Towards a Mathematical Model of Within-Session Operant Responding

Estêvão G. Bittar and Kleber Del-Claro
Universidade Federal de Juiz de Fora

Lucas G. Bittar and Michelle C. P. da Silva
Universidade Federal de Uberlândia

Operant response rate changes within the course of a typical free-operant experimental session. These changes are orderly, and reliably demonstrated with subjects from different species, responding under different experimental conditions. Killeen (1995) postulated that the response rate changes are a function of the interplay between arousal and satiation and offered a mathematical model for this hypothesis. Here we analyze Killeen’s model, demonstrating that, although solid in its principles, it presents some flaws in its implementation. Then, based on the same principles, we build and test a new model of withinsession motivation dynamics. We also demonstrate that, by representing arousal as a variable that ranges between 0 and 1, we can obtain a surprisingly simple model of free-operant response rate.

Keywords: response rate, motivation, arousal, satiation, models

Supplemental materials: http://dx.doi.org/10.1037/a0029086.supp

What are the processes that underlie operant responding? According to Killeen (1994), they are three: arousal, coupling, and time constraints. Behavior is fueled by arousal, constrained by time, and directed by coupling. In an impressive effort, Killeen offered formal models for each of these factors and combined them in an integrative theory called mathematical principles of reinforcement (MPR; Killeen, 1994; Killeen & Sitomer, 2003).

In 1995, Killeen made an attempt to use MPR to account for withinsession changes in operant responding. At that time, McSweeney and her colleagues had already demonstrated that, within the course of a typical free-operant experimental session, response rates show changes that sometimes exceed 450% (McSweeney, Hatfield, & Allen, 1990). Moreover, they demonstrated that these within-session changes in response rates are orderly, generally increasing, decreasing, or increasing up to a peak and then decreasing (McSweeney, Hatfield, & Allen, 1990; McSweeney & Hinson, 1992; McSweeney, Roll, & Weatherly, 1994). These variations are reliably demonstrated with subjects from different species, responding for different reinforcers, operating different operanda, under different rates of reinforcement and under different schedules of reinforcement (McSweeney & Hinson, 1992; McSweeney, Roll, & Weatherly, 1994; McSweeney, Weatherly, & Swindell, 1995b; Roll & McSweeney, 1997).

Because coupling (the association of response and incentives in an animal’s short-term memory [STM]) and time constraints remain relatively constant throughout the course of an experimental session, Killeen (1995) began applying MPR to within-session responding by assuming that the observed changes in response rate must be related to variations in the subject’s arousal as time elapses and more reinforcers are presented and consumed. Next, he expanded his arousal model to present a full description of how arousal first accumulates and then dissipates as the session progresses toward its end. In this article, we revise Killeen’s (1995) model of arousal as applied to within-session responding and discuss how it can be possibly improved. Then, we suggest a new model and test it using behavioral data from our own laboratory as well as data from different researchers.

Modeling Arousal

The model of arousal built into MPR preceded MPR’s elaboration by several years (Killeen, Hanson, & Osborne, 1978). It was first presented to account for adjunctive behavior that generally arises when subjects respond under an intermittent schedule of reinforcement (Falk, 1961; Falk, 1972; Wallace & Singer, 1976). Killeen hypothesized that “adjunctive behaviors are normally occurring parts of an organism’s repertoire, but that their rate of occurrence is excited to supernormal levels by a heightened level of arousal” (Killeen et al., 1978).

As a first step to the construction of his arousal model, Killeen et al. (1978) showed that the presentation of a reinforcer to an organism elicits a state of arousal that decays exponentially over time. If a new reinforcer is presented during this decay, the arousal elicited by the second reinforcer adds to what’s left of the arousal elicited by the first, promoting an accumulation of effects. In a session where various reinforcers are successively presented, the average arousal A at time t is given by the following equation (Killeen et al., 1978):

\[ A_t = aR(1 - e^{-t/\mu}) \]

where \( R \) is reinforcement rate, \( Q \) is the jolt of arousal engendered by each reinforcer, \( \mu \) is the time constant that controls decay of...
arousal, and \( a \) represents the total time of activation elicited by each reinforcer.

The cumulative process suggested by Equation 1 is depicted in Figure 1A. The vertical lines represent the impulse \( Q \), which decays exponentially according to \( \mu \). The integral of the decay curves is given by \( Q \mu \), justifying the interpretation given to parameter \( a \). Because Equation 1 describes the average arousal between reinforcers, the curve generated by it would lie just below the bold curve that touches the arousal peaks.

Applied to within-session responding, the accumulation of arousal may explain the early session increases in response rate (Killeen, 1995). Such warm-up effects failed to be explained by training effects, recovery from handling, and habituation of exploration (McSweeney & Johnson, 1994; McSweeney, Swindell, & Weatherly, 1998; Roll & McSweeney, 1997). According to Killeen (1995), warm-up occurs when successive reinforcers drive the organism to an increasingly high activation state. In support of this hypothesis, it should be noted that within-session responding peaks earlier when reinforcers are scheduled to be presented at high frequency (McSweeney & Hinson, 1992).

