



Time's crooked arrow: optimal foraging and rate-biased time perception

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Time perception is critical to animal behaviours requiring anticipation of future events based on present information about the environment. Most models of animal foraging assume that animals are capable of measuring absolute time despite evidence that animals measure time with predictable biases in mean and variance. We incorporate the evidence for a rate-biased subjective time perception into a classic model of optimal foraging, the marginal value theorem. If acceleration of the clock rate is proportional to food intake rate and time is perceived similarly when in transit between patches as it is while waiting in a patch following eating, organisms are predicted to follow the predictions of the marginal value theorem exactly. However, a nonlinear relationship between clock rate and food intake rate, unequal wait and transit time perception, or any lag in the clock predicts characteristic suboptimal behaviour. We discuss how this mechanism for suboptimal behaviour compares with others in the literature and how it can be recognized in experiments.

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Many models of animal foraging assume that organisms are able to perceive the passage of time accurately. For example, models of either the optimal time or the optimal intake rate at which to leave a patch depend on the ability to measure time. The underlying assumption of absolute temporal perception is unquestioned in many models of animal foraging (Charnov 1976; Stephens & Krebs 1986; Adler & Kotar 1999). However, some evidence suggests that animals are unable to measure temporal events objectively and that temporal perception is influenced by factors external to the animal (Roberts 1998; Shettleworth 1998). The present investigation aims to elucidate the consequences of rate-biased time perception for animal foraging by incorporating empirical observations of time perception into a classical optimal foraging model, the marginal value theorem (Charnov 1976).

Perception of time has been shown to be influenced by many factors, including temperature (Wearden 1991; Wearden & Penton-Voak 1995), diet (Meck & Church 1987), external click trains (Penton-Voak et al. 1996), intertrial interval (Spetch & Rusak 1989), time of day (Meck 1991), food deprivation (Zeiler 1991) and drugs (Maricq et al. 1981).

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Rate-maximizing foragers might be most confounded when the rate of food intake itself alters the perception of time (Killeen & Fetterman 1988; Bizo & White 1997). Figure 1 presents the data of Bizo & White (1997), where pacemaker rate is calculated by assuming that the behavioural state that correlates with a given behavioural response is the result of passage through sequential states at a rate governed by an internal Poisson process (for details on this calculation see Bizo & White 1995). The result in Fig. 1 typifies the large effect of food intake rate on behaviour. We interpret this as an effect on perceived time. We use the term pacemaker rate to describe a generalized behavioural response to food intake rate, without assuming any particular internal mechanism. That is to say, although we can predict the animal's behaviour by increasing the rate of an external clock, we do not assume the animal possesses such a clock.

Where this result applies to animals in the wild, feeding animals would tend to behave as if more time is passing than animals that are feeding less often (Killeen & Fetterman 1988; Fetterman & Killeen 1991; MacEwen & Killeen 1991; Raslear et al. 1992; Morgan et al. 1993; Bizo & White 1997; but see Bizo & White 1995). For example, an animal that encounters an extremely rich patch relative to those in its past will experience a slowing of the flow of external events as its temporal assessment mechanism speeds up to match its rate of resource intake. As a consequence, the animal will perceive its food intake rate

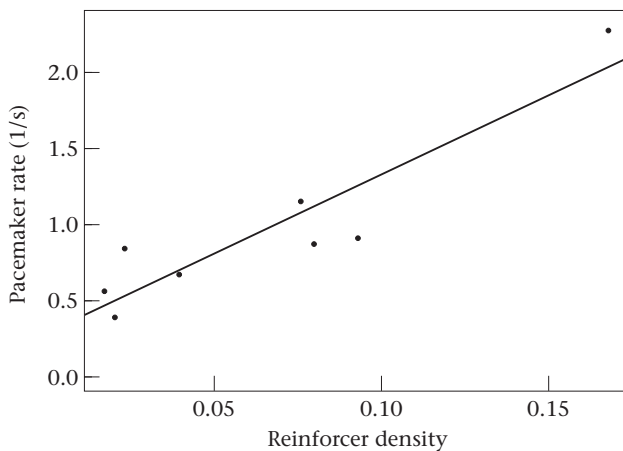


Figure 1. The relationship between resource intake and the speed of the internal pacemaker. The horizontal axis represents the seconds of access to food per second of experiment, averaged over the duration of the experiment. The vertical axis represents the estimated pacemaker rate for pigeons responding in a two-alternative free-operant psychophysical choice procedure. The line represents a linear regression with an approximate slope of 9.5/s, which is in general agreement with the slope of 10.7/s found by Fetterman & Killeen (1991) and of 10.8/s found by Killeen & Fetterman (1988). Drawn from data supplied by L. Bizo (from Bizo & White 1997).

