The psychophysiology of time perception and temporal decision making

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Abstract

Time is a fundamental dimension of our perception of the world and therefore of critical importance to the organisation of human behaviour. Without the ability to perceive time we would not be able to navigate the world in an effective way. We would not be able to perceive the causality between events, nor would we be able to account for the future. However, despite its significance, our perception of time is not veridical, and appears to be labile to many external and internal factors. (A pertinent example is the apothegm “time flies when you’re having fun”, which reflects the temporal distortions we often experience during rewarding periods.) This thesis was aimed at characterising a novel source of volatility in time perception — the effect of reward consumption — and to assess the implications of non-veridical time perception for human decision making.

The first study sought to characterise the effect of different primary rewards on interval timing. Participants performed a novel variant of a duration production paradigm, while they received different volumes of fruit juice on a trial-by-trial basis. The consumption of fruit juice lead to systematic overproductions of time (from 2-5 seconds) and this effect scaled with the volume of the consumed juice. Another four reward types were subsequently tested: money (a secondary reward), water (a tasteless, noncaloric reward), aspartame (a sweet, noncaloric reward), and maltodextrin (a tasteless, caloric reward). Maltodextrin also produced a similar effect on time productions. This pattern of results suggested that the observed effect was
likely to be due to the common caloric content of both fruit juice and maltodextrin. In sum, the first study demonstrated a novel association between biologically relevant rewards and time perception.

The second component of this thesis investigated the proposition that temporal decision making (i.e. decision making that involves time) operates on subjective representations of time. To explore this proposition, the second study investigated whether there was a relationship between individuals’ time perception and their temporal decision making. Participants performed both a temporal reproduction task and a temporal discounting task, while undergoing electrocardiography. The results provided no evidence that parameters from the temporal reproduction task were correlated with discount rates in the temporal discounting task. This did not support the idea that time perception and temporal decision making were related, at least as they were operationalised in this study. However, the behavioural measures from both tasks were independently related to some indices of autonomic nervous system function as measured by electrocardiography, suggesting distinct physiological correlates for both psychological processes.

The third study was designed to assess whether factors that impact time perception also affect temporal decision making. Participants fasted for four hours, and then completed a task similar to a patch-leaving foraging paradigm, incentivised with monetary rewards. Participants gave up waiting for rewards significantly earlier when they experienced higher rates of reward. Participants who consumed a caloric drink in between blocks also gave up waiting significantly earlier, compared to those who consumed water (i.e. participants who consumed the caloric drink were less patient). These results suggest that the consumption of biologically relevant rewards altered time-dependent decision making.
Overall, these findings support the notion that time perception can be affected by an individual’s homeostatic state, and further suggest that different homeostatic states can influence time-dependent decision making processes. Taken together, these experiments provide evidence that our experience of time may be part of a psychophysiological mechanism which may act to optimise ecological decision making.
I, Bowen J Fung, declare that this work is original and entirely my own. I conducted all studies reported here with assistance from other members of the Decision Neuroscience Laboratory at the University of Melbourne. I drafted all empirical manuscripts and revisions were created with the assistance of the manuscript’s named co-authors. These co-authors have agreed to the use of these manuscripts within this thesis. This thesis is in accordance with the guidelines for submission of a thesis with publication provided by the School of Graduate Research at The University of Melbourne. I am grateful for the support of my Supervisors, as well as the previous and existing members of the Decision Neuroscience Lab. I would particularly like to express my gratitude to Daniel Bennett, Damien Crone, Christina Van Heer, Katharina Voigt, Daniel Rosenblatt, Simon Lilburn, Hayley Warren, Will Turner, Maja Brydevall, Jessica Paul, and Marina de Saade, for enriching the environment in which this thesis was constructed.
This document puts forward a thesis regarding time perception, reward and temporal decision making. As a whole, this thesis can be organised into two main themes. The first relates to the idea that reward, and factors related to reward, can alter time perception. This idea is primarily motivated by literature showing that the neurotransmitter dopamine has robust effects on our perception of time, and is also critically involved in reward processing. The second main theme relates to the role of time in decision making and the idea that decision processes operate on a non-veridical, subjective representation of time.

There are three specific research questions which fall under these two themes. Firstly, given the neurobiological overlap between time perception and reward processing, can rewards affect time perception in humans? Secondly, provided that temporal decision making operates on subjective representations of time, is there a relationship between an individual’s time perception and their temporal decision making? Thirdly, if temporal decisions operate on subjective representations of time, can the outcomes of these decisions be altered by factors that are known to change time perception?

To address these questions and provide the appropriate background, this document is arranged into 6 chapters, with sub-sections within each chapter. The background and motivation for the research questions is derived from a selective review of the literature, which is presented in Chapter 1 and Chapter 2. These two chapters correspond to the two main themes of time perception and reward, and time perception and temporal decision making, respectively. These chapters include
general definitions, standard measurement procedures, contemporary psychological and biological models, and some details regarding the neurophysiology of both time perception and temporal decision making. Subsequent to each review is a summary of the literature, and the research questions germane to each chapter are constructed.

The three research questions above correspond to the empirical research presented in Chapter 3, Chapter 4, and Chapter 5, respectively. Chapter 3 constitutes the first series of experimental studies and provides evidence that time perception is affected by caloric primary rewards. Chapter 4 investigates the relationship between time perception and temporal decision making, and identifies some autonomic cardiac signals that are associated with individual differences in both time perception and temporal decision making. Chapter 5 is the final empirical chapter, and provides evidence that caloric primary rewards can affect ecological temporal decision making. Each of these empirical chapters has been accepted for publication in peer-reviewed journals. These chapters are therefore presented in the native format of their respective journals. As they are presented as stand-alone journal articles, a brief preface and discussion are provided to contextualise each one in relation to the overarching document. Chapter 6 contains a general summary and detailed discussion of the findings from the experimental studies, how they relate to each other, and how they address the research questions.

In this document, Figures and Tables are numbered first according to the chapter in which they belong, and then sequentially where they appear (e.g. the third figure of Chapter 2 is Figure 2.3). Figures and Tables in journal formatting are referenced according to the conventions of the journal. Note that all references to chapters, sections, tables, and footnotes are hyperlinks in electronic copies of this thesis. The work in this thesis was supported by a Faculty of Business and Economics
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The psychophysiology of time perception and temporal decision making

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List of abbreviations

ANS - Autonomic nervous system.
BeT - Behavioural theory of timing.
ECG - Electrocardiography/Electrocardiogram.
EEG - Electroencephalography/Electroencephalogram.
FI - Fixed interval.
fMRI - Functional magnetic resonance imaging.
GSR - Galvanic skin response.
HF-HRV - High frequency heart rate variability.
HR - Heart rate.
HRV - Heart rate variability.
LF-HRV - Low frequency heart rate variability.
MTV - Marginal value theorem.
SBF - Striatal beat frequency.
SDNN - Standard deviation of R-R intervals.
SET - Scalar expectancy theory.
SN - Substantia nigra.
SNC - Substantia nigra pars compacta.
SNS - Sympathetic nervous system.
TIMERR - Training-integrated maximized estimation of reinforcement rate.
PI - Peak interval.
PSE - Point of subjective equality.
PNS - Parasympathetic nervous system.
Chapter 1: Time perception and reward

“It's a poor sort of memory that only works backwards.” — Lewis Carroll, 1875.

In physics, time is a singular, fundamental quantity, inexorably bound to the second law of thermodynamics. Physical (or objective) time, is defined by its measurement. Psychological time, on the other hand, is both relativistic and multifaceted. Noted at least as early as 1865 (Mach), psychological time differs from objective time. Psychological time can be subdivided into distinct concepts such as simultaneity, succession, order, continuity, and duration (Pöppel, 1997). (“To be conscious of a time interval at all is one thing; to tell whether it be shorter or longer than another interval is a different thing.” — James, 1890.) For humans and other organisms, one could argue that the paramount function of time is in casual inference and prediction (Hume, 2003). All behaviours unfold over time, and as a result, time is an implicit dimension of all behaviours whether they relate to movement, identification, feeding, communication, co-operation or competition (Marshall & Kirkpatrick, 2015). However, above and beyond merely learning from and acting in a time-ordered environment, humans also experience time as an abstract perceptual sensation.

“There is a certain emotional feeling accompanying the intervals of time, as is well known in music. The sense of haste goes with one measure of rapidity, that of delay with another; and these two feelings harmonise with different mental moods.” — William James, 1890.
It is this perceptual experience of duration, how it differs from objective time, and how it relates to decision making, that are the primary concerns of this thesis. In other words, this thesis concerns behaviours for which time intervals are a significant predictor. Most frequently discussed will be the perception and measurement of durations in the order of sub-seconds to seconds, often referred to as interval timing. Interval timing stands in contrast to other aspects of time perception, such as the experience the psychological present or the “specious present” (“…the short duration of which we are immediately and incessantly sensible.” — James, 1890), which is often the focus when investigating temporal simultaneity or temporal order. Interval timing also relates to the representation of duration in memory, as well as the construction of expected future durations. The latter is particularly important to the second theme of this thesis, as all decisions have consequences that are necessarily constrained to the future, at arbitrarily long delays. Throughout the remainder of this document it can be assumed that findings from the literature relate specifically to these durations (anywhere from ~200 ms to a minute), unless specifically indicated otherwise. Similarly, the terms ‘interval’, ‘duration’, and ‘period’ will be used synonymously.

The majority of key papers on interval timing (as highlighted by a citation-based ranking, Teki, 2016) are concerned with four inter-related issues regarding the nature of potential timing mechanisms. In essence, these constitute ongoing debates about whether there are different or common mechanisms for different aspects of timing behaviour. Firstly, there is the difference between implicit and explicit timing; implicit timing referring to the passive temporal epiphenomenon of any sensorimotor information (e.g. reaction time) and explicit timing referring to situations in which the psychological measurement of duration is overtly cued. Some researchers cite differential neural activity as evidence for separate mechanisms (Coull & Nobre,
2008; Lewis & Miall, 2003), whereas others point to similarities in the statistical characteristics as reflecting a fundamentally common mechanism (Piras & Coull, 2011; Rammsayer, 1989). Secondly, given that there does not appear to be a dedicated sensory organ for time perception, there is a distinction between intrinsic and dedicated models of timing (Ivry & Schlerf, 2008). In intrinsic models, temporal processing is distributed amongst other sensory processing mechanisms, thus each sensory system keeps its own “time” (Buhusi & Meck, 2005; Buonomano & Laje, 2010; Karmarkar & Buonomano, 2007). On the other hand, dedicated models of timing propose that there exists a centralised, universal timing mechanism that generally subserves all sensory and motor systems (Treisman, Faulkner, Naish, & Brogan, 1990). Thirdly, and relatedly, there is some debate as to whether perceptual judgements of time and the timing of actions rely on the same (Buonomano & Laje, 2010; Chen, Penhune, & Zatorre, 2008; Coull, Vidal, & Burle, 2016; Rammsayer, 1989; Simen, Vlasov, & Papadakis, 2016) or different mechanisms (Wiener, Turkeltaub, & Coslett, 2010). Finally, researchers have also debated whether there is a common mechanism (Ivry & Hazeltine, 1995; Lewis & Miall, 2009), or different mechanisms (Ivry & Spencer, 2004; Wiener et al., 2010) for different scales of time, with a particular focus on differences between sub- and supra-second time scales.