Besides its utility, Equation 1 is incomplete. It disregards the loss of reinforcer efficacy that inevitably occurs across successive presentations as a result of processes such as satiation and habituation. Those processes are generally claimed to be responsible for the late session decreases in responding observed in many operant sessions (DeMarse, Killeen, & Baker, 1999; Killeen, 1995; McSweeney, 2004).

Seeking to incorporate satiety effects in his arousal model, Killeen (1995) postulated that, across an experimental session, a linear decrease in deprivation \( (d) \) occurs as a function of time. He also postulated the existence of a motivational drive \( (h) \) linked to deprivation in a simple linear or exponential relation. The linear case would be expressed as \( h_t = \gamma d_t \), where \( \gamma \) is a proportionality constant. The exponential case would be expressed as \( h_t = e^{\alpha d_t} - \Theta \), where \( \Theta \) represents a minimum threshold that must be exceeded before responding is initiated. Finally, he suggested that the motivational drive \( h \) combines multiplicatively with the value \( (v) \) of the reinforcer to determine the reinforcer’s specific activation \( a \), so that \( a = vh \). Consequently, Equation 1 must be rewritten as:

\[
A_t = v h R (1 - e^{-\theta t}).
\]  

The model entailed in Equation 2 is depicted in Figure 1B and 1C. Panel B describes the accumulation and decay of arousal considering a linear decay of \( h \). Panel C describes the same process, but assuming an exponential decay of \( h \). Again, the curve generated by Equation 2 is not depicted in the figure, but it would follow closely below the thick lines that touch arousal peaks.

Figure 1. Models of arousal. The ordinates represent the animal’s arousal level, and the abscissas represent time. The vertical lines illustrate the jolt of arousal elicited by each reinforcer, which decays exponentially as demonstrated by the thin lines. Successive presentation of reinforcers produces an accumulation of effects, resulting in an average level of arousal approximated by the thick line. A presents the seminal model of Killeen et al. (1978), where the jolt of arousal is constant. In B and C, arousal is pushed down by satiation-based drive decay (Killeen, 1995). Drive decays linearly in B and exponentially in C. D represents the model elaborated in the present study. Note that, in D, the thick line does not violate the thin lines of arousal decay.
The Modeling Mistake

Although capable of drawing a bitonic function of arousal along successive reinforcers, Equation 2 presents a modeling mistake. After the peak, the arousal curve is pulled down by the increasingly smaller motivational drive \( h \). As it can be seen from Panels B and C of Figure 1, the general arousal \( A \) assumes a null value when \( h \) comes to 0. However, because arousal elicited by each reinforcer decays exponentially, and because exponential decay curves never reach 0, the general arousal \( A \) could never be completely extinguished.

The reason why Equation 2 produces such a distortion is because all the terms in it are multiplied by the motivational drive \( h \). Drive \( h \) is a direct function of deprivation \( d \). Therefore, it decays as deprivation does. However, as we can see from Figure 1B and 1C, at some point each new reinforcer will begin to reduce the general arousal, producing some sort of “negative arousal.” This moment is represented in Figure 1 as the point where the thick line (which illustrates the general level of arousal) crosses the thin lines (which illustrate the course of the arousal elicited by each reinforcer). After this point, the vertical lines that illustrate the jolts \( Q \) of arousal and that always depart from the remaining arousal from the previous reinforcer would be representing a subtraction of arousal. It could be argued that, after satiation, the reinforcing stimulus becomes aversive, inhibiting instrumental behavior. But this argument would be invalid for two reasons. First, the subtraction of arousal occurs significantly before drive \( h \) reaches a null value. Second, in the context of a free-operant session where subjects work to produce reinforcers, after the crossing point they would be working to produce aversive stimuli—if we assume arousal to be related to operant responding, as Killeen (1994) does. Given the problems entailed in Equation 2, we propose a new model of the dynamics of arousal.

Fixing the Bug

To offer a new model of arousal, we first return to Killeen’s model of arousal as originally presented (Killeen et al., 1978). Immediately after the presentation of a reinforcer, the animal’s level of arousal \( A \) will be given by:

\[
A_1 = Q,
\]

where \( Q \) is the jolt of arousal engendered by the reinforcer. The quantity \( A_1 \) will decay exponentially over time, according to the function

\[
A_t = A_1 e^{-\frac{t}{\beta}},
\]

where \( \beta \) is the exponential time constant.