to be lower than it truly is, underestimate the quality of the patch, and leave too soon.

To assess the consequences of the environmental effect on time perception, we analyse an optimal foraging model well established in the literature, the marginal value theorem (Charnov 1976). A substantial amount of empirical evidence supports the qualitative conclusions of the marginal value theorem (reviewed in Stephens & Krebs 1986; also see Zeiler 1991; Cassini et al. 1993; Jiang & Hudson 1993; Bonser et al. 1998). Many animals appear to be rate maximizers and leave patches when the rate of resource intake is approximately equal for all patches and also stay longer in patches as transit times between patches increase. However, there is ample evidence that animals often fail to obey the quantitative predictions of the marginal value theorem (Pyke 1983; see reviews in Stephens & Krebs 1986; Shettleworth 1988). Animals may stay longer than expected (e.g. Cassini et al. 1990, 1993; Crowley et al. 1990; Kamil et al. 1993; Shipley & Spalinger 1995), leave too early (e.g. Alonso et al. 1995), or alter their foraging behaviour based on other environmental cues such as predator abundance, resource height, or social interactions (e.g. Jiang & Hudson 1993; Holtcamp et al. 1997; Livoreil & Giraldeau 1997).

One hypothesis to explain these discrepancies is that animals fail to forage optimally with respect to the marginal value theorem because they are unable to measure time accurately. Animals with rate-biased time perception are unable to measure travelling time between patches or time spent in a patch absolutely. We assume that the timing mechanism of the animal can be approximated with a variable rate pacemaker, without making any specific assumptions about how the animal achieves this. In the behavioural theory of timing (BET) the animal may

measure rates via arousal level (Killeen et al. 1978) or the rate or length of a sequence of behaviours associated with a particular environment (Killeen & Fetterman 1988). In the scalar expectancy theory (SET) the animal may measure rates as the number of internally generated pulses received by a particular part of the nervous system that acts as an accumulator (Church & Gibbon 1982). These two models for understanding the psychological features of animal timing have both received a great deal of attention and varying degrees of support (see Church & Gibbon 1982; Gibbon et al. 1988; Killeen & Fetterman 1988; Kacelnik et al. 1989; Gibbon 1995; Machado 1997; Staddon & Higa 1999). While we recognize that the general interpretation of the variable rate data shown in Fig. 1 is most appropriate to the BET, we feel that the behaviour that generated this data is not incompatible with mechanisms hypothesized by SET under the influence of external modulators, which could influence the rate or accuracy of accumulated temporal events.

A variety of other optimal foraging models have empirical support besides the marginal value theorem, including, for example, efficiency maximizing and utility maximizing. These models and the support for them are detailed elsewhere (for an introduction to utility maximizing see Stephens & Krebs 1986; Real 1992; for efficiency maximizing see Ydenberg et al. 1994). But these too depend on time perception when foragers must make decisions based on time allocated to different choices. The argument that we develop for the marginal value theorem is, therefore, likely to have relevance in these contexts as well. Another important feature of time perception that has been used to understand errors in foraging is that described by Weber's law. Weber's law is that the perceptual increase in variance of the perceived interval is proportional to the duration of the interval encountered (Shettleworth, 1998). Excellent work has been done on this subject as it pertains to foraging in variable interval environments and it is an important feature of cognitive models of animal foraging (Gibbon et al. 1988; Brunner et al. 1992; Todd & Kacelnik 1993).

