

## **How Associations Become Behavior**

Stefano Ghirlanda<sup>1,2,3</sup> and Magnus Enquist<sup>3</sup>

<sup>1</sup>Department of Psychology, Brooklyn College

<sup>2</sup>Departments of Psychology and Biology, CUNY Graduate Center

<sup>3</sup>Centre for the Study of Cultural Evolution, Stockholm University

### **Author Note**

Correspondence should be addressed to Stefano Ghirlanda, Department of Psychology, Brooklyn College, 2900 Beford Ave., Brooklyn NY 11215. Email: sghirlanda@brooklyn.cuny.edu. Submitted to Neurobiology of Learning and Memory.

**Abstract**

The Rescorla and Wagner (1972) model is the first mathematical theory to explain associative learning in the presence of multiple stimuli. It uses the concept of associative strength to predict behavior, but does not explicitly connect the two. This study proposes that behavior can be described by a collection of Poisson processes, each with a rate proportional to an associative strength. The model predicts that the time between behaviors will follow an exponential or hypoexponential distribution. This prediction is supported by two data sets on autoshaped and instrumental behavior in rats.

## How Associations Become Behavior

### Introduction

The Rescorla and Wagner (1972) model is the first mathematical model to account for associative learning in the presence of multiple stimuli, such as in blocking, overshadowing, and relative validity. It is hard to overstate its success in balancing simplicity and effectiveness, and in inspiring research (Miller, Barnet, & Grahame, 1995; Pearce & Bouton, 2001; Siegel & Allan, 1996).

The main theoretical construct of the Rescorla and Wagner model is associative strength: a number that quantifies the intuitive notion of association. With their famed learning equation, Rescorla and Wagner spelled out a rigorous theory of how associative strength changes with experience. Yet, when linking associative strength to behavior, they assumed merely that larger values yield stronger or more frequent behavior. This was sufficient to account for many learning phenomena (Bouton, 2016; Pearce, 2008), but it weakened the model's connection with behavior and tempered earlier ambitions to predict response probabilities precisely (Bush & Mosteller, 1955; Estes, 1950). Most subsequent models have followed Rescorla and Wagner, resulting in relatively little work on how associative strength relates to behavior. Yet, associative strength cannot be said to accurately capture how learning changes an animal's internal state, if it cannot be connected firmly to behavior.

Here we attempt to link associative strength with the rate at which behavior occurs, drawing inspiration from quantitative behavior analysis and connecting it with associative learning theory (Killeen, Hall, Reilly, & Kettle, 2002; Sanabria, Daniels, Gupta, & Santos, 2019). Formally, we explore the hypothesis that each associative strength influences the rate of a Poisson process that generates behavior (see Methods). This hypothesis may apply to stimulus-response, stimulus-stimulus, or other associations, and to learning theories other than Rescorla and Wagner's. It is about how associations become behavior, not how they are learned or what entities they link. In other words, the Poisson hypothesis makes precise predictions about behavior under constant conditions, including relevant factors such as stimuli, associative strength, and

motivation. However, the hypothesis is silent about what representations are associated and what causes associations to change. For this reason, we do not consider learning below. Rather, we evaluate the Poisson hypothesis by looking at steady-state behavior (Blough, 1975). We consider the relationship between the Poisson hypothesis and learning in the Discussion.

A potential connection between Poisson processes and behavior was suggested to us by data on stimulus summation in rabbit Pavlovian conditioning. Here, the probability of a conditioned response (CR) to the joint presentation of two conditioned stimuli (CSs) is consistently smaller than the sum of CR probabilities to each CS (Kehoe, 1982, 1986; Kehoe & Graham, 1988; Kehoe, Horne, Horne, & Macrae, 1994). If  $A$  and  $B$  are the CSs, and  $p_X$  is CR probability to  $X$ , many experiments fit the formula

$$p_{AB} = p_A + p_B - p_A p_B \quad (1)$$

The term  $-p_A p_B$  seems hard to reconcile with Rescorla and Wagner's (1972) assumption that  $v_{AB} = v_A + v_B$  (where  $v_X$  is the associative strength of  $X$ ) and, more generally, with the widespread assumption that  $v_{AB}$  is a linear function of  $v_A$  and  $v_B$  (Pearce, 1987; Wagner, 2008). However, Ghirlanda (2022) showed that  $v_{AB} = v_A + v_B$  is compatible with Equation (1) if (and only if) the relationship between associative strength and CR probability has the form

$$p_X = 1 - e^{-bv_X} \quad (2)$$

with  $b$  a positive constant. In fact, using  $v_{AB} = v_A + v_B$  in Equation (2) yields

$$\begin{aligned} p_{AB} &= 1 - e^{-b(v_A + v_B)} \\ &= 1 - e^{-bv_A} e^{-bv_B} \\ &= 1 - (1 - p_A)(1 - p_B) \end{aligned} \quad (3)$$

which simplifies to Equation (1).

Ghirlanda (2022) justified Equation (2) from empirical data and normative arguments, but did not provide a mechanistic model for it. The link with Poisson processes stems from the serendipitous observation that, in the experiments yielding Equation (1), a CR was recorded when

at least one response occurred during CS presentation. If responses are generated by a Poisson process with rate  $bv$ , then the probability that *no response* is observed during the CS is  $e^{-bv}$  (where  $b$  includes the duration of the CS as a factor, see Equation (5) in Methods, with  $n = 0$ ). Thus the probability of at least one response is the complement  $1 - e^{-bv}$ . In summary, a Poisson process may explain the origin of Equation (2), which, in turn, is necessary to reconcile associative models with data from summation experiments.<sup>1</sup>

In Methods, we flesh out the idea that associative strengths influence behavior through Poisson processes. We show that it is compatible with standard associative learning theory and derive testable predictions from it. In Results, we show that the predictions are supported by data about autoshaped and instrumentally conditioned behavior in rats. In the Discussion, we consider related models from behavior analysis, open questions, and implications for animal learning and cognition.

