

Optimal timing

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In recent years, there has been a growing attempt to evaluate time perception and timed behavior against an optimal benchmark. What does an optimal timer look like? And how does one behave? In the first part of the review, we give some preliminary evidence to suggest animals build a generative model of elapsed time. In the second part of the review, we give some preliminary evidence that animals estimate their own timing measurement error, and compute the statistically optimal response time constrained by this error. Lastly, we discuss the optimal timing framework as an alternative language in which to think about behavior.

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Current Opinion in Behavioral Sciences 2016, 8:276–281

This review comes from a themed issue on **Time in perception and action**

Edited by **Warren H Meck** and **Richard B Ivry**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 23rd February 2016

<http://dx.doi.org/10.1016/j.cobeha.2016.02.031>

2352-1546/Published by Elsevier Ltd.

Introduction

Animals extract temporal information from their environment, and use this information to guide their behavior. Over the past half-century, scientists have discovered an impressive set of principles that seem to guide these processes. The most notable example is Weber's Law [1], in which both the standard deviation and mean of a temporal estimate scales with the true interval such that their ratio is constant ($\sigma/\mu = \omega$). Another notable result is that timed behavior is often governed by an internal threshold for when to abruptly start or stop responding [2,3]. Findings like these are now so robust in the literature that any model that does not produce them is immediately discarded.

These results were found using standard psychophysical and conditioning approaches. Each approach carries with it a guiding framework and a language in which to communicate. The approach we take in this article is to view “man as a intuitive statistician” [4•]. This framework uses the

language of statistics. Humans and other animals make *inferences* about the state of the world given the data. Animals *estimate* time intervals, and those estimates have *measurement error*, which can themselves be estimated. A natural question to ask in this framework is, How good are the inferences? This question is explored in the first section of this review.

Behavior, then, is the output of a statistical decision-making process that acts on inferences [5•]. Behavior is a two-stage process: the animal makes inferences about the state of the world, and then acts on those inferences with either a computed or cached strategy [6]. A natural question to ask here is, How good are the strategies? This question is explored in the second section of this review.

It is important to note that this framework (and the language it uses) is meant to guide research, not reflect mechanism. It may be that the brain really uses Bayes' Rule to make inferences about temporal intervals [7,8•], and then uses Statistical Decision Theory to decide how to act. Or it may not. Either way, the approach has already led to unique results and may be well on its way to finding new guiding principles that inspire more biologically plausible process models. And, as a worst-case scenario, this framework gives us a principled benchmark from which animal behavior can be compared. Another way to say this is that an *as-if* model (i.e. the animal behaves as if it were Bayesian) is often more useful than a misleading process model.

Optimal inference

Time perception is the output of a generative model acting on an internal clock. To an intuitive statistician, time intervals are inferred from some internal mechanism that marks the passage of time. (The neurobiological details of this mechanism are still largely unknown.) This time-keeping mechanism is accurate, but like any other measurement device, it comes with measurement error (e.g. noisy neurons). This creates uncertainty about elapsed time, and means that animals should not just report the read-out of their internal clock like a wrist-watch. This is why the intuitive statistician builds a generative model of elapsed time. Given this, optimal timing requires by definition that animals make inferences about elapsed time, given the statistics of their internal time-keeping mechanism(s).

Bayes' Rule provides the critical mathematics. An ideal Bayesian timer computes the most probable (posterior) elapsed time t by combining prior information with the current noisy read-out of an internal clock (likelihood).