While the above distinctions are clearly important for any comprehensive model of time perception, they will not be discussed in much more detail here for a number of reasons. Firstly, research into these distinctions is plentiful (see Teki, 2016) and ongoing, and the experiments presented here do not further this research agenda. Secondly, most of the above distinctions do not place constraints on the specific role of time perception in decision making, which is the main focus of this thesis. The general consensus arising from this research is that distinct, but overlapping mechanisms are employed for different tasks (e.g. Wiener et al., 2010). If timing is
Indeed stratified into component systems, it is a reasonable assumption that perceptual timing will apply to perceptual decisions, and motor timing to motor decisions. Likewise, decision processes within certain sensory domains should be agnostic as to whether timing mechanisms are either intrinsic to those domains or centralised (although this may not apply to multimodal decision processes). It is also clear that decision making is a necessary part of explicit timing, as subjects are required to make some decision about duration (indeed, this may be one of the key differences between implicit and explicit timing). In summary, while the majority of published research articles in the time perception field have focused on dissecting the component aspects of a hypothetical timing mechanism, the following review instead focuses only on a subset of the literature relevant to the aims of this thesis.

In the subsequent sections of this chapter, the standard terminology and procedures used to measure time perception will be outlined. This chapter will also discuss some popular psychological models of time perception, in order to provide a framework to understand how external and internal factors might affect time perception. Subsequently, it will detail some of the neurophysiological mechanisms that are associated with time perception, including the relationship between time perception and the neurotransmitter dopamine. Given that dopamine is related to the psychological constructs of motivation and reward, this chapter will focus specifically on how factors related to motivation and reward can influence time perception. Finally, this chapter will summarise this selective review and clarify the first research question of this thesis.
1.1 THE MEASUREMENT OF PSYCHOLOGICAL TIME

The measurement of psychological time has a rich history (Eisler, 1976; Grondin, 2001; Stevens, 1951; Stevens & Galanter, 1957; Woodrow, 2002), and various methodologies have been developed to assess the psychophysics of time perception in both humans and non-human animals (Grondin, 2008). A non-exhaustive list of these time measurement procedures is shown in Table 1. In this section, I will describe a selection of these paradigms in detail. I will also describe a number of fundamental characteristics of timing behaviour that are evident when measuring time perception, and which many models seek to explain.

To ensure communicative clarity in the face of nuances in different measurement techniques, it will also be useful to define some of the terminology which will be used throughout the remainder of this thesis. Firstly, measurements of time perception elicited from subjects in any manner will be referred to as ‘estimates’ or ‘estimations’, although it should be noted that in the wider literature an estimation can refer to a measurement from a specific procedure. I also adopt the terminology of ‘target time’ to refer to the specific intervals that subjects respond to, agnostic of the time measurement procedure. For example, in an estimation procedure, subjects might be asked to retrospectively quantify an elapsed target time of 1 minute (which they may underestimate or overestimate), whereas in a production procedure, subjects might be asked to make an indicative response after a 1 minute target time (which they may underproduce or overproduce).
### Table 1. Time perception measurement procedures. Adapted from Riemer (2015).

<table>
<thead>
<tr>
<th>Method</th>
<th>Task</th>
<th>Description</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimation</td>
<td>Estimation</td>
<td>Numerical quantification of an interval</td>
<td>Zakay &amp; Fallach, 1984</td>
</tr>
<tr>
<td>Production</td>
<td>Production</td>
<td>Emulation of a numerically defined target interval</td>
<td>Ivry &amp; Hazeltine, 1995</td>
</tr>
<tr>
<td>Reproduction</td>
<td>Reproduction</td>
<td>Emulation of a reference interval</td>
<td>Mioni, Stablum, McClintock, &amp; Grondin, 2014</td>
</tr>
<tr>
<td></td>
<td>Ratio setting</td>
<td>Emulation of a proportion of a reference interval</td>
<td>Allan, 1978</td>
</tr>
<tr>
<td></td>
<td>Tapping synchronisation</td>
<td>Entrainment to an external rhythm which may be discontinued</td>
<td>Ivry &amp; Keele, 1989</td>
</tr>
<tr>
<td></td>
<td>Peak-interval</td>
<td>Multiple responding around a pre-trained target interval</td>
<td>Meck &amp; Buhushi, 2010</td>
</tr>
<tr>
<td></td>
<td>Bisection</td>
<td>Categorisation of a probe interval as more similar to short or long reference interval</td>
<td>Wearden, Rogers, &amp; Thomas, 1997</td>
</tr>
<tr>
<td></td>
<td>Generalisation</td>
<td>Categorisation of a probe interval as equal or unequal to reference interval</td>
<td>Wearden &amp; Bray, 2001</td>
</tr>
<tr>
<td></td>
<td>Discrimination</td>
<td>Categorisation of a probe interval as shorter or longer than reference interval</td>
<td>Treisman, 1963</td>
</tr>
<tr>
<td></td>
<td>Ratio judgement</td>
<td>Rating of a probe interval as proportion of reference interval</td>
<td>Wearden &amp; Jones, 2007</td>
</tr>
</tbody>
</table>
Of the time perception paradigms shown in Table 1, two of the most common are the peak-interval interval procedure and the temporal bisection paradigm. In the peak-interval procedure (which is often used in non-human animal research), subjects must first learn a response schedule (often referred to as a fixed-interval schedule, or FI trials) whereby responses are reinforced at a specific target time. Once this schedule has been learned, probe trials (“peak” trials, or PI trials) are not reinforced, and last longer than standard trials. Responses from these probe trials are aggregated, and this leads to a response curve that summarises the response rate across the trial duration (Figure 1.1). The key statistic from this method is the duration at which the response rate is at its maximum (the peak time). This is usually treated as the subjects estimate of the target time.
Notably, on a trial-by-trial basis, responses in the peak-interval procedure fall into a break-run-break pattern (Schneider, 1969), with a distinct time at which responses change to a high rate (often around half the target time) and then back to a low rate (often around 1.5 times the target time, Balci, 2014). This is opposed to an alternative possibility of smooth acceleration and deceleration of responding, which would also lead to the observed smooth response curves in aggregate. Because of this break-run-break pattern, data from the peak-interval procedure are occasionally presented as the durations for the start time (of high responding), peak time, and stop time.
In the temporal bisection procedure, subjects are first trained to identify a ‘short’ and ‘long’ reference interval. In testing, subjects are asked to categorise probe intervals (typically intermediate between the ‘short’ and ‘long’ references) as closer to the ‘short’ or ‘long’ reference. The psychometric function describes the proportion of ‘long’ categorisations as a function of the duration of the probe interval (Figure 1.2). The key statistic from this method is the duration at which the proportion of short and long categorisations is equivalent, otherwise known as the point of subjective equality (PSE). This can be treated as the subjects’ estimate of the arithmetic average of the reference intervals¹.

In both the peak-interval procedure and temporal bisection, if durations are underestimated or overestimated, the response curve will shift horizontally to the right or to the left, respectively.
Figure 1.2. Psychometric curve from a temporal bisection procedure. Subjects’ time estimates are at the time where proportion of categorisations of ‘short’ and ‘long’ are equivalent (i.e. 0.5). Adapted from Wearden and Ferrara (1996).

Crucially, even within each of the paradigms listed in Table 1, variations in experimental design can lead to different results. For example, in a duration reproduction paradigm, subjects are shown a stimulus, the duration of which they must subsequently reproduce. The reproduced intervals have been shown to differ systematically dependent on whether subjects self-initiate the reproduction or are prompted by an external cue, and whether they make two discrete responses or a
single continuous response in order to delineate the target interval (Mioni et al., 2014). The modality of the stimuli used to present temporal information in these procedures is also important. For example, auditory stimuli are consistently judged to be longer than visual stimuli when most other factors are controlled for (Droit-Volet & Meck, 2007; Lustig & Meck, 2011). Moreover, whether subjects count subverbally can also affect time estimates, and therefore participants are often simply instructed not to count to avoid this issue (Rattat & Droit-Volet, 2011). Given these subtle differences in estimates due to variations in different paradigms, results are often best framed as relative, rather than absolute differences in time estimates.

While the data obtained from comparison methods (such as temporal bisection) depict a probabilistic *psychometric* function (i.e. one that relates duration to the likelihood of a particular decision), data from estimation, production, and reproduction methods depict a *psychophysical* function that directly relates subjective time to objective time (Figure 1.3; Eisler, 1976; Grondin, 2001; Stevens & Galanter, 1957; Woodrow, 2002).
Two of the more popular psychophysical functions used to describe this relationship are Steven’s power law (Kane & Lown, 1986; Stevens & Galanter, 1957) and the Weber-Fechner logarithmic law (Killeen & Weiss, 1987; Treisman, 1963). The choice between these two reflects the long-standing conflict of whether log or power laws more accurately capture psychophysical properties (Dehaene, 2003; Eisler, 2009; Krueger, 1989). The Weber-Fechner function is

\[ \psi = k \log(\phi) + c \]

where \( \psi \) denotes subjective duration, \( \phi \) denotes objective duration, transformed by a scaling parameter \( k \) and an intercept \( c \). A three parameter version of Steven’s law is
\[ \psi = \alpha (\phi - \tau)\beta \]

with a scaling parameter \(\alpha\), and shift parameter \(\tau\) (usually close to zero) and an exponent \(\beta\). This subtraction form of the law is useful when capturing ranges near the absolute threshold of duration discrimination (Marks & Stevens, 1968). However, when above this threshold, a two parameter version that excludes the shift \(\tau\) is also commonly used (i.e. \(\psi = \alpha\phi^\beta\)).

Importantly, the use of these psychophysical functions is entirely descriptive, and agnostic to potential mechanisms subserving time perception. Thus, while differences in the parameters of the psychophysical function can be used to assess manipulations of time perception (e.g. Kornbrot, Msetfi, & Grimwood, 2013) or associations with existing personality traits (e.g. Glicksohn, Leshem, & Aharoni, 2006), they do not imply any specific changes to cognitive mechanisms. However, these functions can be incorporated into models of temporal decision making in order to reflect subjective rather than objective representations of time in the decision making process (e.g. Takahashi, Oono, & Radford, 2008; Zauberman, Kim, Malkoc, & Bettman, 2009).

There are also some characteristics properties of timing behaviour revealed by these functions that many mechanistic time perception models seek to address. For example, intuitively, it is more difficult to accurately estimate longer durations. (This can be seen in the response distributions in Figure 1.3, which grow increasingly more dispersed.) Empirically, this inaccuracy has been shown to increase proportionally to the target time. This is known as scalar variance, or the scalar property, which more precisely states that the standard deviation of time estimates scales proportionally with their mean (this is a special case of Weber’s law, Gibbon, 1991). The scalar
property has been shown to hold across many different time perception procedures (Gibbon, Church, & Meck, 1984; Piras & Coull, 2011; Wearden & Bray, 2001), as well as across different non-human animal species (e.g. Gibbon, 1977; Sargisson, Lockhart, McEwan, & Bizo, 2016). Because the standard deviation scales in proportion to the target time, the canonical measure of variability in time perception is the coefficient of variation (CV); the standard deviation of time estimates divided by the mean time estimate for a given target time (often denoted as $\gamma = \sigma / \mu$). For the scalar property to hold, the CV should remain approximately constant across different tested durations. It is vital to note that a number of studies have found violations of the scalar property, as evidenced by relative increases in precision at longer target times (Bizo, Chu, Sanabria, & Killeen, 2006; Eisler & Eisler, 2010; Grondin, 2012; Lewis & Miall, 2009; Wearden & Lejeune, 2008). In particular, Lewis and Miall (2009) used both production and reproduction paradigms with a large range of different intervals (from 68 ms to 16.7 mins), and found that the CV decreased as an approximately logarithmic function of target time. Thus, while often considered to be a fundamental feature of time perception, the scalar property may not be as robust as previously observed.