## Methods

### The Poisson model

Let  $v$  be an associative strength influencing a behavior in a given stimulus situation. We consider the hypothesis that the behavior occurs according to a Poisson process with rate proportional to  $v$ . A Poisson process is a mathematical model for events (here, behaviors) that occur at random times. The process has one parameter, a positive number called the rate. With rate  $a$ , the probability of one event occurring in any small (infinitesimal) interval  $dt$  is  $a \times dt$ , and the probability of two or more events is negligible. Our hypothesis is then that  $a = cv$ , where  $c$  summarizes non-associative factors, such as motivation, which we assume constant in this paper. This hypothesis formalizes the intuition, present already in Rescorla and Wagner (1972), that a larger associative strength corresponds to a higher probability of the relevant behavior.

A Poisson process has two basic properties (Feller, 1971; Resnick, 1992). First, the times between consecutive events, referred to as “waiting times,” are distributed exponentially with rate

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<sup>1</sup> Ghirlanda (2022) shows that Equation (2) is compatible also with summation data for which Equation (1) does not hold.

*a*. These are often referred to as inter-response times (IRTs) in psychology. Formally, the probability density of a waiting time  $t$  is:

$$p_a(t) = ae^{-at} \quad (4)$$

with mean time  $1/a$  and variance  $1/a^2$ . Second, the number of events occurring during any interval of length  $T$  follows a Poisson distribution:

$$\Pr_a(n \text{ events in time } T) = \frac{(aT)^n}{n!} e^{-aT} \quad (5)$$

with mean and variance equal to  $aT$ . Of note, Equations (4) and (5) hold only for Poisson processes, so that either can be used to test whether data follow a Poisson process. Below we use Equation (4) because it does not depend on defining a fixed length for observations, which is not trivial in the data we analyze because different responses are intermixed. For example, it would be incorrect to define a rate of lever pressing for a rat by simply counting the number of lever presses in a fixed-duration trial, because during a trial the rat is likely to experience conditions with different rates, such as early vs. late in the trial or inside vs. outside the food magazine. In addition to Equation (4), we also check the “memoryless” property of Poisson processes: at any time  $t$ , the waiting time distribution is the same regardless how long ago the last event occurred. This property implies that consecutive waiting times are uncorrelated. It is a necessary consequence of the Poisson hypothesis, although it also holds for other stochastic processes (Feller, 1971; Resnick, 1992).

For brevity, we say that a behavior “is Poisson” if it follows a Poisson process. The next sections show that the Poisson model fits naturally with how associative strengths are commonly understood.

### ***Stimulus control***

Stimulus control refers to changes in behavior caused by changes in stimulation (Ghirlanda & Enquist, 2003; Mackintosh, 1974). Associative learning theory analyzes stimulus control by assuming that stimuli are perceived as arrays of elements that can be shared across

stimuli (Blough, 1975; Pearce, 1987; Rescorla & Wagner, 1972; Wagner, 2008). Most commonly, a stimulus' associative strength is broken down into fractional associative strengths attributed to each of its elements.<sup>2</sup> The Poisson model is consistent with this approach if we assume that elemental associative strengths combine to obtain a Poisson rate. Thus two stimulus elements with associative strengths  $v_1$  and  $v_2$  would yield a Poisson process with rate proportional to  $v_1 + v_2$ .

The argument extends to elements with continuous activation. If  $x = \{x_1, \dots, x_s\}$  represents the activation of  $s$  elements, we can calculate an aggregate Poisson rate as

$$v(x) = \sum_{i=1}^s x_i v_i \quad (6)$$

which yields the standard associative theory of stimulus control (Blough, 1975; Ghirlanda, 2015; Wagner, 2008). Inhibition can be accommodated by allowing elemental associative strengths to be negative, and assuming that only overall positive rates give rise to behavior (Ghirlanda, 2022).

### ***Timing of behavior***

Learned behavior occurs at specific times, such as a protective Pavlovian CR that occurs immediately before a noxious US. If Poisson processes are memoryless, triggering behavior regardless of elapsed time, how can they control timed behavior? This puzzle can be resolved with time-varying stimulus representations, i.e., allowing element activation in Equation (6) be a function of time, such as time since CS onset. An associative mechanism can leverage such a representation by tuning the associative strengths of each stimulus element in such a way that total associative strength is maximal when a response should be produced. As with Equation (6) itself, this approach is common in associative learning models of timing (Buhusi & Schmajuk, 1999; D. V. Buonomano & Karmarkar, 2002; Enquist & Ghirlanda, 2005; Grossberg & Schmajuk, 1989; Machado, 1997).

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<sup>2</sup> Alternatively, associative strength is attributed to whole stimuli, and elemental composition is used to compute how associative strength generalizes across stimuli (Pearce, 1987). The two approaches are equivalent (Ghirlanda, 2015, 2018).

***Choice***

When two or more behaviors are considered, we assume that each behavior follows an independent Poisson process with its own rate. Which behavior occurs next depends then on which process first generates an event. We call this “Poisson choice.” This simple model has two appealing properties.

First, Poisson choice agrees with the matching law (Baum, 1974; Herrnstein, 1974), assuming that Poisson rates are proportional to reinforcement obtained. In fact, if behaviors 1 and 2 are independently Poisson with rates  $cv_1$  and  $cv_2$  determined by underlying associative strengths, then they occur in the ratio  $v_1/v_2$  (with  $n$  behaviors, behavior  $i$  occurs with frequency  $v_i/(v_1 + \dots + v_n)$ ; Feller 1971; Resnick 1992). Deviations from the basic matching law can be accommodated following Baum (1974), i.e., assuming that rates are not determined by reinforcement alone.

Second, Poisson choice is robust to how we categorize behavior. Suppose a rat can press a lever with its paws or with its snout, but we cannot or do not want to tell the two apart. In this case, our observations of lever pressing will still be Poisson, with rate proportional to the underlying associative strengths  $v_1 + v_2$  (Feller, 1971; Resnick, 1992).

Stimulus control and choice can be combined by assuming that there is a separate set of associative strengths for each possible behavior, corresponding to multiple copies of Equation (6) with, typically, different values of  $v_1, \dots, v_s$ .