If we assume that satiation decreases the arousing effect of reinforcers, we must consider that, when the next reinforcer is presented, quantity \( Q \) will be slightly smaller. If we assume that \( Q \) also decays exponentially, then

\[
Q_n = Q e^{-\frac{n}{\beta}},
\]

where \( n \) is the number of reinforcers previously consumed and \( \beta \) is a constant that dictates how fast satiation proceeds. When \( n = 0 \), \( Q_0 = Q \).

Considering Equations 4 and 5, at the time a second reinforcer is presented, the arousal level of the subject will be given by:

\[
A_2 = A_1 e^{-\frac{T}{\beta}} + Q e^{-\frac{1}{\beta}},
\]

where \( T \) is the time elapsed since the last reinforcer. Equation 6 simply states that the animal’s arousal at the presentation of the second reinforcer \( (A_2) \) will be the remaining arousal from the first presentation \( (A_1 e^{-\frac{T}{\beta}}) \) plus the new jolt attenuated by a small satiation \( (Q e^{-\frac{1}{\beta}}) \). Following the same process, arousal at the third presentation will be:

\[
A_3 = A_2 e^{-\frac{T}{\beta}} + Q e^{-\frac{2}{\beta}},
\]

And arousal at the \( n^{th} \) reinforcer will be:

\[
A_n = A_{n-1} e^{-\frac{T}{\beta}} + Q e^{-\frac{n}{\beta}}.
\]

Equation 8 is a recursive function. solving it for \( n \), and assuming \( A_0 = 0 \), we can write it as:

\[
A_n = \frac{Q e^{\frac{T}{\beta}} \left( 1 - e^{-\frac{n}{\beta}} \right)}{1 - e^{-\frac{T}{\beta}} + e^{\frac{1}{\beta}}}.
\]

If we want to know arousal \( A \) at moment \( t \) into session, instead of after a number \( n \) of reinforcers, we can assume that reinforcers are presented at an average rate \( R \), which equals \( 1/T \). We can also assume that \( n = Rt \). Then,

\[
A_t = \frac{Q e^{\frac{Rt}{\beta}} \left( 1 - e^{-\frac{Rt}{\beta}} \right)}{1 - e^{\frac{Rt}{\beta}} + e^{\frac{1}{\beta}}}.
\]

The arousal model of Equation 10 is illustrated in Figure 1D. The major difference between Equation 10 and Equation 2 is that, here, the only effect of satiation is that the quantity \( Q \) (vertical lines in Figure 1) becomes increasingly smaller with successive reinforcers. Eventually, new reinforcers will add almost nothing to the general state of arousal. When this happens, the animal’s arousal will decay respecting the natural decay of the reinforcers previously presented. The thin lines in Figure 1D are not violated. It should also be noted that, even when the animal reaches total satiation, Equation 10 predicts it will continue to respond until all the previously elicited arousal dissipates. The effect of satiation is simply to decrease the arousing effect of each new reinforcer—it cannot affect the general arousal level engendered by the reinforcers presented earlier in the session. This is a very important difference from Equation 2, and may help explain at least one instance of what Morgan (1974) termed “resistance to satiation.” As he noticed,

It sometimes happens that an experimenter is careless enough to leave a rat in automated testing apparatus for much longer than the usual session length. When the rat is finally removed, the food cup is often found to be full of reward pellets, that the rat has evidently obtained by lever pressing, but not consumed. (Morgan, 1974, pp. 451–452)
The lever pressing under satiation is sustained by what is left of the arousal that was previously elicited. The animal continues to respond, but its arousal level is not being augmented anymore. Residual arousal rapidly fades, carrying the response rate along with it. This hypothesis is supported by Myers (1960), who reported that “during the accumulation of pellets . . . , the rats’ response rates decline rapidly until responding ceases entirely.”

A Word on a Controversy

Before we proceed to the next step in constructing our model, it is important to clarify that we use the term satiation within a broad definition that includes postingestive factors (e.g., level of sugar in the blood, stomach distension, tissue hydration etc.) as well as preingestive factors (i.e., habituation to the sensory properties of the reinforcer). The relative contribution of post- and preingestive factors to the decrement in responding is still under dispute. While Killeen and his colleagues emphasize the importance of postigestive factors (Killeen, 1995; DeMarce, Killeen, & Baker, 1999), McSweeney and her colleagues have demonstrated that the pregestive factors may overcome the effects of postigestive factors in conditions where these two components of satiation are varied in opposite directions (Aoyama & McSweeney, 2001; McSweeney, 2004). The equations above are silent about this controversy. They simply state that the arousal elicited by each reinforcer (Q) decreases as more reinforcers are presented and consumed. They do not try to answer whether the factors promoting the decay of Q are mainly post- or preigestive.

Constraining Arousal

In MPR, arousal is directed by coupling to produce operant responding (Killeen, 1994; Killeen & Bizo, 1998). Operant responding, in its turn, is constrained by time. This point is important: time constrains responding, not arousal. MPR takes arousal as a linear function of reinforcement rate (Killeen & Bizo, 1998; Killeen & Sitomer, 2003). As such, arousal is free to reach unlimitedly high values as the rate of reinforcement increases.