Another feature reflected in Figure 1.3 is that — in duration reproduction tasks — intervals are increasingly and systematically under-reproduced (Eisler, 2003; Riemer, Rhodes, & Wolbers, 2016; Riemer, Trojan, Kleinböhl, & Hölzl, 2012; Wackermann & Ehm, 2006). This can be quantified by the exponent parameter $\beta$ in Steven’s law, the empirical value of which has been reported to be slightly less than unity (~0.9, Eisler, 1976). The concavity expressed in the psychophysical function as a result of this suggests that memory representations of time may gradually shorten (Wackermann & Ehm, 2006).
Another important characteristic of time perception is that duration judgements depend on one’s preceding experiences with time (Bausenhart, Dyjas, & Ulrich, 2014; Jazayeri & Shadlen, 2010; Levy, Namboodiri, & Hussain Shuler, 2015; Li & Dudman, 2013; Los, Kruijne, & Meeter, 2017; Roach, McGraw, Whitaker, & Heron, 2016; Wiener, Thompson, & Coslett, 2014). This appears to be a consequence of the fact that timing information is subject to the same processes of statistical inference as other sensory systems (e.g. Bennett, 2015), which rely on prior experience and beliefs to generate an internal reference (Bausenhart et al., 2014). This makes sense in a dynamic environment, as agents will be able to exploit changing temporal regularities to learn the probabilistic structure of event timing (Jazayeri & Shadlen, 2010; Li & Dudman, 2013; Los et al., 2017), allowing them to calibrate their behaviour to match the varying distributions of durations they are likely to encounter (McGuire & Kable, 2012). However, this has a number of consequences and implications for the data derived from time perception paradigms, including Vierordt’s Law (Bausenhart et al., 2014). This law indicates that time estimates are biased toward the mean of the sample intervals used in any given procedure (shorter durations will be overestimated, while longer durations will be underestimated, Lejeune & Wearden, 2009). Perhaps relatedly, there are also trial-by-trial contrastive carry-over effects (which appear to be similar to sensory adaptation), where intervals are more likely to be judged as short immediately subsequent to experience with a longer interval, and vice-versa (Gu & Meck, 2011; Heron et al., 2011; Wiener et al., 2014). In addition to these contrastive perceptual effects, there are also carry-over effects from previous responses in time comparison tasks (Wiener et al., 2014). These decisional carry-over effects are additive rather than contrastive, so that sequential time judgments will be positively correlated. This is similar to response autocorrelation observed in other cognitive domains (e.g. category learning, Jones,
Love, & Maddox, 2006; or perceptual discrimination, Fritsche, Mostert, & de Lange, 2017). Ultimately, all of the above effects stem from the fact that time perception is biased by previous experience, which implies that our perception of time can flexibly adapt to different environments, which may be a tradeoff in terms of timing precision (Gibbon & Church, 1990). This idea — that timing imprecision is a consequence of our ability to flexibly adapt to the environment — will be a recurring theme of this thesis.

In the next section, I introduce the ubiquitous clock metaphor, which can reconcile differences in time measurement procedures, as well as provide a cursory review of some other popular and relevant mechanistic models of time perception (for a review of earlier models of time perception, see Grondin, 2001).
1.2 MODELS OF PSYCHOPHYSICAL TIME

The clock metaphor of time perception likens a hypothetical timing mechanism to a pacemaker that emits counts over time, and a reference memory system that accumulates and stores these counts (Treisman, 1963). One major advantage of this pacemaker-accumulator metaphor is its ability to refer to directional inaccuracies in time perception universally, agnostic of the specific paradigm used. To see why this is the case, imagine a consistently inaccurate subject $A$, whose perception of time is measured with two different procedures: a time estimation task and a duration production task. In the estimation task, a 60 s target interval elapses, but subject $A$ estimates that the interval was 50 s. This is an underestimation, and implies that the psychological clock of subject $A$ was “slower” than an objective clock. In the production task, subject $A$ is asked to hold down a button for 60 s. The “slower” psychological clock of subject $A$ leads them to hold the button down for 70 s: an overproduction. These terms — underestimation and overproduction — indicate the same bias in terms of psychological time, although they manifest as negative and positive errors in each paradigm, respectively. The opposite bias in psychological time is also possible: a “faster” psychological clock would result in a relative overestimation and a relative underproduction, in each respective task. The differences between estimation and production are exemplified in this quote:

“In general, a time filled with varied and interesting experiences seems short in passing, but long as we look back. On the other hand, a tract of time empty of experiences seems long in passing, but in retrospect short.” — (James, 1890).

In general, this inversion of relative directional error exists between tasks which involve estimating a target interval that has already elapsed (a retrospective time estimation), and tasks where the time estimation is known in advance of the
target interval (a prospective time estimation). However, the clock metaphor is able to reconcile these differences in the results (Treisman, 1963).

The selective review of time perception models below focuses on pacemaker-accumulator models, at the expense of some popular alternative models (e.g. Church & Broadbent, 1990; Grossberg & Schmajuk, 1989; Staddon & Higa, 1999). The purpose of this selection is fourfold. Firstly, it provides some historical context on the development of a what is fundamentally a single concept. Secondly, it provides some context in terms of which features of this model are neurally plausible. Thirdly, it highlights the idea that the pacemaker rate can be affected by different external factors. Finally, as noted above, the pacemaker-accumulator/clock metaphor is able to reconcile differences in the results from different time perception paradigms, and thus in the remainder of this document changes in time perception will often be related to the rate of this hypothetical pacemaker.

1.2.1 Scalar expectancy theory. There are many different versions of this basic pacemaker-accumulator model (Simen, Rivest, Ludvig, & Balci, 2013; Treisman, 1963), but the canonical (and perhaps most popular) of these models is scalar expectancy theory (SET, Gibbon, 1977). SET extends the pacemaker-accumulator idea to include additional psychological modules: a switch, memory stores, and a comparator (Figure 1.4, Church, 1984).
Multiplicative factors such as the pacemaker rate ($A$) and memory constant ($K^*$) can affect the pacemaker pulse count and result in scalar timing. Adapted from Church (1984).

To process temporal information, the switch controls whether the pacemaker is currently in an ‘off’ or ‘on’ state. When the pacemaker is ‘on’, it generates counts (or pulses) as a Poisson process, which are stored in the accumulator. This count can be transferred to a reference memory which provides the basis for relative comparisons of duration against the current count in working memory. Finally, there is a comparison process which identifies whether the count in working memory matches that in the reference memory.$^2$
SET relies on the characteristics of this modular mechanism to generate timing that follows the scalar property, which, as mentioned in the previous section, manifests as a proportional, multiplicative scaling of the variance of time estimates with their mean (Gibbon, 1991; for the scalar property to hold, the CV should remain constant across different target times). In SET, it is assumed that the distribution of counts generated from the pacemaker is a Poisson distribution (Church, 1984), where the variance is equal to the mean count. Given that longer target times accumulate more counts, this implies that (without further modification of the model) estimates of longer target times should be relatively more accurate, as the standard deviation increases as a square root of the mean (Gibbon, 1977). This would imply that the CV would decrease inversely with the square root of the target time (i.e. “Poisson variance”). Thus, a number of other sources of variance have been proposed in order to account for the scalar property in SET. It was originally proposed that the model can generate the scalar property if the rate of the pacemaker varies symmetrically on a trial-to-trial basis (Church, 1984; Treisman, 1963). It was subsequently noted that the scalar property can be generated by assuming a constant, multiplicative transform in the encoding of the count in memory (Gibbon, 1992). However, the dominant explanation of scalar variance is now generally considered to be a result of the comparison process, which can be based on taking a ratio of the currently stored counts and the total counts in reference memory (Church, 1997). For example, if \( m \) is the count in reference memory and \( a \) is the count in working memory, then a relative comparison rule might be \( (m – a)/m \). Given an arbitrary but constant decision threshold that determines whether this value falls below a criterion value, this modification can also account for the scalar property, as long as the noise in this
comparison process is large relative to the Poisson noise in the pacemaker (Gibbon, 1992). Thus the scalar property in SET is considered to be a product of the decision process rather than the characteristics of the pacemaker itself.

Other empirical characteristics of timing can be accounted for in reference to SET. For example, the systematic discrepancy in the time estimates of auditory and visual stimuli (Droit-Volet & Meck, 2007; Lustig & Meck, 2011) can be explained by auditory signals driving the pacemaker faster than visual signals (Gu & Meck, 2011). Alternatively, auditory signals may be more effective at altering the state of the switch from ‘off’ to ‘on’ (Gu & Meck, 2011). While the switch module usually acts to introduce a non-zero intercept into responses, it has also been proposed to be modulated by attention. This extension of SET, known as the attentional-gate model (Block & Zakay, 1997), allows more or less counts to accumulate according to differences in attentional state.

Ultimately, while SET has provided a useful framework to characterise features of time perception, it has a number of shortcomings. First, it is unclear whether the scalar property is as robust as previously claimed (Bizo, Chu, Sanabria, & Killeen, 2006; Eisler & Eisler, 2010; Grondin, 2012; Lewis & Miall, 2009; Wearden & Lejeune, 2008), thereby undermining one of the primary motivations for the development of SET. Second, an implicit assumption of SET is that the accumulation of counts from the pacemaker is unbounded in order to allow timing for a large range of intervals (Church, 1984). Indeed, humans can (approximately) estimate time over 15 orders of magnitude (Buonomano, 2007). However, with the native computational constraints of the brain, this unbounded count assumption is highly unlikely to be true (Staddon & Higa, 1999). Third, the functioning of the model is partly unexplained, for example, by not specifying how the accumulator can be reset in response to a new trial (Staddon & Higa, 1999). Finally, SET is subject to a classic psychophysical issue,
whereby several different sources of variability can each result in the same distribution of responses in timing tasks (indeed, one article outlines 26 different possible sources of variances in SET, Gibbon, 1984). Thus, the decision to attribute scalar variance to any specific aspect of the model is often complicated (this is usually done by assuming particular correlation structures between start and stop times in individual trial analysis, e.g. Gibbon & Church, 1990; Rakitin et al., 1998). In general, SET has been criticised on the basis that it appears to arbitrarily add modifications to account for the scalar property (Staddon & Higa, 1999).