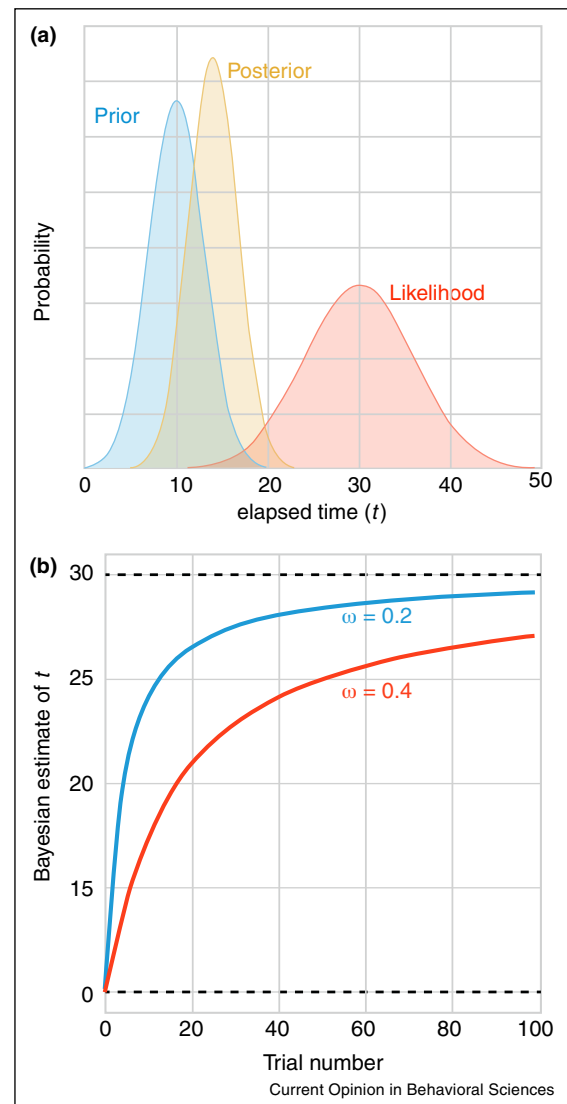
Assume an animal's internal clock reads τ , and has known measurement error ω . The likelihood of obtaining that particular read-out of the internal clock given that t has really elapsed is $p(\tau|t, \omega)$. Since t is unknown, the likelihood is a function that maps any value of t to its likelihood of having generated a clock signal of τ . Assuming measurement error is Gaussian, the likelihood function is also Gaussian, centered around τ . For Gaussian likelihood functions, the most likely time is whatever the clock says. This much is a trivial addition to theory, simply turning a deterministic clock into an inference problem using a generative model.

But prior statistical information goes a long way. An ideal Bayesian timer keeps track of the most probable intervals it has seen in the past, and by extension, knows how probable an interval is, denoted $p(t)$. Both the likelihood and the prior are functions of t . Combining the likelihood and the prior via multiplication (then normalizing) gives the posterior function — the posterior estimate of how probable any t is to be the real elapsed time (see Figure 1). The maximum of this function gives the maximum a posteriori estimate of t (the mean or median are other candidates for optimal time perception. Which one animals use, if any, is an open experimental question).

Bayesian timing makes several predictions that are just beginning to be studied. First is that the statistics of the durations must be able to be learned. Acerbi *et al.* [9] showed humans can learn some higher order statistics from distributions, up to the 3rd moment (skew), but that higher orders were harder to learn (e.g. kurtosis, multimodality). Church and Lacourse [10] showed that rats behave differently when presented with intervals from different distributions that only differ in their higher order statistics (their mean and variance were the same). [11^{*}] showed that monkeys can infer the probability of a reward in real-time, even for bimodal distributions. That is to say, there is strong evidence that humans and other animals can discriminate at least the first few moments of timing distributions.

A second prediction of Bayesian timing is that the manipulation of the prior information can change perception. Jazayeri and Shadlen [12^{**}] asked participants to reproduce the interval they just heard (an auditory tone). The key manipulation in the experiment was that, in each block, the tone durations were uniformly distributed over some range, but the range changed across blocks. Critically, the ranges overlapped to some degree so that the a few of the same intervals were presented in each block. The participants judged these durations differently, overestimating them when they were surrounded by longer intervals relative to when they were surrounded by shorter intervals. In other words, the prior information about which tone durations were likely influencing the

Figure 1



Bayesian time perception. (a) The animal builds a generative model of the elapsed time (yellow) by integrating its noisy clock signal (red) with prior information (blue). The best estimate of the elapsed time is the maximum of the posterior (yellow) distribution (although the mean or median can also be used). (b) The animal learns a new interval through Bayesian updating, where the posterior becomes the prior for the next trial. The Bayesian point-estimate (the MAP of the posterior distribution) follows the traditional learning curve, with learning rates inversely proportional to the Weber fraction (ω).

participants toward reproducing intervals in that range. A similar result was obtained in musicians [13].

A third prediction is that, because prior information is obtained over time and stored, there should be trial-by-trial effects [see 14,15^{*}]. Context effects described above and trial-by-trial effects come about because of changes to the prior information. But trial-by-trial effects are, by definition, short lived. The same interval can be judged

shorter or longer than a referent depending on whether the referent came first or second, or whether the previous trial had a longer or shorter duration [16].

Together, these results suggest that humans and other animals have the capacity to learn the statistics of temporal distributions, store those statistics, and are biased by them. They do so in a way that suggests they are Bayesian timers, although much more work is needed to make that statement with confidence.

Optimal temporal decisions

Writing about the visual system, Marr [17] described three levels of analysis (algorithmic, physical, and computational). These levels apply to study timing behavior, too. Each level of analysis carries with it a framework and a way of thinking about timing behavior. Much of the timing literature fits into the algorithmic camp by developing process models that describe the moment-to-moment changes in intervening variables as a function of time and reward history [18–21]. Optimal timing models, on the other hand, are firmly in the computational camp.