Here, we maintain the assumption that organisms behave under constraints. However, we consider that arousal itself is also constrained, because the hypothesis that organisms can be unlimitedly excited seems unreasonable from a biological point of view. To limit the increase of arousal, we may consider it as a variable that varies in the range of 0 to 1. Then, we multiply its value by its distance to the ceiling. In this way, when arousal is low, its growth is heavily restrained, because the hypothesis that organisms can be unlimitedly excited seems unreasonable from a biological point of view. To limit the increase of arousal, we may consider it as a variable that varies in the range of 0 to 1. Then, we multiply its value by its distance to the ceiling. In this way, when arousal is low, its growth is heavily restrained.

Application to Variable Interval (VI) Schedules

Killeen (1994) demonstrated that the coupling coefficient for VI schedules is given by:

\[ C \approx \frac{\rho \lambda B}{\lambda B + R}. \]  

(13)

where λ is the memory-decay rate and ρ is the coupling constant—related to the proportion of target responses in the overall stream of behavior. For VI schedules, the coupling constant is around 1/3 (Killeen, 1994). Inserting Equation 13 into Equation 12 and solving for B yields:

\[ B = \frac{\rho A}{\delta} - \frac{R}{\lambda}. \]  

(14)

The subtrahend plays a significant role only at very high rates of reinforcement, where the reinforcer effects extend back to the prior
consummatory response, decreasing coupling and reducing re-
sponse rates. Omitting it incurs only a small decrease in goodness
of fit (Killeen, 1995). For the sake of simplicity, our final model
for within-session responding under variable interval schedules
will be given by the following:

\[ B = \frac{\rho A}{\delta}. \] (15)

Next we assess the predictive power of Equation 15 with data
from our own laboratory, as well as data from different research-
ers. But first we refer the reader to Table 1 for a summary of
parameters and variables, their interpretations, and dimensions.

**Experimental Support**

Equation 15 postulates that response rate \( B \) is a function of \( \mu \),
\( \rho \), \( Q \), \( \beta \), \( \delta \), and \( R \). The time constant \( \mu \), which dictates how fast
arousal decays, is a variable probably related to the organism’s
biology, and therefore should remain constant across a large
variety of experimental operations. For most VI schedules \( \rho \) is
estimated to remain close to 1/3 (Killeen, 1994). On the other
hand, parameters \( Q \), \( \beta \), and \( \delta \) can be indirectly manipulated. We
should alter \( Q \) and \( \beta \) by changing the reinforcers’ properties,
such as their quality and size, as well as the deprivation state. We
should alter parameter \( \delta \) through operations that affect response
duration. Finally, the rate of reinforcement \( R \) can be directly
controlled. Now we present empirical data from experiments
where within-session response rates were affected by the oper-
ations listed above. By fitting Equation 15 to these data we can
verify whether its parameters change in the expected directions.
In all experiments the model was fitted to data by nonlinear
least-squares method. The Excel sheet used for parameter esti-
mates is available to the reader as supplementary material to
this article.

**Varying the Rate of Reinforcement (R)**

In an unpublished experiment from our laboratory (Bittar,
2010), six rats (Group 1) pressed levers under VI schedules of
reinforcement with the average interval ranging from 15 to 120 s
in different conditions. The order of the conditions was randomly
determined for each subject, and each condition was maintained in
effect during 15 daily sessions. The reinforcers consisted of 0.1 cc
of water, and the rats were 20-hr water-deprived at the beginning
of each session. Figure 2 shows the within-session response rates
during successive 3-min bins, averaged through the last five ses-
sions during which each condition was in effect. Response rates
conformed to the patterns typically reported in literature (Mc-
Sweeney & Hinson, 1992), increasing under VI 60-s and VI 120-s
schedules and increasing up to a peak and then decreasing under
VI 15-s and VI 30-s schedules. The curves through the data points
were drawn by Equation 15, with parameter estimates provided in
Table 2.

Equation 15 was capable of providing an adequate descrip-
tion of response rates while maintaining parameter estimates at
theoretically consistent values. Because the reinforcer stimulus
and the deprivation level was the same across different condi-
tions, we set parameter \( Q \) at 0.15. Parameter \( \mu \) was set at a
constant 6-min value. Parameter \( \delta \) suffered small variations at
different VI schedules, floating around 0.5 s per response. Parameter \( \beta \), in its turn, behaved in the most interesting way. It
was estimated at 23.6 and 65.2 at VI 15-s and VI 30-s sched-
ules, respectively. Because the reinforcer used in the experi-
ment was a very small amount of water (0.1 cc), it is possible
that the minimum satiation provided by each reinforcer dissipated
between presentations. At the higher rate of reinforce-
ment provided by the VI 15-s schedule, there was little dissi-
pation, and satiation was faster (smaller value of \( \beta \)). At the
lower reinforcement rate, however, dissipation of satiation was
significant, leading \( \beta \) to a higher value on the VI 30-s schedule.
For the VI 60-s and VI 120-s schedules, \( \beta \) took an infinity
value, meaning that all satiation dissipated between reinforce-
ments (i.e., deprivation level remained constant throughout the
session).