1.2.2 Behavioural theory of timing. In SET, the pacemaker mechanism is never specifically identified. The behavioural theory of timing (BeT), is similarly based on a pacemaker-accumulator process, but assumes that agents do not have direct access to an internal pacemaker and instead indirectly measure time via changes in adjunctive behavioural states (behaviours that are not directly related to the task, e.g. a change from the state of ‘preening’ to the state of ‘yawning’, Killeen & Fetterman, 1988). The changes in these states themselves act as discriminative stimuli for timing, rather than the process driving the changes. If an animal is required to make a timed response, its time estimate will be the time at which its behavioural state is coupled most strongly with reinforcement (Killeen & Fetterman, 1988). The idea that animals use their own behaviour for timing discrimination has received some empirical support (Fetterman, Killeen, & Hall, 1998). For example, a recent study showed that as animals learned a target time, they developed a regular and predictable sequence of interim behaviours (Gouvêa, Monteiro, Soares, Atallah, & Paton, 2014). Importantly, temporal categorisations could be predicted on the basis of this sequence of behaviours, justifying BeT’s emphasis on adjunctive behavioural states.
Like SET, BeT also assumes that the transitions between behavioural states occur as a Poisson process. However, there are two key characteristics that differentiate BeT from SET. Firstly, whereas SET assumes that the pacemaker has a fixed rate and that pacemaker counts map linearly to time representations, BeT proposes that different durations are timed using different rates with a fixed decision threshold across durations (i.e. the same average number of behaviours, Killeen & Fetterman, 1988). This overcomes the issue of unbounded accumulation in SET, and also predicts that time estimates should follow a time scale invariant gamma distribution (unless the threshold for responding is very large, Gibbon, 1992).

The second key characteristic of BeT is the source of scalar variance. Instead of assuming that this is generated from the memory or comparison processes, BeT instead assumes that the pacemaker rate is driven by the rate of reinforcement that the animal is receiving (Bizo & White, 1994; 1995). This assumption has its foundation in a study showing that the rate of adjunctive behavioural activity (which the authors characterise as arousal) is a function of cumulative reward delivery (Killeen, Hanson, & Osborne, 1978). This assumption means that for procedures where the rate of reinforcement varies (which is often the case), the scalar property is generated in a similar way to that of introducing symmetrical noise in the pacemaker (Treisman, 1963). When the rate of reinforcement is held constant however, Poisson variance is dominant, and the standard deviation should increase more slowly with target time (i.e. longer target times are proportionally more accurate). This latter point has been supported by empirical data from comparison procedures in which the rate of reinforcement is held constant (e.g. Fetterman & Killeen, 1991 & Platt & Davis, 1983). Ultimately, as a consequence of this formulation, when fit to empirical data, the pacemaker rate varies as a function of different reinforcement schedules (Bizo & White, 1994; 1995; Fetterman & Killeen, 1991).
The idea that reward rate can affect timing behaviour (including temporal decision making) is of critical relevance to this thesis. Specifically, Chapter 3 will present an investigation of the impact of different reward magnitudes on human behaviour in a temporal production task. Furthermore, in their original article on BeT, Killeen and Fetterman (1988) state:

“A faster pacemaker due to higher overall rate of reinforcement means less residence time in any particular state and thus steeper delay of reinforcement gradients. It means that the amount of time an animal perseveres in any food patch or foraging activity will be related to the overall density of food in its environment.”

Chapter 5 explicitly provides evidence for this prediction in the context of human decision making. In Section 1.4, the relationship between reward and time perception will be discussed in more detail. While BeT is not directly used as a model of time perception in any of the subsequent empirical chapters, it is useful to note that this relationship between reward and time perception has precedent in early psychological models.

1.2.3 The opponent Poisson model. The models discussed above do not explicitly outline physiological underpinnings of their constituents. However, a more recent model (of which BeT exists as a special case) maps the different aspects of a pacemaker-accumulation process to hypothetical, but biologically plausible neural processes: the time-adaptive opponent Poisson drift-diffusion model (TOPDDM; hereby referred to as the opponent Poisson model; Simen, Balci, deSouza, Cohen, & Holmes, 2011a; Simen et al., 2013). This model will be briefly outlined in order to demonstrate how pacemaker-accumulator models might be implemented neurally.
The opponent Poisson model can be divided into four hierarchical levels, which are approximately analogous to the modules in the pacemaker-accumulator mechanism (Figure 1.4). At the lowest level (analogous to the pacemaker), individual neurons generate spikes (action potentials) as a Poisson process (Simen et al., 2011a). These spiking neurons either provide excitatory or inhibitory inputs to the second level of the hierarchy, which integrates these signals (analogous to the accumulator). The rate of integration is controlled by balancing these excitatory and inhibitory inputs (i.e. the eponymous “opponency”). The third level of the model consists of a timing circuit which includes the integration population, as well as two other neural populations that act as bistable switches which control initiation and threshold detection respectively (analogous to the switch and comparator, respectively; for more details about the neural properties of these switches see Simen et al., 2011a). Because Poisson processes can approximate diffusion processes under conditions with sufficient elapsing time (Gerstein & Mandelbrot, 1964), the final level of the hierarchy approximates a one-dimensional drift diffusion model (Ratcliff & Smith, 2004; Ratcliff, Smith, Brown, & McKoon, 2016). In other words, elapsed time is represented as a diffusion process with a differential drift rate for different target times (calibrated by the balance of excitatory and inhibitory Poisson spike trains) and a fixed decision threshold (set by a bistable switch). The diffusion coefficient (i.e. the noise) is proportional to the square root of the drift rate. Different target intervals can be learnt by adapting the synaptic weights between the start switch neurons and the integrator neurons (Simen et al., 2011a). Furthermore, a variant of this learning rule (not detailed here) causes the drift rate to vary as a weighted average of the reward rate (Rivest & Bengio, 2011), recapitulating the key principle of BeT.
In general, this model is very similar to BeT (indeed, BeT is a special case of the opponent Poisson model without inhibitory spike trains). As in BeT, a fixed threshold and an adaptive rate overcomes the issue of unbounded accumulation in SET\(^3\). However, whereas BeT attributes the events to changes in behavioural states, the neural integration model equates the Poisson events directly to action potentials (Simen et al., 2011a). Unlike in BeT, there are two opponent pacemaker populations, and as the variances of these sum together, the model predicts inverse Gaussian time estimate distributions (Simen et al., 2011a).

Because of the similarity of the opponent Poisson model to sequential sampling models of perceptual decision making (Ratcliff et al., 2016; Ratcliff & Smith, 2004), this enables a more equivalent treatment of time perception and the decision making procedures that sequential sampling models are typically applied to (Simen et al., 2013). Indeed, the opponent Poisson model has been shown to account for both the scalar property in interval timing tasks, and the more general Weber law that applies to reaction times in decision making tasks (Simen, Vlasov, & Papadakis, 2016), suggesting the possibility of a fundamental mechanism governing each process. This dual applicability also has considerable potential in terms of consolidating time perception with the speed-accuracy tradeoff in decision making (Balcı et al., 2010; Simen, Cohen, & Holmes, 2006). In summary, the opponent Poisson process has considerable utility in equating time perception to a standard model of decision making\(^4\), and importantly, outlines a plausible neural implementation of a pacemaker-accumulator process.

1.2.4 *Striatal beat-frequency*. While there exists a range of other neurally grounded models of interval timing (e.g. Reutimann, 2004), most of these rely on the pacemaker-accumulator idea. One alternative model of neural time representation,
beat-frequency models, instead posit that time is encoded via combinations of neurons with different periodicities (Kononowicz & van Wassenhove, 2016; Miall, 1989). Given that these are relatively popular in the literature, they are worthwhile briefly describing.

A specific instantiation is the striatal beat-frequency model (SBF), which was inspired by neurocomputational models of working memory. These working memory models propose that stimuli in working memory are represented by the ongoing, recurrent excitatory activity in thalamocortical loops (Frank, Loughry, & O'Reilly, 2001). SBF proposes that the oscillations of these recurrent representations are synchronised at stimulus onset, but eventually decohere and oscillate out of phase (Matell & Meck, 2004). This results in specific phase patterns that encodes temporal information (Matell & Meck, 2004). In SBF, these phase patterns are detected by striatal spiny neurons, which can subsequently extract the temporal information by assessing the patterns of synchrony coincident with important events (Matell & Meck, 2000).

Coincidence-detection mechanisms like that of SBF are relatively prevalent in the brain (e.g. Agmon-Snir, Carr, & Rinzel, 1998), highlighting the neural plausibility of a timing mechanism that relies on coincidence detection. Furthermore, the proposed detection mechanism lies in the striatum, which is well known to be associated with time perception and timing deficits (see Section 1.3). Beat-frequency models can also elegantly account for the scalar property (Matell & Meck, 2004). This is due to the fact that the oscillatory phase pattern for any given target time will have a corresponding harmonic series, which scales proportionally to its fundamental wavelength (i.e. target time). Given that there will be higher levels of coincident activity at these harmonics, there will also be higher incidences of responding, which will lead to proportionally scaled error in time estimates (Matell & Meck, 2004).
However, despite the simplicity and general plausibility of beat-frequency models, the known oscillatory properties of neurons are too brief and too variable for SBF to adequately account for empirical timing (Matell & Meck, 2004; Miall, 1989). Further to this, like the extant working memory models (Frank et al., 2001), SBF assumes that stimulus-encoding thalamocortical loops are able to synchronise their activity upon some cue. Currently, this characteristic has not been observed in neural data, and there is no known mechanism that might perform this function.

To summarise this section, many of these models of time perception follow the traditional psychological agenda of predicting the empirical distributions of time estimates seen in the data. While it is not the purview of this thesis to compare models (or even to analyse the specific form of elicited time estimate distributions), there is an acknowledgement in some models that external factors can alter the rate of a hypothetical pacemaker. These factors are discussed in more detail in Section 1.3 and Section 1.4, and include motivational (Treisman, 1963) and pharmacological factors (Meck, 1996). Of particular note, BeT assumes that the rate of the pacemaker is proportional to the rate of reinforcement. The subsequent section will outline some of the neurophysiological findings that further link reinforcement and time perception, and outline some physiological substrates that may fulfil the role of the pacemaker.
1.3 THE NEUROPHYSIOLOGY OF TIME

This section focuses on possible physiological and neurophysiological realisations of the hypothetical pacemaker. It will proceed by first providing some general evidence that periodic biological processes may constitute a pacemaker. It then provides a selective survey of neuroimaging and pathological evidence that implicates particular brain regions in temporal processing. This section also summarises some electrophysiological studies that have focused more specifically on these brain regions. Finally, this section addresses the robust neuropharmacological findings that relate to time perception.

1.3.1 Physiological pacemakers.

"Time is measured by a clock of blood. When one is active, close to the hawk, pursuing, the pulse races, time goes faster; when one is still, waiting, the pulse quietens, time is slow." - Baker & Cocker, 2010.

Some of the models presented in the previous section specifically identify the pacemaker rate with the action potentials of neurons. However, given the resource constraints of the brain, it seems unlikely that the brain would have a dedicated timing mechanism that is isolated from other functionality. There are many biological processes which have implicit periodicity. Thus, one possibility is that the neural processes already underlying these functions can simultaneously provide temporal information to a timing mechanism.

The idea that time perception relies on periodic biological activity is not new. It was proposed as early as 1921 that the natural frequencies of the heart and respiratory system were involved in the perception of time (Goudriaan, 1921). However, a more recent theory has recontextualised this idea on the basis of
functional neuroanatomy (Craig, 2009a), and relies on the anterior insula cortex (AIC) acting as a integrator of afferent visceral signals, and as the locus of awareness of these signals, i.e. interoception (Craig, 2002; 2009b; Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004). It was proposed that this integration process can act as a sort of accumulator for temporal information (Craig, 2009a). This account appears plausible given that there is substantial evidence to suggest that visceral afferent activity may constitute a pacemaker.