***Multi-step behavior***

In most experiments, we do not record every behavior. For example, a rat must approach a lever before being able to press it, but typically we only record presses. In this case, the distribution of times between lever presses is not exponential even if both behaviors are Poisson. This distribution can be calculated as follows.

Suppose approaching and pressing are Poisson with rates  $a_1$  and  $a_2$ . Observing a lever press at time  $t$  implies that the rat had previously approached the lever at a time  $x < t$ , and that the subsequent waiting time for pressing was  $t - x$ . According to Equation (4), the probability of a



waiting time of  $x$  for approaching followed by a waiting time of  $t - x$  for pressing is

$$\Pr(\text{approach at } x < t \text{ followed by and press at } t) = p_{a_1}(x)p_{a_2}(t - x) \quad (7)$$

The time  $x$  is unknown because approach is not observed, but over many observations it is distributed exponentially. We can thus consider all possible values of  $x$  compatible with a press at  $t$ , each with its own probability, in order to obtain the probability of a press at  $t$ . Formally, this means integrating Equation (7) over  $x$ , between 0 and  $t$ :

$$\Pr(\text{press at } t) = \int_0^t p_{a_1}(x)p_{a_2}(t - x)dx \quad (8)$$

$$= \int_0^t a_1 e^{-a_1 x} e^{-a_2(t-x)} dx \quad (9)$$

$$= \frac{a_1 a_2}{a_2 - a_1} (e^{-a_1 t} - e^{-a_2 t}) \quad (10)$$

$$= \frac{a_2}{a_2 - a_1} p_{a_1}(t) + \frac{a_1}{a_1 - a_2} p_{a_2}(t) \quad (11)$$

Repeating the same reasoning for a sequence of  $m$  behaviors leads to

$$\Pr_a(\text{behavior at } t) = \sum_{i=1}^m p_{a_i}(t) \prod_{\substack{j=1 \\ j \neq i}}^m \frac{a_j}{a_j - a_i} \quad (12)$$

where  $a = \{a_1, \dots, a_k\}$ . Equation (12) is known as the “hypoexponential” distribution.<sup>3</sup> It reduces to Equation (4) when  $m = 1$ . We fit this distribution to data as described in the next section.

It is also possible to consider observations that may arise from multiple sequences of behaviors. For example, if we add a “retreat” behavior to our analysis of lever pressing, then many sequences become possible: approach-press, approach-retreat-approach-press, and so on. Each of these sequences contributes to the probability of observing a press at  $t$ . We touch upon these situations in the Discussion (for a complete treatment, see Sanabria et al., 2019; Zucchini, MacDonald, & Langrock, 2016).

<sup>3</sup> When two rates are equal and the denominator  $a_j - a_i$  is zero, the correct probability distribution can be obtained by a Taylor expansion of the exponentials in  $p_{a_i}(t)$  and  $p_{a_j}(t)$ , followed by a limit  $a_j \rightarrow a_i$ .

### Code and data

Code to reproduce our analyses is available at <https://osf.io/7hgyf/>. We analyze two data sets. The first consists of rat autoshaping data from Iliescu, Hall, Wilkinson, Dwyer, and Honey (2018). It is available at <https://osf.io/ka9w3>, and with our code in pre-processed form suitable for our analyses. The second data set consists of rat instrumental conditioning data from George, D. N. (unpublished raw data). Data for 16 subjects are available with our code, data for 32 more subjects are available upon request. Experimental procedures are described below as necessary.

We fit the Poisson model to empirical waiting time distributions using maximum-likelihood estimation, that is, we choose the parameters of the distribution in Equation (12) to maximize the probability that the observed data arise from the distribution. Given  $k$  observed waiting times  $w = t_1, \dots, t_K$ , this probability is

$$L(t, a) = \prod_{i=1}^k \Pr_a(\text{behavior at } t_i) \quad (13)$$

where each probability in the product is computed using Equation (12). We consider the number of terms  $m$  in Equation (12) as a free variable, determined using the Bayesian information criterion (BIC, see James, Witten, Hastie, & Tibshirani, 2013). This is a way of comparing models that penalizes models with more parameters, unless they yield a substantially better fit. We start the fitting process with  $m = 1$  (the exponential distribution) and increase  $m$  so long as BIC values improve. After fitting, we sort the resulting rates in increasing order to aid discussion, although the Poisson model is insensitive to order. (It is the same to wait for a slow process first and a fast process second, or vice-versa.)

Note that, in order to estimate the rate  $a$  in Equation (13), we assume that this rate is constant across the data included in the fit. Because response rates typically vary during an experiment, we try to identify subsets of the data where event rates are at least approximately constant. In this exploratory study, we do this simply by inspecting the data visually, as detailed in Results for each data set.

As a test of the Poisson model, the estimation process is robust to false positives and negatives. A Poisson behavior remains Poisson if equipment misses a random fraction  $q$  of occurrences, in which case we would observe a rate of  $(1 - q)a$ . Similarly, if we spuriously detect behavior with Poisson rate  $a_0$ , the behavior remains Poisson with rate  $a + a_0$ . In both cases, we can still test the Poisson hypothesis despite estimating a biased rate.

We conducted our analyses with R version 4.2.2 (2022-10-31) (R Core Team, 2022) within the Emacs ESS and org-mode environments, versions 18.10.3snapshot and 9.6.4 (Rossini, Heiberger, Sparapani, Maechler, & Hornik, 2004; Schulte, Davison, Dye, & Dominik, 2012). We used packages `data.table` version 1.14.0 for data manipulation (Dowle & Srinivasan, 2021), `ascii` version 2.4 for output formatting (Hajage, 2020), and custom code for fitting the hypoexponential distribution and BIC-guided model selection. Our implementation of Equation (12) is derived from Baumgartner and Gatto (2014).

## Results

To test the Poisson hypothesis, we analyze data about autoshaped and instrumentally conditioned behavior in rats, comparing waiting times between consecutive behaviors to the predictions of Equation (4) and its generalization to multi-step behavior, Equation (12).