Figure 2 also presents data from a different group of five rats
(Group 2) responding under a VI 20-s schedule and yet another
group of three rats (Group 3) responding under a VI 45-s schedule.
Rats on both groups received 30 daily experimental sessions, and
the data points represent the response rate averaged over the last
five sessions during which each schedule was in effect. Apparatus

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Name</th>
<th>Interpretation</th>
<th>Dimension</th>
</tr>
</thead>
<tbody>
<tr>
<td>( B )</td>
<td>Response rate</td>
<td>The number of responses in a time interval divided by the interval’s duration.</td>
<td>1/T</td>
</tr>
<tr>
<td>( Q )</td>
<td>Arousal impulse</td>
<td>The jolt of arousal engendered by the first reinforcer in the session.</td>
<td>1</td>
</tr>
<tr>
<td>( R )</td>
<td>Rate of reinforcement</td>
<td>The number of reinforcers presented in a time interval divided by the interval’s duration.</td>
<td>1/T</td>
</tr>
<tr>
<td>( \mu )</td>
<td>Mu</td>
<td>The time constant of arousal decay</td>
<td>T</td>
</tr>
<tr>
<td>( \beta )</td>
<td>Beta</td>
<td>Constant of satiation.</td>
<td>1</td>
</tr>
<tr>
<td>( C )</td>
<td>Coupling coefficient</td>
<td>The degree to which responses and reinforcers are associated in the animal’s short-term memory.</td>
<td>1</td>
</tr>
<tr>
<td>( \delta )</td>
<td>Delta</td>
<td>The time required for the emission of a single response.</td>
<td>T</td>
</tr>
<tr>
<td>( \rho )</td>
<td>Rho (coupling constant)</td>
<td>The proportion of target responses in the overall stream of behavior.</td>
<td>1</td>
</tr>
</tbody>
</table>
and reinforcer stimuli were the same from the experiment described above. The curve drawn by Equation 15 provided an adequate account of response rates. Estimated parameters are shown in Table 2. Parameters $Q$ and $\mu$ were settled at their typical values (0.15 and 6-min, respectively).

Equation 15 also provided a good fit when applied to McSweeney’s (1992) data. Using lever presses as the target response and 45-mg Noyes pellets as reinforcers, she exposed rats to different VI schedules, presenting her results as proportions (i.e., the number of responses per 5-min component divided by total session responses). We obtained response rate data by multiplying the given proportions by the total session responses and then dividing by 5. Figure 3 demonstrates that Equation 15 provided an accurate description of McSweeney’s results, with the parameter estimates presented in Table 2. Parameters $Q$ and $\mu$ were set at their standard values. Parameter $\delta$ floated around 0.18 s per response. Parameter $\beta$ varied unsystematically, ranging from 32 to 67.4, failing to correlate with the rate of reinforcement. It is probable that parameter $\beta$ is being forced to correct the simplifications that were adopted when constructing the model. Each simplification is a source of error, which $\beta$ may be trying to accommodate.

### Varying the Response Duration ($\delta$)

Melville, Rybiski and Kamrani (1996) trained four rats to press a lever for 45-mg Noyes pellets under a VI 1-min schedule. Then they varied the force required to move the lever from 0.25 $N$ to 1.10 $N$ in different conditions. We fitted Equation 15 to their within-session data, and present the results in Figure 4. The model conformed to the data well, and parameter estimates are presented in Table 3. At all conditions, $\beta$ took an infinity value, indicating that the deprivation level remained constant along the session. Parameters $Q$ and $\mu$ were set at their standard values. Finally, only the parameter $\delta$ changed between experimental conditions. Moreover, the changes were orderly, with $\delta$ values increasing linearly as the required force increased, as shown in Table 3 ($r = .94$). The reader should be reminded that $\delta$ is the time required to emit a response. Because increasing the force required to operate the lever probably increases the time of the lever-press response, the obtained increases in $\delta$ shown in Table 3 were expected in advance. The conclusion here is identical to Killeen’s (1994). After analyzing an experiment of Mazur (1982), he concluded that increasing the lever weight results in increases in $\delta$, while maintaining the arousal level invariant.