For example, if the hypothetical pacemaker is driven by biological periodicity, then one might expect that differences in the rate of the more fundamental biochemical processes underlying these will also result in altered time perception (Hoagland, 1935). This appears to be the case: by assessing a range of different animals species, it has been shown that metabolic rate is positively correlated with the frequency threshold at which a flickering stimulus is perceived as stable (Healy, McNally, Ruxton, Cooper, & Jackson, 2013). Similarly, body temperature — which is associated with the average rate of biochemical processes — is positively associated with pacemaker rate across a variety of different time perception tasks in humans (Wearden & Penton-Voak, 1995). This finding holds whether the cause of the temperature change is natural diurnal variation (François, 1927; Pfaff, 1968), fever (Alderson, 1974; Hoagland, 1933), or direct heating (Bell, 1965; Fox, Bradbury, & Hampton, 1967; Hancock, 1993; Hancock, Vercruysse, & Rodenburg, 1992; Kleber, Lhamon, & Goldstone, 1963; O'Hanlon, McGrath, & McCauley, 1974) or cooling (Baddeley, 1966; Bell, 1975; Lockhart, 1967). However, there are also studies that have failed to replicate this effect (Rammsayer, 1997). Natural variation in core body temperature over the circadian cycle peaks at around 2030 hrs, which has also been
shown to be the point at which temporal judgements of 1 hr are most accurate (Campbell, Murphy, & Boothroyd, 2001). Thus, gross physiological factors like body temperature appear to influence time perception.

Another key construct that is associated with the rate of biological processes is arousal. Arousal is one of two key psychological constructs that have historically had an intimate association with time perception (Gil & Droit-Volet, 2012; Treisman, 1963). The other is attention (Block & Gruber, 2013; Zakay & Block, 1995), which will not be discussed in detail here. A typical arousal-based manipulation of time perception involves the employment of emotional or affective stimuli, such as images of mutilation (Grondin, Laflamme, & Gontier, 2014), or attractive faces (Arantes, Berg, & Wearden, 2013). In general, such stimuli appear to increase the rate of the pacemaker and result in overestimations of the duration of the presented images, regardless of their valence (Corke, Bell, Goodhew, Smithson, & Edwards, 2016; Droit-Volet & Gil, 2009; Droit-Volet & Meck, 2007; Gil & Droit-Volet, 2012; Langer, Wapner, & Werner, 1961). Depression is often considered to oppose arousal, and individuals with depression have been shown to underestimate time in time estimation tasks (Blewett, 1992; Kuhs, Hermann, Kammer, & Tölle, 1991; Mezey & Cohen, 1961). Healthy individuals with depressive symptoms have also been shown to underestimate time in temporal bisection tasks (Gil & Droit-Volet, 2009). Similarly, individuals with narcolepsy, which is an arousal-related disorder, have also been shown to underestimate intervals (Poryazova et al., 2013). There is also both anecdotal and empirical evidence for an acceleration of the pacemaker during acute, arousing incidents that entail danger (Arstila, 2012; Corke et al., 2016; Langer et al., 1961), but there is mixed evidence about whether this constitutes an actual change in sensory processing, or whether it is merely an epiphenomenon of arousal. For instance, take the oddball effect of time perception. In a standard oddball paradigm,
sequences of standard stimuli are shown, followed by an unpredictable oddball stimulus. Participants are asked to judge whether the oddball was shorter or longer than the standards. The typical finding in these studies is that the oddball stimuli are perceived to be longer than the standards (Matthews & Gheorghiu, 2016) and this overestimation has been reported to facilitate information processing, e.g. increased perceptual performance in enumeration of the stimuli (Wutz, Shukla, Bapi, & Melcher, 2015). However, others have found that the rate of perceptual sampling (as measured by flicker-fusion threshold) was not enhanced during arousal induced by free-fall (Stetson, Fiesta, & Eagleman, 2007) which suggests that changes in time perception may be a function of memory rather than perception (Mather & Sutherland, 2011). In an article that slightly predates BeT (and justified the assumption that pacemaker rate is proportional to reinforcement rate) Killeen, Hanson, and Osborne (1978) characterised arousal as the rate of transitions between adjunctive behavioural states. Importantly, they attributed increased arousal to the cumulative delivery of rewards and other incentives (Killeen et al., 1978). This foreshadows the content in Section 1.4, which focuses on how reward and motivation influence the hypothetical pacemaker.

The robust effects of manipulations of psychological arousal on time perception provide some more broad evidence that physiological processes are related to a hypothetical pacemaker. From the effect of psychological arousal, an accompanying effect of physiological arousal might also be expected. However, only a few studies have explicitly investigated this in relation to time perception. One such study used galvanic skin response to measure autonomic sympathetic arousal, and showed that when attention was directed to negative emotional stimuli, arousal was higher and time was overestimated (Mella, Conty, & Pouthas, 2011). Another study related the cardiac pre-ejection period — another index of sympathetic nervous
system influence — to time perception after a stress manipulation (van Hedger, Necka, Barakzai, & Norman, 2017), showing a significant relationship between overestimations of time and increased sympathetic activity, but only at one duration (400 ms) of a number tested. Similarly, a relationship between accuracy in a temporal bisection task and pre-ejection period has also been reported (Cellini et al., 2015), suggesting that decreased sympathetic nervous system activity is associated with better accuracy. One other commonly used index of arousal is the dilation of the pupil (Bradley, Miccoli, Escrig, & Lang, 2008; de Gee et al., 2017). A study using this index showed that the pupil diameters of non-human primates were negatively correlated with saccade latencies on a delayed response visual memory task, suggesting that arousal was associated with an increase in the rate of the pacemaker (Suzuki, Kunimatsu, & Tanaka, 2016). Pupil-diameter has also been used as a proxy for noradrenergic activity (Aston-Jones & Cohen, 2005), which — as a neurotransmitter — will be discussed in greater detail below, as well as another important neuropharmacological index of arousal: dopamine (McClelland, Patel, Stier, & Brown, 1987; Robbins, 1997). In summary, the studies discussed above appear to show that sympathetic measurements of physiological arousal are associated with time perception.

While the above findings provide evidence that time perception is associated with the rate of biological processes, these process (e.g. body temperature, arousal) are related to general nervous system function at a very broad level (Robertson & Money, 2012; Shibasaki, Suzuki, Mizuno, & Tominaga, 2007; Yu, Hill, & McCormick, 2012), and thus these findings do not pinpoint any specific processes that might serve as a pacemaker. While the interoceptive integration theory proposes that it is an aggregate of many signals that drives the pacemaker (Craig, 2009a), there have been a number of suggestions that specific processes are primarily responsible for
pacemaker rate. One such suggestion is that timing information is extracted by directly equating it with neural energy consumption (Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2007). To give a concrete example, the oddball effect (explained above) has been interpreted as a result of relative coding efficiency, where repeated exposure to the standard stimuli decreases the energy consumption needed for neural representation (i.e. repetition suppression), which results in a decrease in the subjective duration associated with the standard stimulus and a relative increase in the subjective duration of the oddball (Eagleman & Pariyadath, 2009). Although it is unclear whether the brain can perform such global self-monitoring of energy usage, it has been suggested that the AIC performs this function (Craig, 2013), consistent with the idea that the AIC acts as a temporal information accumulator.

A significant amount of research has also investigated the possibility that the heart serves as a specific, primary biological pacemaker. However, it is unlikely that a simple linear relationship between heart rate and time perception exists. This has been made clear by one study that manipulated heart rate via exercise, but found no accompanying changes in time perception (Schwarz, Winkler, & Sedlmeier, 2012). However, there are other aspects of cardiac signals apart from mean heart rate that may relate to time perception, for example, heart rate variability (HRV), which is primarily the result of the influence of the parasympathetic nervous system (PNS, Berntson et al., 1997). Individuals with higher HRV have been shown to be more accurate in duration reproduction tasks (Pollatos, Yeldesbay, Pikovsky, & Rosenblum, 2014), and in temporal bisection tasks (Cellini et al., 2015)\textsuperscript{6}. Another study has reported that individuals more accurately reproduced durations when their heart rate slowed down faster during the encoding of intervals (which is a consequence of PNS activity, Meissner & Wittmann, 2011). However, it is important to note that HRV has also been related to attention, self-control, and working memory performance.
which are all components in time perception tasks. Thus, it may be that this relation between cardiac measures and executive function is responsible for the observed results in timing tasks, rather than time perception being specifically modified by cardiac activity. It has also been reported that interoceptive awareness of one’s own heart rate is related to time perception (Pollatos, Laubrock, & Wittmann, 2014), with those with better interoception having been shown to be more accurate in duration reproduction tasks (Meissner & Wittmann, 2011). This is consistent with the idea that the AIC integrates timing information, as the AIC mediates heartbeat perception (Critchley et al., 2004; Khalsa, Rudrauf, Feinstein, & Tranel, 2009) and regulates the cardiovascular system at large (Nagai, Hoshide, & Kario, 2010). It is worthwhile noting that Chapter 4 presents empirical evidence of a relationship between cardiac measures and time perception. Thus, this literature is of particular relevance to this thesis.

In collection, the above studies provide general support for the idea that periodic interoceptive signals are related to time perception (Craig, 2009a). As a whole however, they do not indicate which physiological aspects are necessary or sufficient for timekeeping, nor do they suggest a specific locus for the realisation of a pacemaker. The next section relies on the neuroimaging literature to broadly survey which brain areas may be more specifically critical for timing.

1.3.2 Neuroanatomy and pathology. The development of modern neuroimaging techniques has lead to a recent wealth of data on brain regions that are associated with time perception. In particular, functional magnetic resonance imaging (fMRI) measures the blood-oxygen-level dependent (BOLD) magnetic signal as a proxy measure of neural activation and has provided identification of some brain regions
with reasonably high spatial precision. A number of studies over a range of different timing tasks have provided data that may be used to identify candidate brain regions involved in time perception. However, the review of this literature will be abbreviated here for a number of reasons. Firstly, the experiments reported in this thesis did not employ neuroimaging, and make no contribution to the time perception neuroimaging literature. Secondly, while instrumental in providing some candidate regions that may be involved in temporal processing, due to limited temporal and spatial resolution, fMRI studies have not yet been able to lend strong support to any particular model or computational process that might underlie timing mechanisms. Thirdly, different brain regions respond dynamically to different components of time perception tasks (for meta-analyses see Lewis & Miall, 2003; Macar et al., 2002; Meck, Penney, & Pouthas, 2008; Wiener, Turkeltaub, & Coslett, 2010); it is often unclear whether the responsive regions are involved in the encoding of a time interval (i.e. memory processes), the reproduction of an interval (i.e. motor processes), or the decision process. Given the quantity of literature on this topic, and the content and scope of this review, this section has been constrained to the literature directly relevant to this thesis (exhaustive reviews can be found in Coull, Cheng, & Meck, 2011; Meck, 2003; Merchant, Harrington, & Meck, 2013). In particular, this section aims to justify the subsequent sections’ focus on the activity of dopamine neurons in the basal ganglia.