Here we concern ourselves only with a detailed exploration of rate-biased time perception, where the only nonfood interval (travel between patches) is held constant. Patch assessment is assumed to be based on the rate of perceived continuous food intake once an animal arrives in a patch following a constant travel time from the preceding patch. Although many animals forage in resource environments that are not continuous, where food is parceled out in discrete quantities, results from a continuous approximation appear to generalize well to those environments (Shettleworth 1998).

Our models investigate the consequences of rate-biased time perception by quantifying predicted deviations from the optimal departure time achieved by a hypothetical forager with a perfectly autonomous clock. We first consider organisms where clock rate changes linearly with food intake rate, showing that they can achieve the optimal strategy. We then show three generalizations that lead to characteristic suboptimal behaviour: differences in clock rate when travelling between patches and waiting in a patch, nonlinear dependence of clock rate on

food intake rate, and a lag in clock response. We discuss the conditions where mistakes due to rate-biased time perception are likely to be greatest, and propose behavioural experiments to test the importance of this mechanism. Finally, we discuss the potential benefits of a rate-biased clock for foraging organisms, and attempt to predict when benefits outweigh the potential foraging costs.

MARGINAL VALUE THEOREM

The classical marginal value theorem describes the behaviour of a rate-maximizing animal foraging in an environment consisting of well-defined resource patches separated by empty space (Charnov 1976). Resources within a patch are monotonically depleted during foraging. When an animal leaves a patch, it spends an average transit time, T , between patches before finding another patch. Animals maximize resource intake by choosing the best time, t^* , to leave a patch.

The animal seeks to maximize the rate of intake, R , which is equivalent to the cumulative resource acquired, $F(t)$, divided by the time spent acquiring it, $T+t$, or

$$R = \frac{F(t)}{T+t}. \quad (1)$$

The rate-maximizing patch departure time satisfies the equation

$$F'(t^*) = \frac{F(t^*)}{T+t^*} \quad (2)$$

(Charnov 1976), which specifies the departure time when the instantaneous rate of return in the patch is equal to the global average rate of return. It predicts that animals should leave all patches at equal rates of intake.

RATE-BIASED TIME PERCEPTION

Let the cumulative perceived duration be $aT+Q(t)$, where a is the characteristic rate of the internal clock when the animal is travelling, and $Q(t)$ is the perceived time in the patch at time t . We can rewrite equation (1) in terms of a perceived rate, R_p , as

$$R_p = \frac{F(t)}{aT+Q(t)}. \quad (3)$$

The maximum of R_p occurs for the value of t solving

$$\frac{F'(t)}{Q'(t)} = \frac{F(t)}{aT+Q(t)}. \quad (4)$$

This is the rate-biased marginal value theorem. When the animal's perceived rate of instantaneous intake, food per perceived second, equals its perceived rate of global intake, it should depart. This solution is thus identical to the marginal value theorem except that the optimum is based on perceptual components of the animal's nervous system.

The animal's cognitive faculties operate as a homothetic translation of time, stretching or shrinking time along its axis. When time is perceived absolutely, the forager can achieve the rate-maximizing solution. With rate-biased time perception, the animal may make mistakes by leaving patches at a perceived optimum that is different from the rate-maximizing optimum. In what follows we develop three detailed and testable predictions based on specific instances of this model.

Instantaneous Linear Changes in Clock Rate

To a first approximation, the psychophysical evidence suggests a linear relationship between food intake rate and pacemaker speed (Fig. 1). We assume that $Q'(t)$, the instantaneous pacemaker speed while in a patch, is

$$Q'(t) = b + sF'(t). \quad (5)$$

The slope of the line in Fig. 1 is s , the Y intercept is b . We allow the possibility that the clock rate a during travel (the travel rate) might differ from the baseline rate b when in a patch but not eating (the wait rate). The cumulative perceived time in the patch $Q(t)$ is then

$$Q(t) = bt + sF(t) \quad (6)$$

We can substitute these into the rate-biased marginal value theorem, equation (4), to find

$$\frac{F'(t)}{b + sF'(t)} = \frac{F(t)}{aT + bt + sF(t)}. \quad (7)$$

When solved for $F'(t)$, as in the classical marginal value theorem, we find

$$F'(t) = \frac{F(t)}{\frac{a}{b}T + t}. \quad (8)$$

In the linear case, if an animal experiences the same pacemaker rate when travelling and waiting, this equation matches the classical marginal value theorem, equation (2), and the animal will behave optimally. This is remarkable because it implies that benefits of an increased pacemaker speed (e.g. arousal level) can be enjoyed without reductions in foraging rate.