### Varying the Reinforcer’s Magnitude

Cannon and McSweeney (1995) reported an experiment where three pigeons pecked keys on VI 30-s schedules of

---

**Table 2**

*Equation 15 Parameter Estimates When Applied to Data From Bittar (2010) and McSweeney (1992)*

<table>
<thead>
<tr>
<th>Study</th>
<th>Condition</th>
<th>$\rho$</th>
<th>$\delta$</th>
<th>$Q$</th>
<th>$\mu$</th>
<th>$\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bittar (2010) – Group 1</td>
<td>VI 15-s</td>
<td>1/3</td>
<td>0.54</td>
<td>0.15</td>
<td>6.0</td>
<td>23.6</td>
</tr>
<tr>
<td></td>
<td>VI 30-s</td>
<td>1/3</td>
<td>0.47</td>
<td>0.15</td>
<td>6.0</td>
<td>65.2</td>
</tr>
<tr>
<td></td>
<td>VI 60-s</td>
<td>1/3</td>
<td>0.45</td>
<td>0.15</td>
<td>6.0</td>
<td>$\infty$</td>
</tr>
<tr>
<td></td>
<td>VI 120-s</td>
<td>1/3</td>
<td>0.47</td>
<td>0.15</td>
<td>6.0</td>
<td>$\infty$</td>
</tr>
<tr>
<td>Bittar (2010) – Group 2</td>
<td>VI 20-s</td>
<td>1/3</td>
<td>0.55</td>
<td>0.15</td>
<td>6.0</td>
<td>21.0</td>
</tr>
<tr>
<td>Bittar (2010) – Group 3</td>
<td>VI 45-s</td>
<td>1/3</td>
<td>0.74</td>
<td>0.15</td>
<td>6.0</td>
<td>34.2</td>
</tr>
<tr>
<td>McSweeney (1992)</td>
<td>VI 15-s</td>
<td>1/3</td>
<td>0.21</td>
<td>0.15</td>
<td>6.0</td>
<td>51.6</td>
</tr>
<tr>
<td></td>
<td>VI 30-s</td>
<td>1/3</td>
<td>0.17</td>
<td>0.15</td>
<td>6.0</td>
<td>67.4</td>
</tr>
<tr>
<td></td>
<td>VI 60-s</td>
<td>1/3</td>
<td>0.17</td>
<td>0.15</td>
<td>6.0</td>
<td>33.1</td>
</tr>
<tr>
<td></td>
<td>VI 120-s</td>
<td>1/3</td>
<td>0.16</td>
<td>0.15</td>
<td>6.0</td>
<td>37.2</td>
</tr>
<tr>
<td></td>
<td>VI 240-s</td>
<td>1/3</td>
<td>0.20</td>
<td>0.15</td>
<td>6.0</td>
<td>32.0</td>
</tr>
</tbody>
</table>

*Note.* Parameter $\delta$ is given in seconds, whereas $\mu$ values are given in minutes.
reinforcement. The duration of reinforcers (access to mixed grain) varied from 2 s to 20 s in different conditions. They presented their results as the number of responses per 5-min component divided by total session responses, from which we calculated response rate data. The experimental results and the fitted curves from Equation 15 are depicted in Figure 5. Parameter estimates are presented in Table 4. Response duration was settled at 0.25 s and at its standard value 6 min.

Parameters and were strongly correlated with the reinforcer magnitude, but in opposite directions. As the reinforcer magnitude increased, the jolt of arousal elicited by each reinforcer increased (\( r = .96 \)) while the number of reinforcers needed to produce 63.2% of satiation (\( \beta \)) decreased (\( r = -0.88 \)). In short, we conclude that increasing the reinforcer magnitude affects response rate through a double effect mechanism: \( Q \) is increased and \( \beta \) is decreased.

Varying the Organism’s Capacity

DeMarse, Killeen and Baker (1999) measured the weight of 20 food-deprived pigeons before and after providing 1-hr of access to a food cup. The difference in weight was defined as the pigeons’ eating capacity. The four subjects with greater capacity (\( M = 47.5 \) g) were grouped to form the Group LC while the four subjects with smaller capacity (\( M = 19.2 \) g) formed the Group SC. Then, all pigeons responded under VI 30-s schedules. In different conditions, reinforcers consisted of 2 s or 5 s of access to a hopper containing milo grain. The experimenters also delivered one reinforcer just before the beginning of each session to attenuate warm-up effects (DeMarse et al., 1999). This procedural detail results in the pigeons’ arousal being significantly greater than 0 at the start of the sessions, thus requiring a small adjustment of Equation 15. To account for their data, we added \( Qe^{-\delta t} \) to the arousal model of Equation 11, which is embedded in Equation 15. This term represents the arousal elicited by the presession reinforcer, which decays exponentially throughout the session according to the decay rate \( \mu \).

Results for both groups, averaged from the last five sessions during which each condition was in effect, are presented in Figure 6, with the curves drawn from the adjusted Equation 15.