### Autoshaping

Iliescu et al. (2018) trained 32 rats in operant chambers for 12 40-trial sessions. On a random half of trials, one of two retractable levers was inserted for 10 s, after which it was retracted and food became available in the magazine. On the other trials, the other lever was inserted, but no food was delivered. Thus the levers served as CSs for food delivery and non-delivery. Each trial included 10 s before lever insertion, and 10 s after. Inter-trial intervals (ITIs) varied uniformly between 10 and 50 s. No scheduled stimuli differentiated the pre-CS, post-CS, and ITI periods. The times of lever presses, magazine entries, and magazine exits were recorded. We consider the simple scheme of the rat's behavior shown in Figure 1. The rat can be either outside or (partly) inside the magazine. When outside, it can decide to enter the magazine, to press the lever (when present), or to do "nothing," by which we mean any behavior that is not

recorded. When inside the magazine, the rat can decide to exit or do “nothing.” After pressing the lever, it can press again, enter the magazine, or do “nothing.”

In testing the Poisson model, we are concerned with the distribution of waiting times for the transitions between behaviors. For example, given that the rat is in the magazine, how is the time until it exits distributed? The model predicts an exponential or hypoexponential distribution for all waiting times, provided the hypothesis of constant rate parameters is met. However, response rates generally vary both between and within trials. For example, there are more magazine entries and lever presses right after the insertion of the lever that signals food than at other times. To work with approximately constant rates, we first selected for analysis the last three experimental sessions, in which overall response rates are approximately constant within subjects. Then, within these sessions, we selected the following portions of each trial (see Fig. S1):

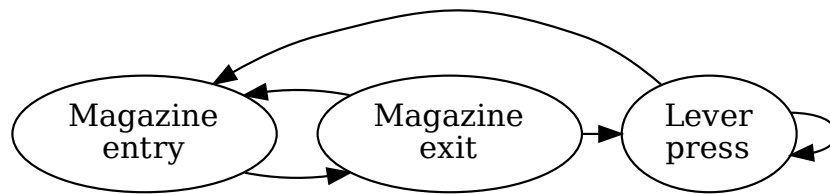
- For the entry-exit, we used data from non-reinforced trials, up to 40 s in the trial. This includes the 10 s pre-CS period, 10 s CS period, the 10 s post-CS period, and the first 10 s of the inter-trial interval, which was undistinguishable to the rat from the post-CS period. The remaining of the inter-trial interval was discarded as the rate of behavior decreases substantially. These intervals include times with and without the non-reinforced lever (which was present only between 10 and 20 s). While this may affect event rates in principle, empirically there was no systematic variation (Fig. S1, top left).

- For the exit-entry interval, we used non-reinforced trials up to 40 s in the trial, but we excluded 2 s after lever insertion and removal because exit-entry intervals are longer at these times (Fig. S1, top right). We also analyzed, separately, reinforced trials starting 5 s after lever insertion and up to 40 s. (The first 5 s following lever insertion have much higher intervals between entry-exit events, see Fig. S1.)

- For the lever-lever, lever-entry, and exit-lever, we used data from reinforced trials, excepting 2 s following lever insertion, during which these behaviors have higher rate.

We excluded from analysis exit-entry rates on reinforced trials because there was no substantial interval within a trial in which these rates are constant (Fig. S1, top right). We also excluded

intervals involving the lever on reinforced trials, because these events are very few.



**Figure 1**

*Possible transitions between the behaviors recorded by Iliescu et al. (2018), when a lever is present in the operant chamber. Without a lever, the only possible behaviors are magazine entry and exit.*

Figure 2 shows that entry-exit intervals in non-reinforced trials follow the Poisson model closely. For most subjects in Figure 2, a simple exponential distribution provides the best fit. For a few subjects, a two-rate hypoexponential is slightly better than an exponential. Entry-exit intervals in reinforced trials and exit-entry intervals in non-reinforced trials show a similar pattern (see Supplementary Material).

Figure 3 shows a strikingly different pattern for the waiting times between consecutive lever presses. These are generally well-described by a hypoexponential distribution with two or three terms, often nearly identical. Waiting times for the exit-lever and lever-entry intervals show a similar pattern (see Supplementary Materials). Table 1 shows that all of the intervals in Figure 1 are described quite well by an exponential or hypoexponential distribution.

The only systematic deviation from the Poisson model appears that, in entry-exit and exit-entry data, small intervals are more frequent than predicted. For example, the first data point is consistently above the model curve in Figure 2. There are at least two potential contributions to this effect. First, rats may sometimes trigger the apparatus in rapid succession, for example, by its whiskers, tail, or other body part crossing repeatedly the infrared beam that records magazine entry and exit (Iliescu, A., pers. comm.). There are no excess short intervals in lever press data,

consistent with lever pressing being harder to trigger accidentally. Second, it is often observed that animals alternate high-rate and low-rate bouts of behavior (Brackney, Cheung, Neisewander, & Sanabria, 2011; Killeen et al., 2002). When this is case, the assumption of constant rate under which the Poisson model predicts an exponential distribution does not hold, and one would have to analyze high-rate and low-rate bouts separately. In Iliescu et al.'s (2018)'s data, this does not seem important. In fact, a mixture of high-rate and low-rate bouts implies a correlation between successive waiting times, because overall short waiting times would cluster together within high-rate bouts, and long waiting times within low-rate bouts. The data, however, show no significant correlations (see Supplementary Material).

### Instrumental conditioning

George, D. N. (unpublished raw data) rewarded lever pressing in three groups of 16 rats on variable-interval schedules, with an average inter-reinforcement time of 30 s. The schedules differed in the distribution of inter-reinforcement times (geometric, Gaussian, or rectangular), which we ignore as it does not affect our results (see Supplementary Material).