Here, behavior is the output of a series of decisions about what response to make, when, and how much [22,23]. Statistical Decision Theory [24,25] provides the critical mathematics although only a small subset of that framework is needed here [see 26,27]. The goal of the animal is to respond at a time that maximizes some value function (or minimizes some cost function). But because of measurement error in the brain's clock, animals cannot always hit that exact time. The result is a distribution of response times whose statistics are only partly controlled by the animal. This creates uncertainty in any timing task, and causes temporal behavior to fall under the category of decision making under risk. The best the animal can do is maximize the expected value given the constraints imposed by the measurement error of the clock.

As long as the animal can estimate its own measurement error, all is not lost. The response distribution (which is a product of a decision to respond and unintended measurement error) is a probability distribution over possible outcomes. Responding at time t results in the reward associated with responding at time t . The expected value of any choice is just the weighted sum of the possible outcomes:

$$E[t|\omega] = \int_{t=0}^{\infty} g(t)p(t|\mu, \omega)dt \quad (1)$$

where μ is the intended response time (the choice), and $p(t|\mu, \omega)$ is the probability of responding at t when the choice was μ with measurement error ω . The animal gets rewarded for the actual response time, not the intended

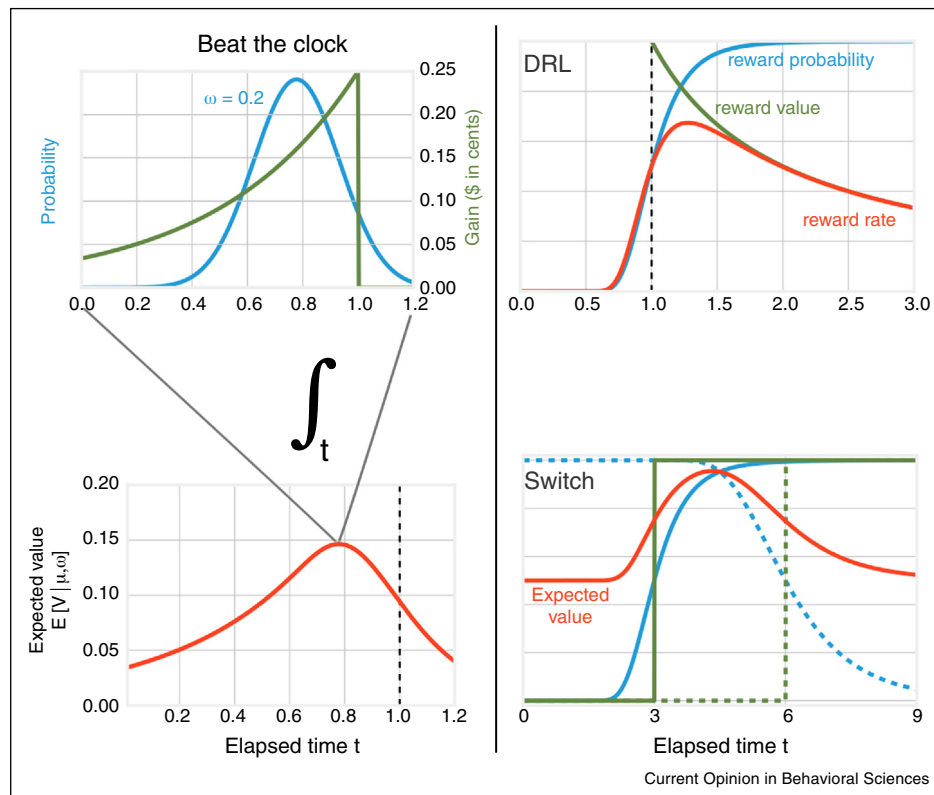
one, so the gain function g is a function of t . The goal of the animal is to choose a response time μ that maximizes $E[t|\omega]$. This time can either be explicitly calculated or easily simulated.

There is now strong evidence that animals ranging from humans to mice come close to choosing the optimal strategy, with some caveats discussed below. The most straightforward test of this optimal strategy is the Beat-the-Clock task, in which participants are rewarded as a function of how close they can get to a target interval without going over [28,29]. The gain function is an exponentially increasing function of time, reaching a peak at the target time, and dropping to zero after. A strategy that ignores measurement error is to choose to respond exactly at the target interval. But this strategy is suboptimal because response time variability means that many of the responses fall beyond the target interval, earning no reward. An optimal strategy is to choose a μ that positions the response distribution just far enough away from the target interval to avoid losing too much reward. Humans earn about 99% of the maximum gain they could (given their measurement error).