As can be seen from the parameter estimates presented in Table 5, the most significant changes occurred in the satiation parameter \( \beta \), as could be predicted. This parameter took smaller values (indicating faster satiation) in Group SC than in Group LC. Within groups, satiation proceeded faster at the 5-s hopper access than at the 2-s hopper access condition. When LC subjects responded for 2-s hopper access, no satiation occurred at all (\( \beta = \infty \)). Parameters \( Q \) and \( \mu \) were settled at 0.3 and 6-min, respectively. Parameter \( \delta \) varied around 0.24-s for Group SC and around 0.31-s for Group LC, indicating that SC subjects responded slightly faster.

Alternative Models

Visual inspection of Figures 2 to 6 leaves us with the impression that Equation 15 provides an adequate description of the experiments cited above. However, does Equation 15 describe data better than alternative models?

To answer this question we fitted two other models of within-session responding to the results from the aforementioned experiments. The first model is from Killeen (1995) and the second from McSweeney, Hinson and Cannon (1996). There’s also a linear model from Aoyama (1998), but as Aoyama and
McSweeney (2001) acknowledged, it cannot account for the bitonic pattern of response rates observed in the behavioral data presented here. Therefore, it was excluded from the analysis below. Before we go on to compare the performance of each of these models, we provide a brief description of these alternative formulations.

**Killeen’s (1995) Model**

We have seen before that Killeen calculates the within-session arousal level as follows:

\[
A_t = v h R (1 - e^{-\frac{t}{\delta}}). 
\]

This is Equation 2, and we have already discussed its limitations. The motivational drive \( h_r \), in its turn, is given by \( h_r = \gamma d_r \), where

\[
d_r = d_0 + (M - mR)t. \tag{16}
\]

**Table 3**

*Equation 15 Parameter Estimates When Applied to Data From Melville, Rybiski, and Kamrani (1996)*

<table>
<thead>
<tr>
<th>Condition</th>
<th>( \rho )</th>
<th>( \delta )</th>
<th>( Q )</th>
<th>( \mu )</th>
<th>( \beta )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.15N</td>
<td>0.52</td>
<td>0.15</td>
<td>6.0</td>
<td>\infty</td>
<td></td>
</tr>
<tr>
<td>0.25N</td>
<td>0.44</td>
<td>0.15</td>
<td>6.0</td>
<td>\infty</td>
<td></td>
</tr>
<tr>
<td>0.50N</td>
<td>0.56</td>
<td>0.15</td>
<td>6.0</td>
<td>\infty</td>
<td></td>
</tr>
<tr>
<td>0.75N</td>
<td>0.72</td>
<td>0.15</td>
<td>6.0</td>
<td>\infty</td>
<td></td>
</tr>
<tr>
<td>1.10N</td>
<td>0.96</td>
<td>0.15</td>
<td>6.0</td>
<td>\infty</td>
<td></td>
</tr>
</tbody>
</table>

*Note.* Parameter \( \delta \) is given in seconds, whereas \( \mu \) values are given in minutes.

\( M \) represents the metabolic rate and \( m \) represents the size of the reinforcers. Equation 16 simply states that deprivation at time \( t \) into session \( (d_r) \) depends on the initial deprivation level \( (d_0) \) attenuated by the balance between the resources that have been spent \( (M) \) and the resources that have been consumed \( (mR) \).

To obtain a prediction of operant response rates, Killeen states the following:

\[
B = \frac{k A_t}{A_t + 1} \tag{17}
\]

This equation postulates that response rate is a hyperbolic function of arousal level, scaled by parameter \( k \)—the maximum response rate attainable at a specific experimental context, given by \( C/\delta \). The entire model has seven parameters \( (k, v, \gamma, d_0, M, m, \text{and } \mu) \). Because parameter \( \gamma \) is redundant with parameter \( v \), it may be fixed at 1. It is also possible to fix metabolic rate \( M \) at 0, assuming that metabolic processes are insignificant in the course of a typical experimental session (Killeen, 1995). Parameter \( m \) may be set at 1, leaving deficit \( d_0 \) to be measured in number of reinforcers. We are finally left with four parameters free to vary: \( k, v, d_0, \text{and } \mu \).

**McSweeney, Hinson, and Cannon’s (1996) Model**

McSweeney et al. (1996) also provided a model of within-session operant responding. After examining the fit of several functions to within-session responding data, they arrived at a three parameter equation given by the following:

\[
P = \frac{a}{e^{bt} - c + T}. \tag{18}
\]

where \( P \) is the proportion of the total-session responses that occur during successive time bins, and \( a, b \) and \( c \) are free.
parameters. The first term promotes an exponential decay of response rate attributed to habituation. The second term promotes a hyperbolic increase of response rate attributed to sensitization. These two processes combine to draw a bitonic pattern of response rate along the course of an experimental session. Contrary to Equation 15 and to Killeen’s (1995) model, Equation 18 is an empirical model. Therefore, its parameters have no theoretical meaning.