George recorded the same behaviors as Iliescu et al. (2018), and we continue to use the scheme in Figure 1. The waiting times distributions are also similar. Entry-exit and exit-entry

### Table 1

*Summary of Poisson model fits to the intervals between successive behaviors, in data from Iliescu et al. (2018). R: Reinforced trials. N: Non-reinforced trials. r: Pearson's correlation coefficient between binned data and Poisson fits across 32 subjects.  $\bar{r}$ : Median of r.*

Interval	$\bar{r}$	$r$ range
Entry-exit N	0.95	0.79–0.99
Exit-entry N	0.87	0.71–0.95
Exit-entry R	0.93	0.59–0.99
Lever-entry R	0.95	0.59–0.99
Lever-lever R	0.94	0.74–0.99
Exit-lever R	0.95	0.93–0.98

waiting times are typically described by exponential distributions, while lever-lever, lever-entry, and exit-lever waiting times by hypoexponential distributions. Model fits for the lever-lever waiting times of subjects 1–16 are shown in Figure 4. See Supplementary Materials for the other intervals. Table 2 mirrors Table 1 in showing that all of the intervals in Figure 1 are described quite well by an exponential or hypoexponential distribution. Like in Iliescu et al.'s (2018)'s data, we found no correlation between consecutive waiting times (Supplementary Material).

Nevertheless, we observe that the model often underestimates the peak of distributions involving lever presses. Possibly, behavior involving the lever is not completely described in terms of unvarying sequences, as we have assumed in our multi-step model, and one needs to consider that engaging with and disengaging from the lever can occur in multiple ways (see Methods).

### The structure of waiting times

Tables 1 and 2 show that the Poisson model fits the data well, but does it provide any insight into behavioral processes? Table 3 shows that the number of terms in the fitted distribution tracks the intuitive complexity of behaviors. Exiting the magazine takes place in a relatively constant stimulus situation (the rat's head is inside the magazine) with few behavioral options. In ~90% of cases, the waiting times are distributed exponentially. In the remaining cases, the best fitting distribution has two rates, but the difference from an exponential is small because the

### Table 2

*Summary of Poisson model fits to the intervals between successive behaviors, in data from George, D. N. (unpublished raw data). Legend as in Table 1.*

Interval	$\bar{r}$	$r$ range
Entry-exit	0.93	0.81–1.00
Exit-entry	0.92	0.78–0.98
Lever-lever	0.94	0.78–0.99
Lever-entry	0.92	0.15–0.98
Exit-lever	0.91	0.52–0.97

second rate is much larger than the first (see subjects 21, 22, 30, 31 in Figure 2). The waiting times for entering the magazine after having exited from it show a similar pattern, but two (occasionally more) terms appear in about one third of cases. The resulting distributions are still almost exponential in shape.

In contrast, waiting times involving the lever are rarely distributed exponentially (transitions exit-lever, lever-entry, and lever-lever in Figure 1). The most common pattern is a hypoexponential distribution with several, almost identical faster rates, and often one slower rate (Figure 3 and Figure 4). The higher complexity of these distributions may reflect the fact that engaging and disengaging with the lever is best analyzed as consisting of several steps, but we cannot test this interpretation with the available data. That some rates are estimated to be nearly identical suggests that they may correspond to the repetition of the same or similar behaviors. Alternatively, some rates could pertain to internal processes underlying behavioral decisions.

### Discussion

The Poisson model of response generation provides a quantitative hypothesis for how associative strengths and other variables become behavior, that is, by influencing the rates of Poisson processes. It is a bold hypothesis as it implies that inter-response time distributions can

#### Table 3

*Number of terms in the best-fitting hypoexponential distribution for all subjects in Iliescu et al. (2018) and George, D. N. (unpublished raw data). The “Lever press” column includes all intervals involving the lever, see Figure 1. N: Number of data sets (for each interval, only subjects yielding at least 50 data points were included).*

	Terms:							
	<i>N</i>	1	2	3	4	5	6	7
Magazine exit	80	71	9	0	0	0	0	0
Magazine entry	101	64	33	3	0	1	0	0
Lever press	193	9	63	55	37	25	2	2



be described completely by combining exponential distributions in various ways. For example, Brackney et al. (2011) found that waiting times between lever presses were described effectively by a mixture of two exponential distributions. This and similar cases are compatible with the Poisson hypothesis, by assuming that the animal switches between two situation with different response rates. The causes of such switches are beyond the scope of the Poisson hypothesis and would be sought in changes in stimuli, motivation, reinforcement, and internal decision processes.

The question remains of whether *all* decision making in animals can be adequately described by combinations of Poisson processes. The literature contains many examples of non-exponential distributions, such as peaked and multi-modal distributions, which have been explained with sophisticated models that include the Poisson process but add such elements as pacemakers, noise, and multiple response rates (Kessel & Lucke, 2008; Killeen et al., 2002; Sanabria et al., 2019). We suggest that it may be possible to keep the unadorned Poisson process as the sole mechanism of response generation, provided behavior is observed in sufficient detail and a full model that includes stimulus control and timing is employed to account for short- and long-timescale variation in response rates (see Methods).

For example, we did not encounter multi-modal distributions in our analysis. One reason may be that we analyzed waiting times between any two responses we had data about, instead of between alike responses as is typically done. To see why this matters, consider the distribution of entry-entry waiting times in the model in Figure 1. An entry-entry event can occur in many ways, such as entry-exit-entry, entry-exit-lever-entry, entry-exit-lever-lever-entry, and so on. The corresponding waiting time distribution is bound to be more complex than those for the elementary transitions in Figure 1. Indeed, the entry-entry distribution is often multi-modal even in Iliescu et al.'s and George's data (Figure 5), while the elementary distributions are adequately described as exponential and hypoexponential. In other words, by using a finer-grained picture of the animal's behavior, we were confronted with simpler distributions that seem compatible with Poisson processes.

To fully evaluate the Poisson hypothesis, we need further development in several areas.