If the transit pacemaker rate were different from the waiting pacemaker rate, then the animal would leave at a nonoptimal time as shown in Fig. 2. If the slowest possible pacemaker rate in a patch exceeds the characteristic transit rate ($b > a$), then animals should leave early, and conversely.

Indirect evidence for a visually driven 'odometer' in honeybee's, *Apis mellifera ligustica* Spinola, was recently provided by Srinivasan et al. (2000). If the mechanism for short interval timing in animals is similarly affected, travelling animals may perceive more rapid passage of time ($a > b$) than an animal waiting at a single location, leading to later than optimal departure times. A trend in the optimal foraging data towards later than optimal departure times would be consistent with this prediction.

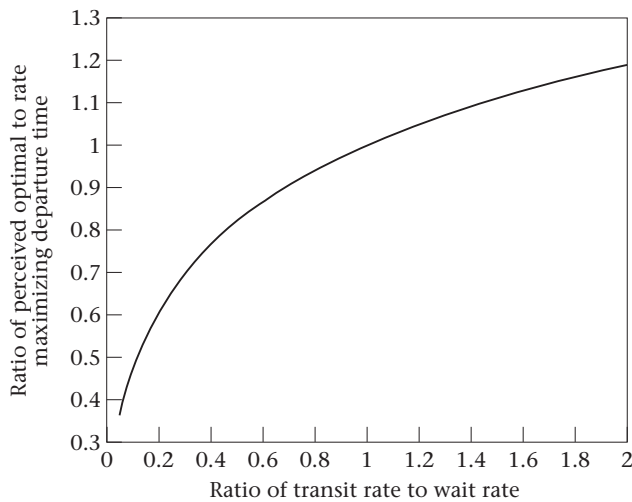


Figure 2. The relative departure time as a function of the ratio of the pacemaker speed during transit, a , to that while waiting, b . Vertical axis values greater than 1.0 represent departures later than the optimum; values less than 1.0 represent departures earlier than the optimum.

Equation (8) may fail to match real cognitive phenomenon for two reasons, which we will subsequently address: the pacemaker might not respond linearly to intake rate, and there might be a lag in the internal pacemaker rate following a change in the external event rate.

Nonlinear Changes in Clock Rate

If the pacemaker has a nonlinear response to food intake rate, the models predict specific deviations based on the curvature of the nonlinear function. In particular, suppose that the pacemaker speed follows

$$Q'(t) = b + sG(F'(t)). \quad (9)$$

for some nonlinear function G . Then perceived time in the patch is

$$Q(t) = bt + s \int_0^t G(F'(\tau)) d\tau. \quad (10)$$

Substituting into the rate-biased marginal value theorem, equation (4), gives

$$\frac{F'(t)}{b + sG(F'(t))} = \frac{F(t)}{aT + bt + s \int_0^t G(F'(\tau)) d\tau}. \quad (11)$$

Appendix 1 uses Jensen's inequality to show that the animal leaves early when the function G is concave down, and late when the function G is concave up.

If animals have an upper limit on perceived time rate, the relationship shown in Fig. 1 would become concave down for sufficiently large values of reinforcer density. This would imply that animals would be more

inclined to leave early if they encountered high reinforcer densities.

Lagged Changes in Clock Rate

The instantaneous linear case is mathematically convenient but the evidence for a lag in rate-biased time perception is convincing for two reasons. First, experiments reporting increases in pacemaker rate involve rewarding the animal with food and then, when the animal is not eating, probing the animal's time perception. The effects of an increased pacemaker rate persist when the animal is no longer eating. Second, animals tested repetitively without rewards show a gradual slowing of the internal pacemaker (Morgan et al. 1993; Killeen et al. 1999).

One simple way to incorporate a lag into the model assumes that the pacemaker rate $Q'(t)$ obeys the differential equation

$$Q''(t) = \alpha (b + sF'(t) - Q'(t)), \quad (12)$$

and thus decays toward the instantaneous value at rate α . If α is large, perceived time approximates the instantaneous linear case. If α is zero, the pacemaker measures absolute time.