Firstly, the previous section implicated the AIC as playing a key role in time perception, specifically as an accumulator of temporal information (Craig, 2009a). There have been a number of fMRI studies consistent with this idea. For example, in a temporal discrimination task using target times of ~500ms, subjects reported increased durations for looming stimuli, compared to static stimuli (van Wassenhove, Buonomano, Shimojo, & Shams, 2008). When the same paradigm was reproduced during an fMRI scanning session, activity in the AIC was observed during the
presentation of looming stimuli (van Wassenhove, Wittmann, Craig, & Paulus, 2011; Wittmann, van Wassenhove, Craig, & Paulus, 2010). Indeed, there have been a number of other fMRI studies that have also demonstrated the involvement of the AIC in time perception across a range of paradigms (e.g. Livesey, Wall, & Smith, 2007; Wittmann, Simmons, Aron, & Paulus, 2010).

Along with the AIC, other cortical areas appear to be involved in aspects of timing behaviour, including anterior and posterior cingulate cortex, prefrontal cortex and dorsolateral prefrontal cortex, inferior frontal gyrus, posterior and inferior parietal cortex, superior temporal gyrus, and the supplementary motor area (Lewis & Miall, 2003; Macar et al., 2002; Meck et al., 2008; Penney, Holder, & Meck, 1996; Wiener et al., 2010). However, the basal ganglia, and in particular the nigrostriatal pathway, have been implicated as part of a core timing mechanism which recur in multiple studies (Coull et al., 2011; Meck et al., 2008; Teki, Grube, & Griffiths, 2012). For example, Harrington et al. (2004) asked participants to complete a temporal discrimination task (where a target time must be categorised as shorter or longer than a reference interval) while they were scanned using fMRI. The study used two reference intervals of 1200 or 1800 ms. The authors found that the coefficient of variation of time estimates was correlated with activation in the right inferior parietal, right caudate, left declive and left tuber, suggesting that these areas were associated with timing accuracy (Harrington et al., 2004).

In another study, Pouthas et al. (2005) asked subjects to complete a temporal generalisation task (where a target time must be categorised as equivalent or different to a reference interval) while they were scanned using fMRI. Either a short (450 ms) or long (1300 ms) reference interval were used in separate trials, delineated by a flashing light. By comparing brain activation during trials in which the short reference was used versus those in which the long reference was used, the authors could
identify which areas were sensitive to interval duration. They found that activation in preSMA, anterior cingulate cortex, right inferior frontal gyrus, bilateral premotor cortex, and the right caudate nucleus corresponded to the duration of the interval. The authors interpreted the activity in each of these regions as attributable to separate timing functions: the caudate and preSMA supported a clock mechanism, the anterior cingulate supported the decision process, and the premotor-inferior frontal regions represented working memory-related activity (Pouthas et al., 2005). These two studies show, respectively, that the activation of the striatum corresponds to both the accuracy (Harrington et al., 2004) and the duration (Pouthas et al., 2005) of time estimates. The involvement of the basal ganglia is also evident in meta-analyses that aggregate studies using different procedures (e.g. Macar et al., 2002; Meck et al., 2008; Wiener et al., 2010).

The other corpus of literature that points to the basal ganglia as a neuroanatomical requisite of time perception relates to pathology (for detailed reviews of disorders that affect time perception see Allmam & Meck 2012; Teixeira et al., 2013). In particular, Parkinson’s patients, who have a loss of dopamine producing neurons in the substantia nigra (Damier, 1999), have robust impairments in time perception across a range of tasks (Carroll, O'Donnell, Shekhar, & Hetrick, 2009; Jones, Malone, Dirnberger, Edwards, & Jahanshahi, 2008; Malapani et al., 1998; Parker, Lamichhane, Caetano, & Narayanan, 2013; Perbal et al., 2005; Smith, Harper, Gittings, & Abernethy, 2007). This manifests as a motor timing impairments (e.g. tapping synchronisation, Elsinger et al., 2003; O'Boyle, Freeman, & Cody, 1996), also seen in the classic Parkinsonian symptom of bradykinesia, as well as perceptual timing impairments (e.g. temporal bisection, Carroll et al., 2009; Elsinger et al., 2003; Parker et al., 2013; Smith et al., 2007). More specifically, it has been reported that
patients tend to underestimate intervals (Lange, Tucha, Steup, Gsell, & Naumann, 1995; Pastor, Artieda, Jahanshahi, & Obeso, 1992), which is consistent with a slower pacemaker.

Apart from Parkinson’s disease, there are also other disorders that affect timing behaviour. Patients with schizophrenia tend to perform poorly on a range of timing tasks, even when accounting for working memory deficits (Bolbecker et al., 2014; Ciullo, Spalletta, Caltagirone, Jorge, & Piras, 2015; Elvevåg et al., 2003; Peterburs, Nitsch, Miltner, & Straube, 2013). Again, it has been suggested that this arises as a result of the impaired function of dopaminergic brain areas, which is a key feature of schizophrenia (Brisch et al., 2014; Guillin, Abi-Dargham, & Laruelle, 2007). More generally, brain regions implicated in timing are similar to those affected in schizophrenia (Andreasen, 1999; Stopper & Floresco, 2014).

Patients diagnosed with attention deficit hyperactivity disorder (ADHD) also often exhibit impairments in the accuracy of temporal reproductions (Barkley, Edwards, Laneri, Fletcher, & Metevia, 2001a; Barkley, Murphy, & Bush, 2001b; Plummer & Humphrey, 2009; West et al., 2000). Some authors have even suggested that time processing deficits directly underlie the impulsive characteristics of this disorder (Barkley, Koplowitz, Anderson, & McMurray, 1997; Noreika, Falter, & Rubia, 2013; Smith, Taylor, Rogers, Newman, & Rubia, 2002). There also seems to be an overlap of the neural time perception network and the regions most impacted by ADHD (Noreika et al., 2013; Rubia, Halari, Christakou, & Taylor, 2009). This neurobiological link is further supported by studies showing that dopamine agonists such as methylphenidate (the most common treatment for ADHD) can alleviate the timing impairments present in the disorder (Rubia et al., 2009).
In summary, fMRI studies of healthy individuals, as well as diseases and disorders in which time perception is affected, point toward the basal ganglia as a core timing mechanism.

1.3.3 Neurophysiology. This section has thus far identified that the dopaminergic areas of the basal ganglia are a recurring feature when it comes to neuroimaging studies of time perception and timing pathology. Recent work has selectively targeted these areas in non-human animals, using electrophysiological and optogenetic techniques in order to measure the activity of individual neurons and neurotransmitters with high precision. Here, I focus on the neural activity in the basal ganglia, although it should be noted that there are other neural populations which have been shown to contain time-related information. This includes posterior parietal cortex (e.g. Jazayeri & Shadlen, 2015; Leon & Shadlen, 2003; Matell, 2014; Matell, Meck, & Nicolelis, 2003). However, these areas have been suggested to primarily be involved in response preparation and decision processes, which may represent downstream integration of timing information (Coull, Cotti, & Vidal, 2016; Matell, 2014; Praamstra, 2006; Shadlen & Newsome, 2001). There is also evidence that the activity of neurons in sub-cortical areas is more representative of timing information than neurons in cortical areas (e.g. Bakhurin et al., 2016; Matell et al., 2003). Later sections will also show that time perception is intimately related with dopamine (Section 1.3.4), which is the primary neurotransmitter of the basal ganglia. Given these reasons, this section focuses exclusively on the basal ganglia.

The basal ganglia are comprised of the ventral and dorsal striatum (which themselves are composed of the nucleus accumbens, and caudate and putamen nuclei, respectively), as well as the globus pallidus, ventral pallidium, subthalamic nucleus and substantia nigra. Notably, the substantia nigra, which is the principle dopamine
producing area, has neural inputs to the striatum. Given that these areas recur in models of time perception (e.g. SBF), imaging studies, and pathology, particular attention has been paid to these areas in terms of electrophysiological investigation (Chiba, Oshio, & Inase, 2015; Gouvêa et al., 2015; Soares, Atallah, & Paton, 2016).

One of the first electrophysiological studies of time perception was conducted using a fixed interval reinforcement schedule, where rats responses would earn reward after a target time (Matell et al., 2003). The target times, 10 and 40 s, were randomly interleaved between trials, and occurred with a probability of 25% and 75%, respectively, in order to keep reinforcement rate balanced. Once trained, the rats showed a distribution of responses that peaked at each target time with approximately equal rates. While they performed this task, the activity of anterior dorsolateral striatum neurons was recorded (as well as neurons in the anterior cingulate cortex). The researchers found that the different target times could account for variability in the firing rates of a subset of the striatal neurons (and the cortical neurons). Furthermore, the target times could be predicted from the firing rates of these neurons, even when the firing rate of only a single neuron was tested. This strongly suggests that these neurons coded duration information (Matell et al., 2003). Notably, the responses of the neurons either had a peak at the target time or had a ramp-shaped function that peaked at the target time, and these patterns resemble decision and accumulation processes, respectively.

More recent experiments have supported and extended this idea. For example, using a similar fixed interval paradigm while recording neural activity from medium spiny projection neurons in the rat striatum, researchers re-established that responses of these neurons covaried with the animal’s time estimates (Mello, Soares, & Paton, 2015). This neural activity also predicted the time of inaccurate response when animals were adapting to a novel target time (Mello et al., 2015). Of relevance to BeT
(where adjunctive behaviours during an interval serve as discriminative stimuli for time estimates; Section 1.2.2), the neural activity was also affected by interim behaviours. This multiplexing of temporal information with sensorimotor information supports BeT’s assumption that transitions in behavioural states mediate timing (Fetterman, Killeen, & Hall, 1998; Gouvêa, Monteiro, Soares, Atallah, & Paton, 2014). However, some neurons appeared to exclusively code for duration, suggesting the possibility of a purely perceptual representation. The researchers also found that neural activity was scaled to the target time, demonstrating a neural encoding of time that was relative rather than absolute, which supports the concept of a variable rate pacemaker.

Another electrophysiological study also found that neural activity in the striatum was predictive of time estimates (Gouvêa et al., 2015). In this study, infusions of muscimol (a neurotoxic GABA agonist) into the striatum significantly impaired timing behaviour, while leaving other behaviours intact, demonstrating the necessity of these neurons for time perception (Gouvêa et al., 2015).

Perhaps the most compelling demonstration of the importance of the basal ganglia in time perception comes from Soares, Atallah, and Paton (2016), who used optogenetic techniques to directly and specifically manipulate neural activity in mice during a temporal bisection task. This study also used both pharmacogenetic suppression and fibre photometry to provide additional evidence that basal ganglia neurons affected time perception. However, the optogenetic results constitute a direct, causal manipulation of these neurons, therefore this experimental aspect is focused on below. The optogenetic procedure involved injecting a viral vector that carried photosensitive channelrhodopsin and halorhodopsin into tyrosine-hydroxylase expressing neurons (dopamine producing neurons) in the substantia nigra pars compacta (SNC), which project to the striatum. These neurons could then be selectively activated or
inhibited via light stimulation of different wavelengths, resulting in an increase or decrease of dopamine levels in the striatum, respectively. The researchers found that after activating these neurons, timing functions were shifted rightward, indicating an underestimation of time consistent with a slowing of the pacemaker, while after inhibition, timing functions were shifted leftward, indicating an overestimation of time consistent with an acceleration of the pacemaker. Notably, this study focused on the role of the SNC (which is the afferent dopaminergic input to the dorsal striatum) rather than the dorsal striatum itself. Neurons in the SNC respond in a similar manner to those in the ventral tegmental area (Ilango et al., 2014). However, it is unknown whether dopamine neurons in the ventral tegmental area also affect timing in a similar manner.

