves and with other operants. We conclude from their data that drinking became excessive under the FT schedule as a result of adventitious reinforcement, and that it was displaced by magazine entries that were reinforced toward the end of the FT, and throughout the VT, along with, in all likelihood, other adjunctive responses, and simple locomotion. Their data show that SID developed more slowly than ME in terms of peak heights. Learning is retarded when reinforcement is delayed (see, e.g., Killeen & Pellón, 2013, Figure 1) and as SID becomes sequestered toward the start of the interval, it incurs longer delays of reinforcement. Any argument both that SID and ME should be learned with equal speed, and that they were the only behaviors that compete for expression, would be disproved by the less-than-perfect negative correlations found in the data reported in the target article. Any argument that SID and ME did not compete, would need another mechanism to explain the many correlations between them those authors observed that were nudging  $-0.9$ .

There is a substantial literature showing that SIB covaries with motivational operations on the primary reinforcer (e.g., hunger for pellets), not the SIB (for the latest installment, see Castilla & Pellón, 2013). In a 3-hr session rats will consume up to 50% of their body weight in water. Scaled up to your size, this is more water than you could carry for more than a few steps. Having consumed that much water, we think it unlikely that a signal that food is not immediately forthcoming would shift you into a motivational state akin to thirst produced by water deprivation, or that postprandial drinking itself could be transformed into such a motivational state. We could be wrong. We do know that neutral signals that food is unavailable do not elicit drinking. It is natural for food and drink to go together, and that explains the origins of SID as a postpellet phenomenon. It does not explain its excessiveness. That, as we and Patterson and Boakes agree, is because of the entrainment of such responses by the primary reinforcer—to conditioning.

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## Appendix

### The Competing Traces Model

Delay of reinforcement gradients are assumed to be exponential in shape, with amplitude  $a$  and rate of decay  $\lambda$ . Although they are to be conceptualized as a decaying trace of memory of the response, giving its residual strength  $S$  at the time of reinforcement, it is convenient, and mathematically equivalent, to treat them as taking the argument of time-to-reinforcement, rather than time since response (Killeen, 2011). For ME, this is

$$S_{M,t} = a_M e^{-\lambda_M(T-t)} \quad (\text{A1})$$

where  $t$  is time through trial, and  $T$  is the time at which the reinforcer is delivered. A similar equation is written for drinking, and their relative strength  $s$  is computed as the proportion

$$S_{D,M,t} = \frac{a_D e^{-\lambda_D(T-t)}}{a_D e^{-\lambda_D(T-t)} + a_M e^{-\lambda_M(T-t)}} \quad (\text{A2})$$

Dividing through by the numerator permits us to reduce the four parameters to two

$$S_{D,M,t} = \frac{1}{1 + a e^{-\lambda(T-t)}} \quad (\text{A3})$$

with

$$a = a_M/a_D, \lambda = \lambda_M - \lambda_D \quad (\text{A4})$$

Equation A2 is Killeen and Pellón's (2013) Equation 3.

There is another strong competing response not under the control of the forthcoming reinforcer, but of the last reinforcer. This is ME caused by postprandial investigation of the magazine (MPP) that competes strongly with all other responses. Although for symmetry this should simply appear in the denominator as  $a_{MPP} e^{-\lambda_{MPP}t}$ , to remain consistent with Killeen and Pellón, and to save a gratuitous parameter (an arbitrarily large value for  $a_{MPP}$ ), we incorporate that as a numerator in A2

$$S_{D,M,t} = \frac{k(1 - e^{-\lambda_{MPP}t})}{1 + a e^{-\lambda(T-t)}} \quad (\text{A5})$$

The parameter  $k$  is a scale parameter that adjusts for the calibration of the measurement instrument. This is the equation that drew the curve for the FT 30 licking shown in Figure 3, using the parameters  $k = 1$ ,  $\lambda_{MPP} = 0.13/s$ ,  $a = 66$ , and  $\lambda = 0.224/s$ .

To compute the strength for the VT schedule, think of it as an embedded set of probabilistic FT schedules. If the VT is, say an arithmetic progression with  $N = 10$  intervals of  $T_i = 6, 12, \dots, 60$  s, then for the first 6 s interval evaluate the 10% probability of food

(Appendix continues)

at 6 s, the 10% probability of food at 12 s, 10% at 18 s, and so on out to 60 s. Because the process is symmetric for competing responses, we may focus on the denominator of A5, and write it for the first interval on the VT

$$1 + \frac{1}{N} \sum_{i=1}^N ae^{-\lambda(T_i-t)} \tag{A6}$$

if the first interval doesn't deliver, then when  $t$  exceeds  $T_1$ , the probability that each in succession will pay off increases to 1-in-9, and the denominator becomes

$$1 + \frac{1}{N-1} \sum_{i=2}^N ae^{-\lambda(T_i-t)} \tag{A7}$$

We continue this process until we reach the last interval. Although with some spreadsheet ingenuity this is not a difficult computation, it may be made simpler by idealizing the VT as having as many intervals as seconds in the longest interval  $T$ , and evaluate at every second. Then the probability of reinforcement at the end of that second is  $1/(T-t+1)$  up to  $T$ , and rather than a series of piecewise summations, the denominator becomes

$$1 + \frac{1}{T-t+1} \sum_{i=t}^T ae^{-\lambda(T-i)}, \text{ for } t \leq T \tag{A8}$$

At this grain size of 1 s, it would be simplest to replace the summation by an integral, but the readers will not be further taxed with that nuance.

Equation A5, with Equation A8 as its denominator, drew the curve through the VT L data using the same parameters as given above.

To predict ME, we must switch the terms in Equation A2. That is simply achieved by using  $1/a$  rather than  $a$  in Equation A8, and  $-\lambda$  in place of  $\lambda$  in Equation A8. With those substitutions, and the same values for the constants except for  $k$  (reduced to 0.67), Equation A5 with Equation A8 as the denominator drew the curves through the ME data in [Figure 3](#).

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