First, the terms of the hypoexponential distribution, Equation (12), or of more general Markov models, should be better connected to behavior. We have assumed that these terms reflect unobserved behaviors (or internal processes), but we have been unable to test this assumption with available data. Using higher-resolution behavioral data would resolve this uncertainty. For example, we can use pose-estimation software to reduce video data to low-dimensional vectors describing the animal's posture and relationship with the environment (Bohnslav et al., 2021; Mathis et al., 2018), then use classification algorithms to sort these vectors into different behaviors (Fujimori, Ishikawa, & Watanabe, 2020; James et al., 2013), and finally evaluate the waiting times between these behaviors. These analyses might also cast light on individual differences, such as those apparent in Figures 3 and 4, by showing the behavioral origin of waiting time distributions. The approach can be eventually developed into full individual-level Markov models (Sanabria et al., 2019).

Second, we have not developed the Poisson hypothesis for continuous response, such as the force of biting or of lever pressing in rats (Daunton, 1973; Herrick, 1964) and the amount of nictitating membrane closure in rabbits (Kehoe, Graham-Clarke, & Schreurs, 1989). One possibility is to draw inspiration from the neural control of muscle force (Bawa, 2002; Burke & Howells, 2016; Enoka & Duchateau, 2017). For example, we could assume that a stimulus can activate many elementary Poisson processes, akin to how a muscle contraction results from the activation many motoneurons. Response strength would then depend on how many Poisson processes are activated, and by their rates.

Third, the Poisson hypothesis must be merged with learning and timing models to investigate changing response rates. For example, a behavior's rate can be set to vary across trials according to the associative strength predicted by the Rescorla and Wagner (1972) model, and according to timing models within trials (Buhusi & Schmajuk, 1999; D. Buonomano, 2005; Grossberg & Schmajuk, 1989; Machado, 1997). We have not pursued these possibilities here because we wished to evaluate the Poisson hypothesis independent of assumptions about learning and timing, and because there is no accepted model that captures within- and between-trial

changes in behavior. Establishing whether the Poisson hypothesis can be successfully combined with models of learning and timing is an exciting task for future research.

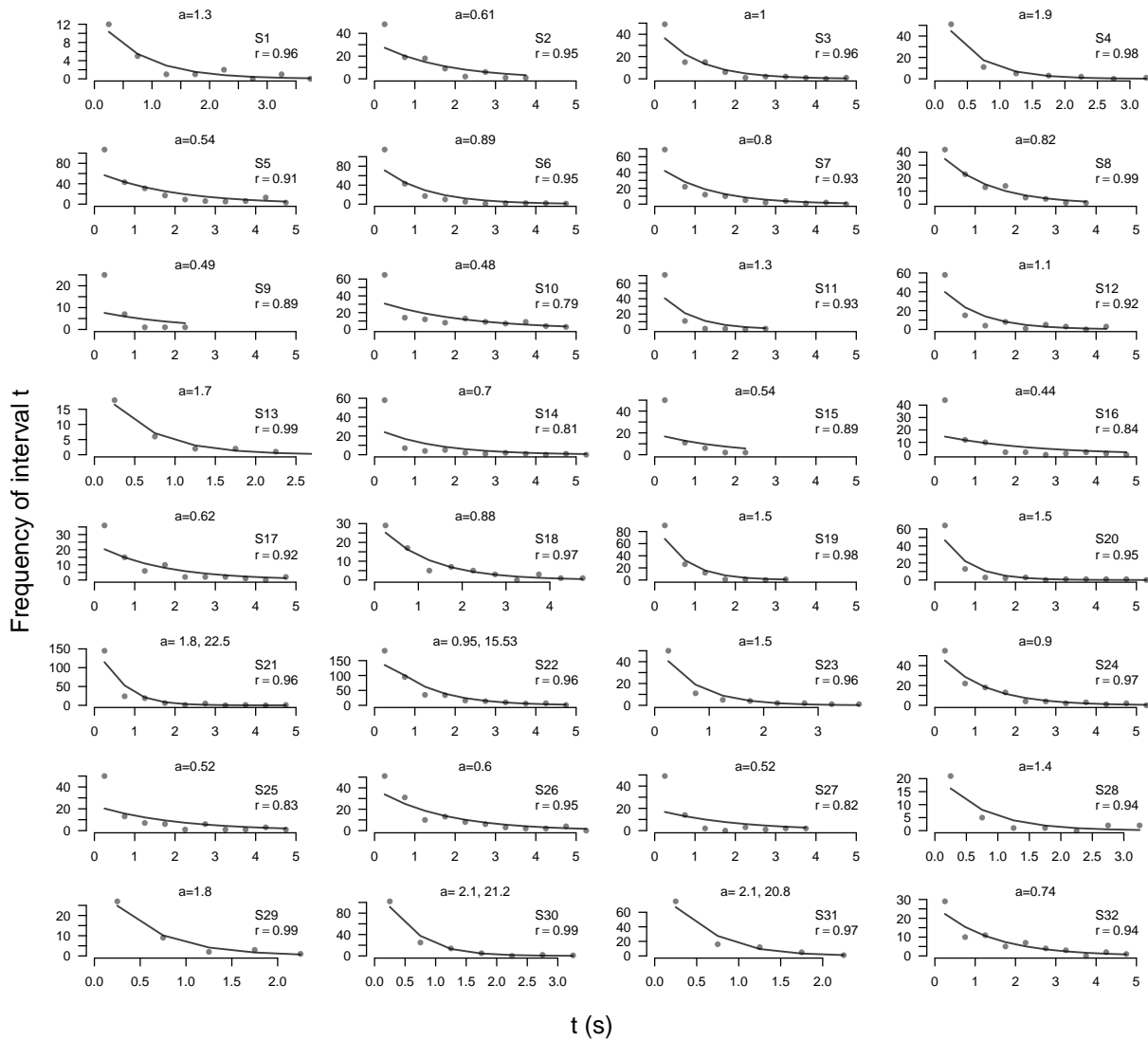
If it can be developed into a satisfactory description of behavior, the Poisson hypothesis suggests new approaches to outstanding issues. One is the extent to which organisms plan ahead. In the Poisson model there is no planning because choice of behavior depends only on the values of associative strengths, and because the exponential distribution is memoryless (see Methods). Looking for deviations from the Poisson model may be a valuable strategy to detect more complex decision making.