In summary, there is a growing consensus that the neurons in the basal ganglia form a network that is critical for time perception and that dopaminergic neurons are specifically involved in timing. In the next section, I will detail some other findings that relate to dopamine, as well as some other neurotransmitters.

1.3.4 Neuropharmacology. The section above highlighted the importance of the basal ganglia (in particular the striatum and substantia nigra) in time perception. These areas are canonically associated with the neurotransmitter dopamine. Dopamine is typically thought to play an important role in motivation (Berridge, 2007) and reward (Schultz, 1998), and how these constructs relate to time perception will be detailed in the Section 1.4. The canonical finding is that dopaminergic activity in the striatum encodes a reward prediction error — the differences between expected and experienced reward — which guides learning about actions (Schultz, 1998). However, in addition to its associations with motivation and reward, as a pharmacological agent, dopamine has been routinely acknowledged to play a significant role in time
perception, in what some refer to as the ‘dopamine clock hypothesis’ (Balcı, 2014; for reviews of the role of dopamine in time perception see Coull et al., 2011; Jones & Jahanshahi, 2009).

The predominant example of this comes from non-human animal studies, which have pharmacologically manipulated dopamine during time perception tasks. When given dopamine agonists (e.g. methamphetamine) during a peak interval procedure, rats’ response rates peaked earlier, as if their pacemaker was accelerated (Buhusi & Meck, 2002). When given dopamine antagonists (e.g. haloperidol), peak responses were later, commensurate with a slowing of the pacemaker (Buhusi & Meck, 2002). When both drugs were delivered simultaneously, rats’ peak responses were similar to that of a control condition (Maricq & Church, 1983). Concurrent fMRI imaging and dopamine precursor depletion has demonstrated reduced activity in the putamen and supplementary motor area during time perception tasks (Coull, Hwang, Leyton, & Dagher, 2012).

To add to this evidence that dopamine is important for the rate of the hypothetical pacemaker, genetic knockout of the gene for the dopamine transporter (DAT, which increases extracellular levels of dopamine) has been shown to cause either a total loss of temporally sensitive behaviour (Meck et al., 2012) or earlier peak responses in mice (Balcı et al., 2010). Similarly, genetic over-expression of the D₂ receptor has been shown to cause later peak responses (Drew et al., 2007). Many studies also report an increase in the variance of responses (i.e. non-directional impairments) in timing tasks due to dopamine antagonists (Coull et al., 2012; Rammsayer, 1999; 1993; 1997). Nevertheless, the bulk of evidence has generally supported the idea that increasing dopamine levels increases the speed of the pacemaker (Abner, Edwards, & Douglas, 2001; Buhusi & Meck, 2002; Cevik, 2003; Cheng, Macdonald, & Meck, 2006; Cheng & Liao, 2007; Cheng, Hakak, & Meck,
2007; Cheung et al., 2006; Chiang et al., 2000; Maricq & Church, 1983; Maricq, Roberts, & Church, 1981; Matell, Bateson, & Meck, 2006; Matell, King, & Meck, 2004; Meck et al., 2012), and that decreasing dopamine levels decreases the speed of the pacemaker (Buhusi & Meck, 2002; Cheng & Liao, 2007; Drew, Fairhurst, Malapani, Horvitz, & Balsam, 2003; Lustig & Meck, 2005; MacDonald & Meck, 2005; 2006; Maricq & Church, 1983).

However, all of the above studies were performed on non-human animals (with the exception of Lustig & Meck, 2005). A study by Lake and Meck (2013) tested human participants on a peak-interval procedure while under the influence of amphetamine (which increases synaptic dopamine levels in the striatum) and found different patterns of results across individuals, dependent on how much they liked the drug (as measured via self-report questionnaire). Importantly, the degree of amphetamine induced euphoria has been positively correlated to the amount of dopamine release in ventral striatum (Drevets et al., 2001). Individuals who did not like the drug (and performed more poorly on a baseline reaction time task used to measure attentional lapses) had earlier peak response times after ingesting amphetamine, consistent with the animal literature and consistent with an acceleration of the pacemaker (these same participants also exhibited later peak response times after treatment with haloperidol). However, individuals who reported liking the drug more (and who had better performance on the attentional task) had significantly later peak response times after ingesting amphetamine. (Peak response times were unaffected by haloperidol in these individuals.) The authors of this study concluded that in the latter participants, the euphoria and positive affect induced by amphetamine competed for attentional resources (Buhusi & Meck, 2009), and thus caused underestimations of time in this group. They liken this explanation to the “time flies when you’re having fun” idiom: if attentional resources are reallocated to positive
experiences, then it might be expected that time ought to be underestimated. The results of this study would suggest that the effect of dopamine on time perception is a function of pre-existing individual differences (Lake & Meck, 2013).

Support for the idea that individual differences moderate the effect of dopamine on time perception has also been put forward by human studies that have assessed genotype in combination with time perception (Balcı, Wiener, Çavdaroğlu, & Coslett, 2013). Here, researchers used a variant of the peak interval procedure while rewarding participants for correct responses with either a small or large monetary reward. They found that the contingency of large monetary rewards could cause individuals to begin responding earlier than when they could earn smaller monetary rewards. However, there was no change in the peak response time, nor the timing of response termination. This might suggest a simple change in response strategy rather than a change in pacemaker rate. Additionally, this finding only applied to those whose genotype indicated either high levels of prefrontal dopamine availability and high D₂ receptor density or low levels of prefrontal dopamine availability and low D₂ receptor density (the COMT-Val158Met polymorphism regulates prefrontal dopamine catabolism, and the DRD2/ANKK1-Taq1a polymorphism regulates D₂ receptor density in the striatum). The authors of this study concluded that the effect of reward magnitude on response timing was dependent on individual genetic differences in prefrontal/striatal dopamine functioning.

Other corollaries of dopamine function can be seen in other physiological measures. For example, some researchers have previously suggested that the spontaneous rate of eye blinks reflects the tonic level of striatal dopamine (Karson, 1983; Taylor, 1999). While the relationship between tonic dopamine and spontaneous eye blink rate has attracted some contention (van der Post, de Waal, de Kam, Cohen, & van Gerven, 2004), given the striatum’s central location in the brain, and the
difficulty of making direct and precise measurements of dopaminergic activity, this proxy seems to have high utility if robust. However, despite the popularity of the dopamine clock hypothesis and the wealth of studies that pharmacologically manipulate dopamine, only one study has investigated the association between spontaneous eye blink rate and time perception (Terhune, Sullivan, & Simola, 2016). In this study, participants completed both a visual and an auditory temporal bisection task while eye blink rate was recorded. The authors reported that individuals overestimated durations if they had blinked prior to the judgement on the previous trial. However, an important caveat of this study is that, even if taken as a robust index, spontaneous eye blink rate has typically been assumed to be associated with tonic levels of dopamine. If the association between temporally local changes in blink rate and time perception is to be interpreted as relating to dopaminergic function, then it must be assumed that local eye blink rate also reflects more phasic dopaminergic activity. So far there is little evidence of this. Similarly, that the presence of eye blinks during a 800-2100 ms (variable) interval, anywhere from 2350-6150 ms before the time judgement, should be associated with this judgement appears rather ad-hoc (Terhune et al., 2016). However, despite the interpretability issues, this study was unique in looking at intra-individual differences in timing due to endogenous factors, and provides an exemplar of how these types of non-invasive physiological measures can be used to investigate time perception.

Some further caveats about the above findings may help to explain some conflicting and inconsistent evidence. Pharmacologically, drug delivery affects dopamine levels in a non-specific way (i.e. not exclusively in striatal areas but also in the prefrontal cortex). This is especially the case when different dopaminergic agents are used (e.g. amphetamine, methamphetamine, cocaine, haloperidol, remoxipride, sulpiride, SCH-23390) and thus precise comparison between these manipulations is
difficult. Furthermore, some of these agents target specific subtypes of dopamine receptors (i.e. D₁, D₂, and D₃ receptors), which have entirely different (sometimes opposing) effects on neural activity. Similarly, some agonists (e.g. amphetamine) also affect noradrenaline, and to a lesser degree serotonin (Seiden, Sabol, & Ricaurte, 1993), which themselves both have effects on time perception (see below). There is also an issue with variability in the pharmacodynamics and metabolism of ingested drugs, the progress of which develops over a relatively long period that may have distinctly different stages of effects on behaviour. Furthermore, the dynamics of dopamine exhibit non-linear dose-response curves for a range of functions (Cools & D'Esposito, 2011; Floresco, 2013; Gjedde, Kumakura, Cumming, Linnet, & Moller, 2010; Monte-Silva et al., 2009), and these can be difficult to characterise due to individual differences. The effects of drug-based dopaminergic manipulations are therefore difficult to characterise due to their non-specificity, and possible collateral effects that impact timing behaviour in myriad ways. It should also be noted that as dopaminergic manipulations also affect motivation, it is rather difficult to attribute the deficits in timing behaviour specifically to time perception, as motivational deficits may also lead to impairments in performance.

Ultimately, the optogenetic study of Soares, Atallah and Paton (2016) discussed in the previous section, overcomes many of these confounding factors and speaks more definitively to the dopamine clock hypothesis. To reiterate, this study found that dopamine release in the striatum was consistent with a decrease in the rate of the pacemaker (Soares et al., 2016). Given this finding, it is likely that previous suggestions of a positive relationship between dopamine and pacemaker rate may have been complicated by motivational effects. For example, if positive affect causes
attentional reallocation from time perception to euphoria, it would be difficult to
disentangle the effect of euphoria using gross pharmacological manipulation,
particularly in non-human animals.

Apart from dopamine, other neuromodulators are also known to affect time
perception, albeit to a less-well characterised degree. Specifically, the catecholamine
noradrenaline, which is typically associated with activity in the peripheral nervous
system, seems to play a role in timing behaviour. Noradrenaline has an established
relationship with arousal (Berridge, 2008; Coull, Jones, Egan, Frith, & Maze, 2004),
and as discussed above, arousal is known to have an effect on time perception
consistent with an increased pacemaker rate. However, when noradrenergic neurons
are lesioned in rats, they tend to make earlier responses, which is consistent with an
increased pacemaker rate (Al-Zahrani, Al-Ruwaitea, Ho, Bradshaw, & Szabadi,
1998). Similarly, noradrenergic agonists (clonidine) have been shown to lead to
rightward shifts in peak-times in rats, while antagonists (idazoxan) lead to leftward
shifts, suggesting that noradrenaline decreases pacemaker rate (Penney et al., 1996).
In humans, the noradrenaline re-uptake blocker reboxetine has been shown to increase
accuracy in temporal discrimination (Rammsayer, Hennig, Haag, & Lange, 2001)\(^8\). In
some of the above studies, as some effects only occur for longer target times (> 200
ms), noradrenaline has been proposed to affect timing via attentional mechanisms,
rather than affecting the pacemaker rate via arousal (Penney et al., 1996; Rammsayer
et al., 2001). Thus, while noradrenaline ought to affect timing behaviour consistent
with an increase in pacemaker rate, findings have not been entirely in support of this
idea and therefore its precise effect has not been well characterised in terms of
existing theoretical models.
Serotonin (5-HT), a monoamine neurotransmitter, also appears to affect time perception (Wittmann et al., 2007). Specifically, one study has shown that ingestion of psilocybin (a 5-HT$_{2A/1A}$ agonist) can cause increased underestimations of time in a reproduction task, consistent with a shortened representation of time in memory (Wackermann, Wittmann, Hasler, & Vollenweider, 2008). This finding has been corroborated by a genetic study, showing that 5-HT-related genes are associated with shortened duration representations in a duration discrimination task (Sysoeva, Tonevitsky, & Wackermann, 2010). 5-HT lesions in non-human animals also appear to cause timing deficits, but there have been a number of conflicting results in this literature that are not reconcilable with a standard pacemaker-accumulator model (Al-Ruwaitea, Al-Zahrani, Ho, Bradshaw, & Szabadi, 1997; Chiang, Al-Ruwaitea, Ho, Bradshaw, & Szabadi, 1999; Ho, Velázquez-Martínez, Bradshaw, & Szabadi, 2002). However, one reasonably robust finding is that increased serotonin increases patience in time-dependent decisions, whereas decreased serotonin leads to impatient decisions (Eagle et al., 2008; Ho et al., 2002; Miyazaki, Miyazaki, & Doya, 2012; Miyazaki et al., 2014; Schweighofer et al., 2008; Tanaka et al., 2007; Worbe, Savulich, Voon, Fernandez-Egea, & Robbins, 2014; Yates et al., 2014).