For simplicity, we assume that transit times are long enough for the pacemaker rate to have decayed to the transit rate upon arrival in a patch. The solution of this linear differential equation can be written as the integral

$$Q'(t) = \int_0^t (b + sF'(t - \tau))g(\tau) d\tau + \int_t^\infty ag(\tau) d\tau \quad (13)$$

with $g(\tau) = ae^{-a\tau}$. We will demonstrate our results for any form of $g(\tau)$, thus modelling the pacemaker rate more generally as a weighted average over prior environments.

A typical time course for the lagged pacemaker rate is presented in Fig. 3 (solid line) compared with that for the pacemaker with instantaneous rate changes (dotted line). The pacemaker rate initially increases to match the steady state food intake rate and then decreases to the waiting rate, b , as the resource depletes. Initially the animal's pacemaker is running at the transit speed. As the animal begins to find food, its pacemaker speeds up. At some point the pacemaker will again slow down as food depletes. Then the pacemaker rate will have caught up, and overshoot, the slowly decreasing steady state rate.

In Appendix 2 we show that any lag of this form will induce the forager to leave early if the transit rate is equal to the wait rate, or $a=b$. This result is shown graphically in Fig. 4, where the ratio of perceived optimal departure time to rate-maximizing departure time is plotted against the lag rate. Notice that for very slow and very fast lag rates the ratio approaches equality.

DISCUSSION

Animals behave as if time is passing at a rate that is a linear function of the rate of food intake (Killeen &

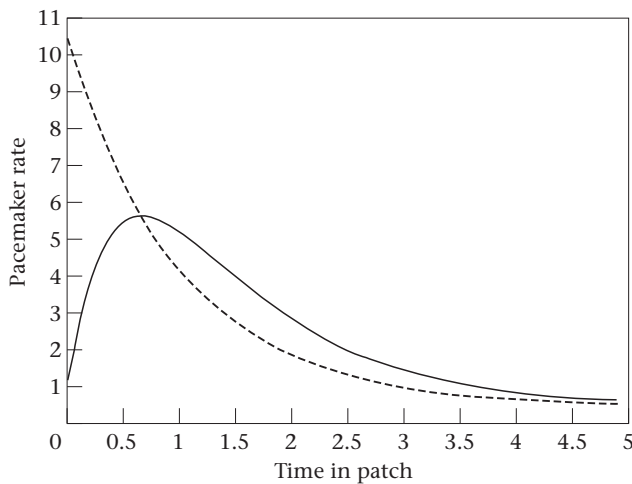


Figure 3. Time course for pacemaker rate with a lag (solid line; $\alpha=2$) and without a lag (dotted line; $\alpha=0$; other parameters are $a=1$; $b=0.5$; $\beta=1$; $s=10$). A horizontal line at the value of 1.0 would represent absolute perceived time.

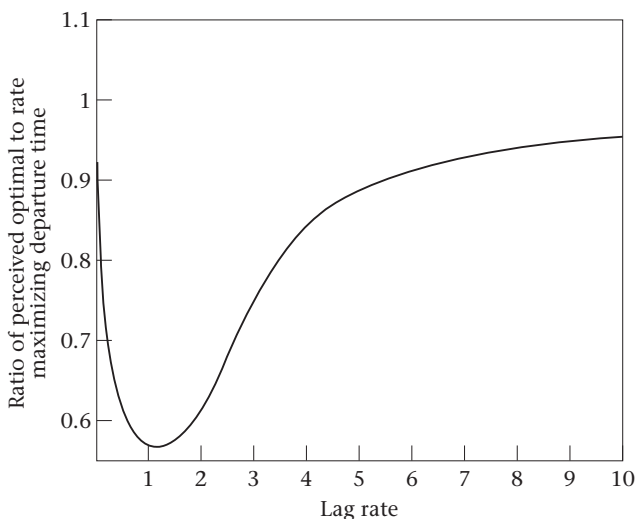


Figure 4. Relative error of perceived optimal departure time to changes in lag rate. Parameter values are as in Fig. 3, except $a=b=1$.