Comparing the Fits

We used the least-squares method to fit Equation 17 (Killeen, 1995) and Equation 18 (McSweeney et al., 1996) to data from all the experiments mentioned above. Then we compared the relative goodness of fit of these models and Equation 15 using the bias-corrected Akaike Information Criteria (AICc), which is preferred over traditional AIC when working with small sample sizes (Spiess, & Neumeyer, 2010). The Akaike weights for all models for all conditions of all experiments are presented in Table 6. At each condition these weights can be interpreted as the probability of a specific model being the best model among its competitors (therefore, Akaike weights in a row must always add up to 1). Equation 15 performed better than the alternative models in 19 of 25 comparisons (76%). McSweeney’s model performed better in 5 comparisons (20%) and Killeen’s model in one (4%).

Besides often providing a better fit to data, Equation 15 also provides a better fit to theory. While McSweeney’s model is admittedly empirical, Killeen’s model has some flaws in its construction. The model outlined here, on the other hand, is solidly grounded in MPR’s core principles (Killeen, 1994). As a consequence, its parameters have clear theoretical meanings, assuming values that are immediately interpretable and easy to compare and understand.

Table 4

<table>
<thead>
<tr>
<th>Condition</th>
<th>$\rho$</th>
<th>$\delta$</th>
<th>$\phi$</th>
<th>$\mu$</th>
<th>$\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-s</td>
<td>1/3</td>
<td>0.25</td>
<td>0.03</td>
<td>6.0</td>
<td>53.7</td>
</tr>
<tr>
<td>5-s</td>
<td>1/3</td>
<td>0.25</td>
<td>0.05</td>
<td>6.0</td>
<td>63.7</td>
</tr>
<tr>
<td>8-s</td>
<td>1/3</td>
<td>0.25</td>
<td>0.04</td>
<td>6.0</td>
<td>33.9</td>
</tr>
<tr>
<td>15-s</td>
<td>1/3</td>
<td>0.25</td>
<td>0.09</td>
<td>6.0</td>
<td>10.7</td>
</tr>
<tr>
<td>20-s</td>
<td>1/3</td>
<td>0.25</td>
<td>0.10</td>
<td>6.0</td>
<td>16.9</td>
</tr>
</tbody>
</table>

Note. Parameter $\delta$ is given in seconds, whereas $\mu$ values are given in minutes.
In the present study, we relied on simple assumptions to derive a formal model of arousal dynamics. The assumptions were as follows: (a) reinforcers arouse organisms, (b) the arousal decays over time, (c) the arousal accumulates, (d) reinforcers lose their arousal effect through successive presentations, and (e) there is a limit to the degree an organism can be aroused. The first three assumptions were also present in Killeen’s (1995) model of arousal dynamics. However, the process by which successive reinforcer presentations affect arousal was not clearly devised, leading his model to a modeling mistake. Killeen’s arousal model also lacks a ceiling. Later, additional assumptions were made to allow the prediction of response rates. They were as follows: (f) a fraction $C$ of an organism’s arousal is directed to emission of target responses, and (g) time constrains responding. These two principles are not new, and they are at the core of MPR (Killeen, 1994).

These seven assumptions were formally elaborated, resulting in an equation that describes response rate as a function of six variables: (1) the arousal impulse $Q$, (2) the time constant of arousal decay $\delta$, (3) the constant of satiation $\mu$, (4) the coupling coefficient $C$, (5) the response duration $\beta$, and (6) the rate of reinforcement $R$. Application of the model to experimental data from different laboratories demonstrated its generality and comparison with alternative models attested to its adequacy. The model provided a good description of the responding of rats and pigeons working for different reinforcers under different experimental conditions.

The parameters of the equation changed in the predicted ways when they were fitted to behavioral data. The arousal impulse $Q$ correlated with the reinforcers’ magnitude. The constant of satiation $\mu$ correlated with the reinforcer magnitude, with the organism’s capacity, and sometimes with the rate of reinforcement. The response duration $\beta$ correlated with the force required to respond. The time constant of arousal decay $\delta$ remained invariant across experimental manipulations, always settled at 6-min. This value of $\delta$ was also estimated by Killeen et al. (1978), who measured how fast pigeons’ activity decays after a single feeding.

Besides providing a consistent model of arousal dynamics, the present study demonstrates the utility of within-session responding.
operative responding data. Because schedules of reinforcement are generally held constant throughout the session, observed variations in response rate must be primarily attributed to changes in processes such as arousal, satiation, and habituation. As a consequence, within-session data provide a valuable means to clarify the relation between performance and important motivational variables.

Finally we demonstrated that, by representing arousal as a parameter in the range of 0 to 1, we can formalize MPR (Killeen, 1994) in the simplest and most intuitive form of Equation 12.

References


Received December 12, 2011
Revision received April 10, 2012
Accepted May 3, 2012