The Poisson model also speaks to the relationships between mechanistic and normative models of learning. Mechanistic models, such as most associative models, attempt to construct algorithms that describe observations of learning, like the Rescorla and Wagner (1972) equation. Normative models, on the other hand, attempt to understand learning by asking how a rational agent would learn. For example, the Rescorla and Wagner (1972) equation can be derived by assuming that the goal of learning is error minimization under computational constraints such as limited short-term memory (Enquist & Ghirlanda, 2005; Haykin, 2008; Widrow & Hoff, 1960). Mechanistic and normative approaches are not necessarily in contrast (Hogan, 2017; Tinbergen, 1963), although which one is more fruitful is a matter of discussion (Beckers, Miller, De Houwer, & Urushihara, 2006; De Houwer, Hughes, & Barnes-Holmes, 2016; Gallistel & Wilkes, 2016; Gershman & Niv, 2012). Within this debate, Ghirlanda (2022) showed that Equation (2) enables associative systems to perform probabilistic inferences often deemed beyond their reach (Cheng, 1997; Holyoak & Cheng, 2011). Here we showed that Equation (2) emerges from an elementary decision-making mechanism, the Poisson process. This strengthens the idea that simple mechanisms can behave, effectively, as if following sophisticated rules of inference, thus going part of the way toward reconciling mechanistic and normative models.

### **Acknowledgments**

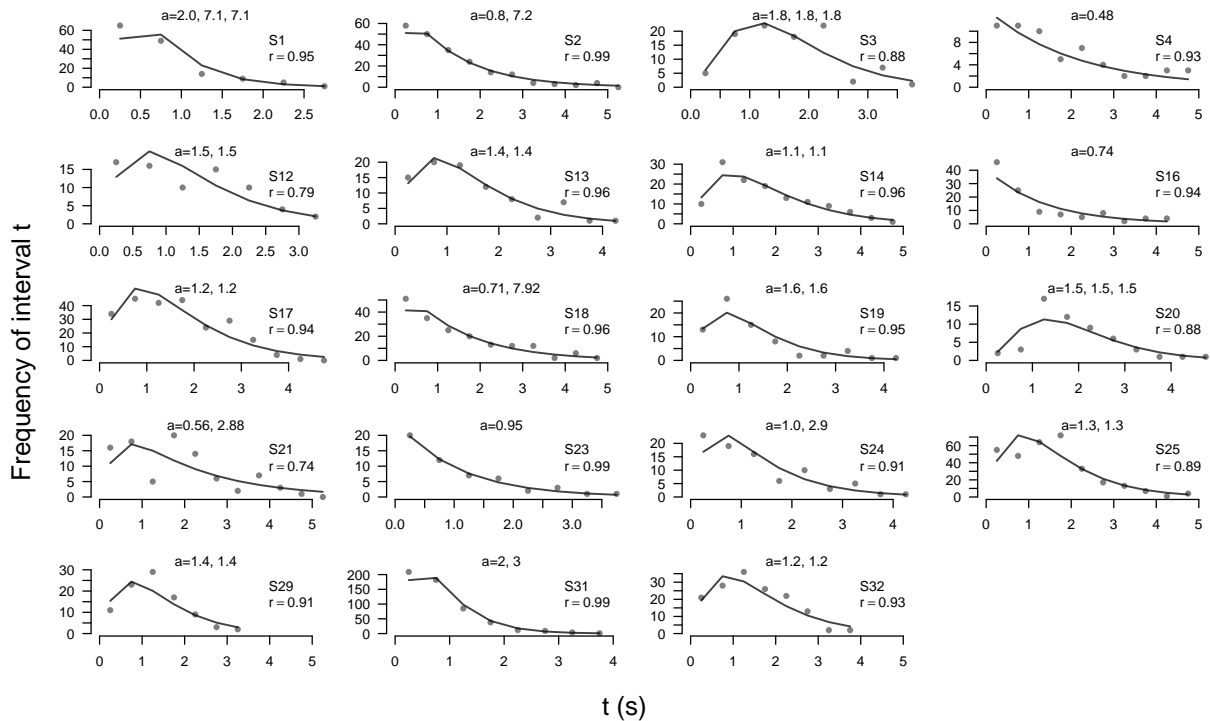
We thank Adela Iliescu for help with interpreting data files, David George for sharing unpublished data, Peter Killeen for pointing us to behavior-analytical models, Victor Navarro and

three anonymous reviewers for comments.