Fetterman 1988; Raslear et al. 1992; Fetterman & Killeen 1991; MacEwen & Killeen 1991; Morgan et al. 1993; Bizo & White 1995, 1997), and therefore, maximizing animals that forage with this rate-biased time perception are likely to make stereotypical mistakes. We describe the consequences of a linear increase in time sense with food intake along with three deviations. In particular, instantaneous linear increases in perceived time can match optimal foraging behaviour when travel times and in-patch waiting times are perceived identically. When instantaneous changes are nonlinear, animals leave early or late if the perceived time with food intake rate function is concave down or up, respectively. Lagged changes in perceived time lead to early departure times when travel and waiting times are perceived equally, but are sensitive to transit times and patch depletion rate where travel and waiting times are perceived differently.

The rate-biased marginal value theorem generates several testable predictions about animal foraging behaviour. First, it suggests that animals that appear to leave patches in accordance with the marginal value theorem are capable of this behaviour for one of four reasons.

(1) They contain an autonomous pacemaker that is not tuned by interaction with the environment.

(2) They arrived at the optimal departure time over successive generations as a consequence of natural selection acting directly on departure time, independent of perception.

(3) They have a lag-free linear clock where transit rate is equal to the wait rate.

(4) Deviations from optimal behaviour are too small to detect due to limits on experimental accuracy.

All of these possibilities are testable and relevant to our understanding of animal foraging behaviour and its cognitive control. We discuss each below.

The possibility that animals contain an absolute pacemaker for making foraging decisions contradicts the psychophysical evidence for subjective time perception. However, this data is primarily based on the responses of vertebrates, for example, rats in Raslear et al. (1992), pigeons in Fetterman & Killeen (1991), and humans in Penton-Voak et al. (1996). Other animals may have an absolute time sense.

If an animal does not have an absolute time sense, then natural selection may find the optimal departure time via other perceptual mechanisms, but this is likely to be most successful only in stable and predictable environments. Varying the resource depletion curves or waiting times in an experiment can reveal whether animals are using relatively inflexible mechanisms to make optimal departure decisions. Such inflexible mechanisms could be based on cues other than time perception, such as bio-kinetic cues as in the wapiti, *Cervus elaphus*, which leave grazing sites when the lateral angle of the neck reaches a critical inclination (Jiang & Hudson 1993). A testable prediction that follows from this argument is that animals that have evolved foraging strategies in more resource stable environments should be less likely to use time perception mechanisms than animals evolving in more resource heterogeneous environments. When resources arrive in unpredictable quantities, time perception is required to assess their relative abundance.

As we have shown, however, rate-biased time perception can lead to optimal departure times if the clock is lag-free and linear with respect to changes in resource abundance. To date, the majority of tests on the presence or absence of lag in time perception are assessed during periods without reward (Morgan et al. 1993; Killeen et al. 1999). A more complete survey of time perception would look at animals over a wide range of slowly increasing or decreasing intake rates. Perceived time during transit could be measured by manipulating transit times, which must be undertaken following a cue that signals food at a given location. This experiment would require only slight modifications to experiments previously undertaken to test foraging predictions of scalar expectancy theory (Kacelnik et al. 1989; Brunner et al. 1992).

If the animal in question does experience lagged changes in time perception as resource abundance changes, then we are left to conclude that, in the absence of some other mechanism for assessing optimal departure times (as described above), the animal is not foraging optimally in the marginal value theorem sense. Based on the assumptions made in the model, the animal is unable to perceive the optimal departure time accurately.

It is useful to summarize an animal's alternatives and their consequences. The animal can use an autonomous clock to make optimal foraging decisions, but then it must pay the price of untuned arousal. It can forage using nontemporal cues, but then it must forage in predictable environments. It can use an aroused clock to match perception to environmental cues, which will allow optimal foraging decisions except in the case where there is a lag in the clock response to resource level or the travel rate does not equal the wait rate. In the lagged case, the animal will always fail to forage optimally in the marginal value theorem sense, although it may certainly be foraging optimally in other senses. That is to say, using a rate-biased mechanism to appropriately tune arousal level implies a possible catch-22 in animal behaviour: if animals do not create their own perceptual price associated with foraging in heterogeneous environments, they may pay the price of inappropriately tuned perception (i.e. overlooking predators or food, or paying too much attention to them when there is no apparent reason to suspect their presence). A possible conclusion of this argument, taken with the empirical evidence for rate-biased time perception, is that it is more important to be perceptually calibrated with an environment than it is to maximize resource intake rate. This further supports an efficiency maximizing argument of animal foraging (Ydenberg et al. 1994).