A closely related task is the differential reinforcement of low rates (DRL) task [30,31**]. Here, participants are rewarded if (and only if) the time between responses is greater than some target interval. In this case, Eqn (1) reduces to be the fraction of responses greater than the interval — the probability of a reward. Dividing by the time between rewards μ gives the reward rate (Figure 2: DRL). Humans, rats, and mice earn more than 90% of the maximum possible gain on this task [32,33]. An interesting caveat is that the 10% discrepancy from optimality was systematic; animals responded earlier than they should have. Further, rats trained on very long intervals (greater than 25 s) were highly suboptimal, and largely did not account for their own measurement error. These results are an important deviation from theory that should be studied in more detail.

Humans, rats, and mice can choose a time to switch from one option to another in a way that nearly (about 98%) maximizes reward ([34**,35]; [Figure 2: Switch]). Recent evidence suggests the decision about when to switch is made by rapidly integrating previously learned task parameters, rather than hill-climbing a reward function [36**]. And mice nearly maximize reward on the related bisection task [37,38], but humans do not maximize reward when they have to make a series of timed decisions in a row [39*]. Humans can optimally compensate for experimentally added response time variability [40*], but there is preliminary evidence that rats and mice do not. Further, humans can optimally decide how long to view a stimulus before executing a movement [41], but have trouble optimally planning a sequence of movements in time [42].

Figure 2



Statistical Decision Theory in action. **(Left panels).** In the Beat-the-Clock task, participants are rewarded for responding as close to a target interval without going over. The expected value of a chosen response time depends on the gain function, and on the response distribution (which depends on the measurement error in the clock; top figure). The time with the highest expected value is the optimal choice (bottom figure). **(DRL).** In the DRL task, participants are rewarded for responding after a target interval. Because animals naturally discount future rewards, the gain function decays over time (green). The reward rate function (red) is the element-wise multiplication of the gain function and the probability of a reward (blue). **(Switch).** In the switch task, participants are asked to switch their response at the appropriate time in order to classify a tone as either short or long. The expected value (red) is the weighted average of correctly saying short (solid curves) and correctly saying long (dashed curves).

Together, these results suggest that for simple tasks, humans and other animals take into account their own measurement error when deciding when to respond, and do so in a way that comes close to maximizing reward (or reward rate). But this ability may break down fairly quickly when taxed. Like any discipline in its infancy, we should focus on cataloging the ways in which animals depart from the optimal benchmarks with the hope that a pattern will emerge.

One possible source of departure is that the optimal model is wrong. This is the 'Is it plugged in?' alternative because it's the first one to look for, and sometimes right. For example, the Random Dot Motion task [43] is the standard task for studying the speed-accuracy tradeoff in perceptual decisions [44]. If the benchmark were to optimize accuracy, participants would fail to be optimal. So, too, if the benchmark were speed. Finding the appropriate benchmark (in this case, it may be reward rate [44,45]) is the key first step.

Another possible point source of departure is suboptimal inference [46••]. In this section, we assumed for simplicity that the animals knew the target intervals veridically. But this information, along with the task structure itself, has to be learned through experience. In the Beat-the-Clock and DRL tasks (described above), animals have to infer the target interval using only their estimated response time and whether a reward occurred or not. This is a hard statistical inference to make, and it may be that the animals came close enough, but were not dead-on.

Lastly, animals may use heuristics instead of explicitly maximizing value functions. There is a strong case for this in human economic decision-making tasks [47] but has not been studied rigorously in the timing domain. Of course, there are other alternatives not mentioned here. But the point is that having a solid theoretical benchmark grounded in as few free parameters as possible is ideal for studying behavior because it forces us to rigorously specify the task, posit the goals of the behavior, and gives a

concrete starting point for studying deviations from the optimal strategies.

Conclusion

Every generation dating back to the 1930s has suggested in some form that animals build generative models of their environment [4,48–50,51*]. Some of these suggestions have been verified in the brain; there really are cognitive maps in the hippocampus [52–54], and it is starting to look like some brain areas integrate evidence in favor of hypotheses [55,56]. Moreover, brains certainly have the capacity for Bayesian updating [7], but they do not always act as if they do [57,58]. There is also quite a bit of evidence suggesting animals use cached strategies that can be highly suboptimal [see 59]. These disparate findings have caused controversy for generations, and the debate is likely to rage on.

The important thing is that we don't throw the baby out with the bathwater. These debates have generated a tremendous amount of original research that has given scientists insight into behavior at every level of analysis. We hope timing research is no different.

Conflict of interest statement

Nothing declared.

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