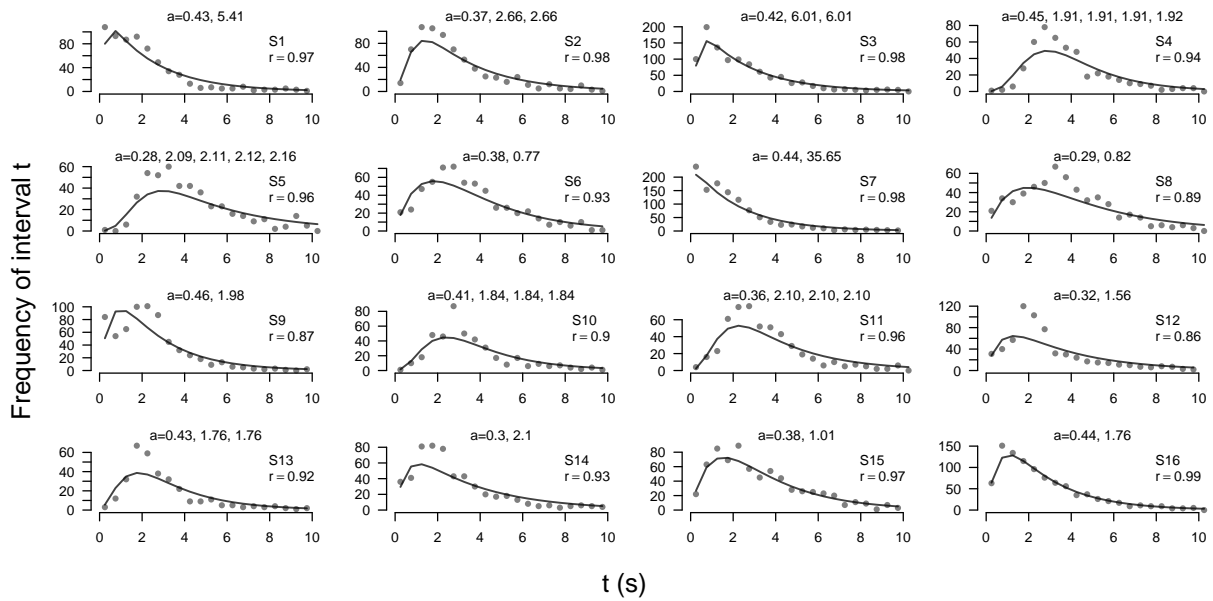
**Figure 2**

*Empirical distribution of entry-exit intervals (circles) compared to the best-fitting exponential or hypoexponential distribution (line), in data from Iliescu et al. (2018). Data are binned in 0.5 s intervals. For each bin, the predicted value is calculated as  $P_a(x_2) - P_a(x_1)$ , where  $P_a$  is the cumulative distribution function with fitted parameters  $a$  (see top of each panel) and  $[x_1, x_2]$  is the bin.  $S_i$  indicates subject  $i$ , and  $r$  is the Pearson's correlation coefficient between observed and fitted values.*



**Figure 3**

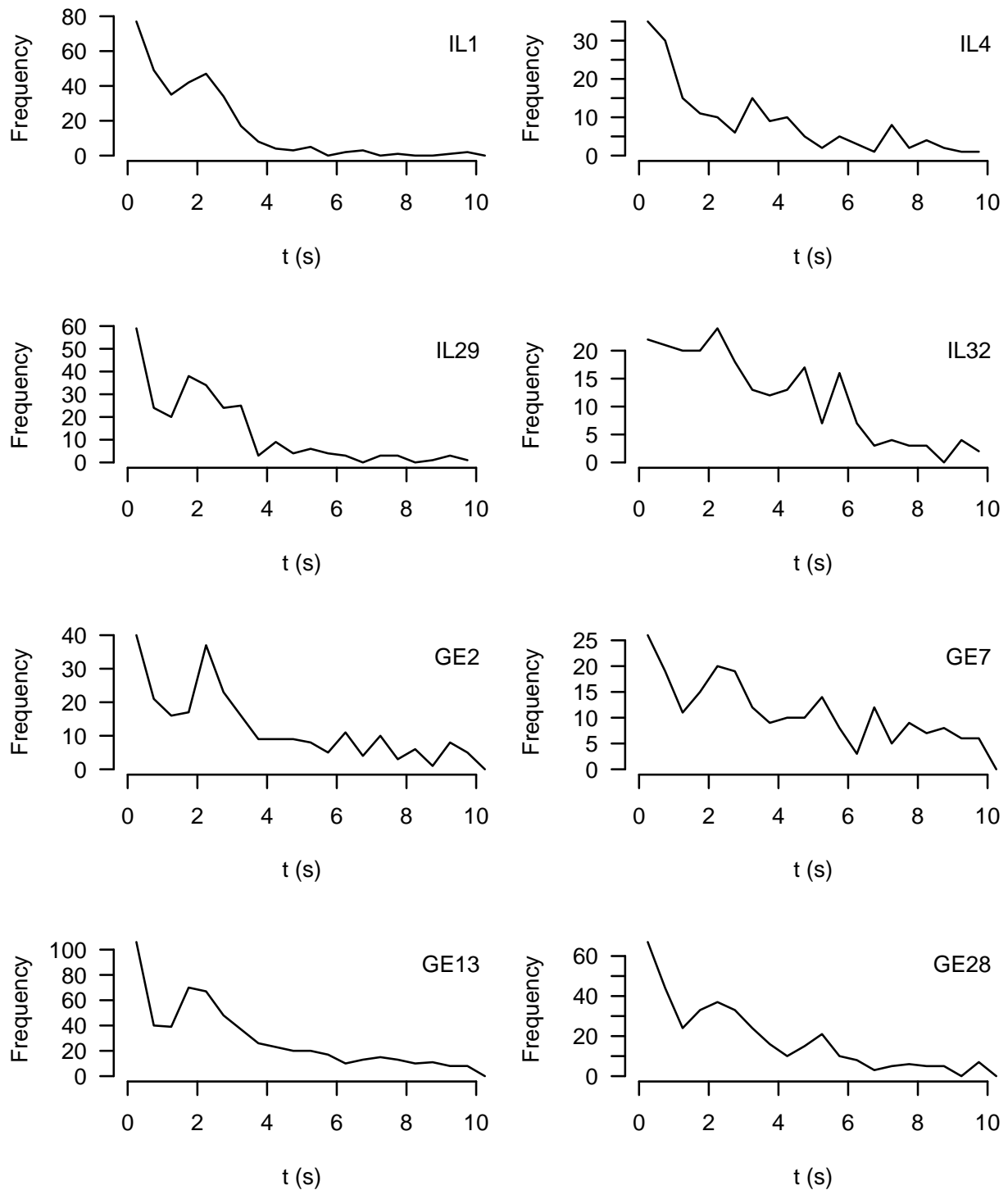
*Empirical distribution of lever-lever intervals (circles) compared to the best-fitting exponential or hypoexponential distribution (line), in data from Iliescu et al. (2018). Individuals performing fewer than 50 lever-lever transitions are excluded. See Figure 2 for details.*



**Figure 4**

*Empirical distribution of lever-lever intervals (circles) compared to the best-fitting hypoexponential distribution (line), in 16 subjects from George, D. N. (unpublished raw data).*

*See Figure 2 for details.*

**Figure 5**

Waiting time distributions for entry-entry intervals in some subjects from Iliescu et al. (2018), labeled IL, and George, D. N. (unpublished raw data), labeled GE.



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