Rate-biased time perception may be a consequence of variable arousal states during times when increased cognitive processing is beneficial (Killeen et al. 1978). Animals may increase arousal during foraging bouts for several reasons. If a particular location is profitable it will benefit animals to learn as much about the location as possible. Allocation of a limited attention to multiple features of an environment reduces an animal's sensitivity to any specific feature of the environment, leaving the animal vulnerable to predators, parasites, or bad food decisions (Metcalf et al. 1987; Godin & Smith 1988; Dukas & Ellner 1993). Fast reaction times are required in particular environments for both competitive and escape reasons. It is therefore of some import to be able to increase the total amount of attention that can be allocated during times of specific need. Enhanced arousal in the presence of predators may be an underlying mechanism leading animals to leave dangerous or unfamiliar patches sooner than they leave safe or familiar patches (see Holtcamp et al. 1997). It is not surprising then that hippocampal activity, known to be critical to spatial, temporal and olfactory learning (Thompson et al. 1982; Meck et al. 1984; Meck 1988; Ono et al. 1995; Wood et al. 1999) is directly correlated with behavioural arousal (Day et al. 1991; Thiel et al. 1998).

The evolutionary trade-off leading to variable rate pacemakers may come in terms of the high metabolic cost of nervous tissue. By weight, nervous tissue is 22 times more metabolically expensive than muscle (Aiello 1997). Adaptive behaviour requires a coevolution between the nervous system and the environment such that the costs of operating the nervous system are compensated for by the benefits that the nervous system accrues. Thus, it is beneficial to control the operational costs of the nervous system by tuning its output to match the specific needs of the environment. Evidence of a trade-off in arousal has been established for circadian schedules (Meck 1991) as well as in encounters with food (Killeen et al. 1978). A metabolic hypothesis is further supported by evidence for higher metabolic rate and other measures of cerebral activity (such as cerebral blood flow or cerebral lactate output) during wakefulness versus sleep and during tasks involving mental computation (Madsen et al. 1992; Ikeda et al. 1995).

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Appendix 1

The general case for nonlinear clock adjustments

We are interested in knowing what happens to the optimal departure time, t^* , when we include the nonlinear term in equations (9)–(11). Using the implicit function theorem, we can find dt^*/ds evaluated at $s=0$. We begin by rewriting equation (10), noting that t^* is now a function of s ,

$$\frac{F'(t^*(s))}{b+sG(F'(t^*(s)))} = \frac{F(t^*(s))}{aT+bt^*(s)+s\int_0^{t^*(s)} G(F'(\tau))d\tau}. \quad (14)$$

The derivative of this equation is then taken with respect to s . Solving for dt^*/ds and simplifying we get

$$\frac{dt^*}{ds}\Big|_{s=0} = \frac{F(t^*)}{F'(t^*)} \frac{(F(t^*)G(F'(t^*)) - F'(t^*)\int_0^{t^*} G(F'(\tau))d\tau)}{b(\frac{a}{b}T+t^*)^2 F''(t^*)}. \quad (15)$$

To determine the sign of this equation we know that $F(t)>0$ and $F'(t)<0$ and assume that $F''(t^*)<0$ (diminishing returns). We need only determine the sign of

$$F(t^*)G(F'(t^*)) - F'(t^*)\int_0^{t^*} G(F'(\tau))d\tau. \quad (16)$$

If equation (16) is positive, then $dt^*/ds<0$; the animal leaves early. If negative, then $dt^*/ds>0$; the animal leaves late.

We can determine the sign of equation (16) using Jensen's inequality (Gradshteyn & Ryzhik 1979). Jensen's inequality states that $E(G(x))\leq G(E(x))$ whenever the function $G(x)$ is concave down (the reverse is true when the function is concave up). In this case, $\int_0^{t^*} G(F'(\tau))d\tau$ can be incorporated into Jensen's inequality by recognizing that

$$\int_0^{t^*} \frac{G(F'(\tau))}{t^*} d\tau \leq G\left(\int_0^{t^*} \frac{F'(\tau)}{t^*} d\tau\right), \quad (17)$$

where

$$\int_0^{t^*} \frac{F'(\tau)}{t^*} d\tau = E(F'(t^*)) \quad (18)$$

and

$$\int_0^{t^*} \frac{G(F'(\tau))}{t^*} d\tau = E(G(F'(t^*))). \quad (19)$$

Therefore,

$$F(t^*)G(F'(t^*)) - F'(t^*)\int_0^{t^*} G(F'(\tau))d\tau \geq F(t^*)G(F'(t^*)) - F'(t^*)t^*G\left(\frac{F(t^*)}{t^*}\right) \geq 0. \quad (20)$$

Dividing through by t^* ,

$$\frac{F(t^*)}{t^*}G(F'(t^*)) - F'(t^*)G\left(\frac{F(t^*)}{t^*}\right) \geq 0. \quad (21)$$

Letting $y=F'(t^*)$ and $x=F(t^*)/t^*$,

$$xG(y) - yG(x) \geq 0 \quad (22)$$

Rearranged slightly, this equation is

$$\frac{G(y)}{y} - \frac{G(x)}{x} \geq 0. \quad (23)$$

This is true for concave down functions when $y<x$, which we know to be true given that $F'(t^*)<F(t^*)/t^*$ (which follows from the fact that $F'(t)<0$). Therefore,

$$\frac{dt^*}{ds}\Big|_{s=0} < 0. \quad (24)$$

In the concave down case, the animal leaves early. When the pacemaker function is concave up, the same argument applies and the animal leaves late.

Appendix 2

Effects of lag with linear clock adjustments

Suppose that the pacemaker rate obeys

$$Q'(t) = \int_0^t (b+sF'(t-\tau))g(\tau)d\tau + \int_t^\infty ag(\tau)d\tau$$

for some weighting function $g(\tau)$ where $\int_0^\infty g(\tau)d\tau=1$. Let

$$\Gamma(t) = \int_0^t g(\tau)d\tau$$

be the cumulative weight until time t .

If we suppose that $a=b$, this simplifies to

$$Q'(t) = \int_0^t sF'(t-\tau)g(\tau)d\tau + a.$$

The perceived elapsed time is then

$$\begin{aligned}
 Q(t) &= \int_{i=0}^t Q'(t) dt \\
 &= at + \int_{i=0}^t \int_{\tau=0}^i sF'(\hat{t}-\tau)g(\tau) d\tau dt \\
 &= at + \int_{\tau=0}^t \int_{i=\tau}^t sF'(t-\tau)g(\tau) d\tau dt \\
 &= at + \int_{\tau=0}^t sF(t-\tau)g(\tau) d\tau
 \end{aligned}$$

where we used the Fundamental Theorem of Calculus (Adler 1998) and the fact that $F(0)=0$ to compute the inner integral.

Because $F'(t)$ is a decreasing function and F is an increasing function

$$Q'(t) = \int_0^t sF'(t-\tau)g(\tau) d\tau + a > sF'(t)\Gamma(t) + a \quad (25)$$

$$Q(t) = \int_0^t sF'(t-\tau)g(\tau) d\tau + at < sF'(t)\Gamma(t) + at. \quad (26)$$

Rearranging the rate-biased marginal value theorem (equation 4) and using these inequalities,

$$\frac{F'(t)}{F(t)} = \frac{Q'(t)}{aT+Q(t)} > \frac{sF'(t)\Gamma(t)+a}{aT+at+sF(t)\Gamma(t)}.$$

Cross-multiplying and cancelling like terms gives

$$F'(t) > \frac{F(t)}{T+t}.$$

Therefore, an organism with a lag always leaves when its rate of intake is higher than the global optimum given by the marginal value theorem (equation 2), and thus leaves too early.