While these other neurotransmitters are no doubt relevant to timing behaviour, given the critical role of the basal ganglia and the robustness of pharmacological manipulation, the literature has primarily focused on the role of dopamine in time perception. It is central to this thesis that dopamine neurons are also involved in reward processing, as Chapter 3 provides empirical evidence for an effect of reward on human time perception. In the next section of this chapter, I will discuss how the psychological factors associated with dopamine affect time perception, which will lead to the postulation of the first research question.
1.4 REWARD AND MOTIVATION

In the previous section I have presented literature that describes a relationship between dopamine and time perception. In this section, I focus on the psychological factors that are known to rely principally on dopamine, and explicitly address the relationship between time perception, motivation, and reward. I will first explain how dopamine relates to each of these respective constructs, before reviewing the literature that has more directly investigated associations between motivation and reward in both humans and non-human animals.

It should be noted that much research into the neurobiology of reward and motivation typically focuses on the mesolimbic dopamine pathway. This is in contrast to time perception research, which is more often related to the nigrostriatal pathway (this is also commonly associated with movement). However, these pathways are not independent and the nigrostriatal pathway has also been shown to be critical for reward processing (Wise, 2009).

There are numerous definitions of motivation and reward (Kleinginna & Kleinginna, 1981), thus, for clarity, some definitions of these constructs will be provided. The hedonistic principle defines motivation as the process of maximising pleasure (Young, 1959). Motivational states therefore relate to reward-directed behaviour, including approach, behavioural activation and invigoration (Kleinginna & Kleinginna, 1981). In regard to this thesis, the most important part of this definition is the temporal sequence: motivation is the behavioural or cognitive state of an agent due to a prospective reward (Botvinick & Braver, 2015). Notably, some researchers have proposed that the behavioural energisation that would conventionally be considered to be an aspect of goal-directed motivation may also occur generally, when a reward is not specified (Niv, Joel, & Dayan, 2006).
A general psychological definition of reward is any appetitive stimulus that can cause a positive affective experience and that can (but does not necessarily, White, 1989) act as a reinforcer. A dichotomy is often drawn between primary rewards (those that are essential for survival, e.g. food, sex) and secondary rewards, which derive their value from primary rewards (e.g. money, Peters & Büchel, 2010; Sescousse, Caldú, Segura, & Dreher, 2013). Both primary and secondary rewards appear to have similar, but differentiable neurobiological effects (Kim, Shimojo, & O'Doherty, 2011; Levy & Glimcher, 2012). Both typically activate dopaminergic brain regions (Valentin & O'Doherty, 2009), while there are disassociations between the specific identity of the reward in the orbitofrontal cortex (Sescousse, Redoute, & Dreher, 2010). In the subsequent section, it can be assumed that primary rewards are used in non-human animal studies, and secondary rewards are used in human studies, unless indicated otherwise.

1.4.1 Dopamine and motivation. Many researchers have drawn a distinction between the motivation toward reward (“wanting,” Berridge, 2007) and the hedonic experience of reward receipt (“liking,” Wise, 1980). A clear difference is in the timing of these states relative to reward: “wanting” ought to occur during the anticipation of reward, while “liking” ought to occur during consumption of reward. There has been much debate about which one of these constructs the dopaminergic system principally subserves, or whether they are even mutually exclusive (Bromberg-Martin, Matsumoto, & Hikosaka, 2010a), and it is unclear precisely which motivational processes (e.g. arousal, effort, persistence) are influenced by midbrain dopamine (Salamone & Correa, 2012).
However, proponents of the incentive salience hypothesis propose that the main function of midbrain dopamine is in motivating behaviour, and that dopamine function is neither necessary nor sufficient to act as a hedonic signal (Berridge, 2007). Evidence for this comes from studies showing, for example, that dopamine depletion in the ventral striatum can impair high-effort reward seeking (Aberman & Salamone, 1999; and for review see Salamone, Correa, Farrar, & Mingote, 2007). Motivational deficits are also present in dopaminergic diseases like depression and schizophrenia (Salamone, Koychev, Correa, & McGuire, 2014).

Because dopamine appears to play such a critical role in motivation, many of the observed effects of dopaminergic manipulations on time perception (Section 1.3.4) may actually be a result of motivational changes rather than changes in perceived time. This is particularly the case in non-human animal studies, where learning the timing task necessarily involves reinforcement and motivated responding. However, motivational factors themselves affect time perception in humans, possibly via dopaminergic mechanisms.

1.4.2 Motivation and time perception. Early experimental studies first demonstrated an effect of motivation on time perception by incentivising subjects to complete irrelevant tasks before interrupting them and eliciting a time estimate. For example, Rosenzweig and Koht (1933) — who refer to motivation as “need-tension” — asked subjects to complete an unsolvable puzzle and told subjects that the puzzle constituted a practice (low motivation) or a test (high motivation). While no inferential statistics were provided, the authors reported a tendency for durations in the low motivation condition to be overestimated relative to durations in the high motivation condition.
(over durations of 1-10 mins). Other similar early experiments also report these
tendencies with similar paradigms, which differed slightly in their manipulation of
motivation (Meade, 1959; 1963).

One key proposal that has been advanced to account for these findings is that
in highly motivated states, agents are engaged with their goals, and “lose track of
time” (Meade, 1963). Such an effect has been explained by assuming a common,
finite, attentional resource for temporal and non-temporal information (Alonso,
Brocas, & Carrillo, 2014; Buhusi & Meck, 2009). In terms of the clock metaphor, if
more of this attentional resource is allocated to one’s goals, temporal information
processing is inhibited, and less counts accumulate in the memory store (Zakay &
Block, 1995). This idea has been shown to generalise to task engagement in general,
especially in dual task paradigms, where a time estimation must be made concurrently
with another non-temporal task. The results from these paradigms have indicated that
time is consistently underestimated relative to when the distractor task is not present,
suggesting that the distractor task interferes with the accumulation of counts (Brown,
1997). Thus, one explanation for the effect of motivation can be attributed to a lack of
attention to time.

However, more recently, this has been questioned by a study using an
experience sampling method (Conti, 2001). In this study, participants were queried
about their current activities, intrinsic and extrinsic motivation, time awareness, time
estimation, checking of time, and perceived speed of time during normal behaviour
over a five day period. It was found that higher intrinsic motivation was associated
with a lack of attention to time and underestimations of time. Importantly, while this
finding would seem to recapitulate the idea that task engagement leads to a lack of
attention to and underestimations of time, these factors were *independently* associated with time perception after controlling for the other. Thus, a lack of attention to time cannot fully account for the relationship between motivation and time perception.

Some studies have used more explicit incentives to assess how motivation can influence time perception. For example, using a version of the peak-interval procedure modified for humans, Balcı, Wiener, Çavdaroğlu, & Coslett (2013) assessed the effect of increased monetary reward payoff on timing. Here, participants were instructed to bracket the target time by holding a response key. If the response was initiated after, or terminated before the target time, the reward was not received. The study found that when larger rewards were available, participants with particular genetic polymorphisms (low PFC dopamine and low D2, or high PFC dopamine and high D2) initiated their responses earlier. However, as these participants did not also terminate their responses earlier, this was taken as a strategic change in the decision process rather than a change in pacemaker rate (see Balcı, 2014).

Another more recent experimental study relates to physiological factors, in addition to motivation (Gable & Poole, 2012). Given the relevance of physiological factors to this thesis, this study merits particular attention. In this study, images of appetising food (designed to elicit high-approach motivation), as well as generally positive (low-approach motivation) and neutral images were used as stimuli in a temporal bisection procedure (Gable & Poole, 2012). In the tested ranges (400 ms - 1600 ms), the high-approach motivation images were significantly underestimated relative to the other stimuli. This effect was moderated by the time since participants had last eaten, suggesting that hunger might increase the motivation toward the food stimuli (Gable & Poole, 2012). Ultimately, the results of this study are consistent with the above findings, which in sum support the idea that motivation is associated with a decrease in the rate of the hypothetical pacemaker and with underestimations of time.
Importantly, intrinsic motivation is predictive of persistence (Gottfried, 1985; 1990). This is suggestive of another, ecological explanation for why motivation could affect time perception. In the general case, if there exists a mechanism that causes underestimations of time during motivated states, this may prolong goal pursuit, which could generally be considered to be an adaptive mechanism (Gable & Poole, 2012). However, such a mechanism could also be maladaptive. For example, casinos (and virtual/online environments) are often enriched with stimulating and rewarding cues. If such cues trigger the same motivational mechanism and induce underestimations of duration (Noseworthy & Finlay, 2009), this may encourage this individual to stay in the environment longer than they ordinarily would, which (given the nature of casinos) will presumably result in a net loss of reward.

1.4.3 Dopamine and reward. In contrast to the incentive salience hypothesis, earlier studies implicated dopamine as the principle neurotransmitter responsible for the hedonic nature of “liking” (Wise, 1980). The perspective has rapidly evolved (in part due to computational models of behaviour), and dopaminergic signals are now more often conceptualised as a reinforcement signal that facilitates learning, rather than directly causing pleasure. This is due to the classic finding that phasic dopamine activity constitutes a reward prediction error (Schultz, 1998), commensurate with prescriptive models of reinforcement learning (specifically temporal difference learning, Sutton & Barto, 1998), and the growing causal evidence that supports this account (Adamantidis et al., 2011; Chang et al., 2016; Kim et al., 2012; Schoenbaum, Esber, & Iordanova, 2013; Steinberg et al., 2013). In one sense, the role of dopamine in reinforcement learning combines the previous “wanting” and “liking” aspects into “learning” the associations between actions and rewards. Nonetheless, these constructs are still useful to distinguish dopaminergic activity during the anticipation
of reward and the actual consumption of reward. Given its dominant involvement in
time perception, this section will largely focus on dopaminergic factors, but it should
be noted that other neurotransmitters are also involved in reward processing
(Nakamura, 2013).

The precursor to the current model of dopamine response was the finding that
dopamine neurons in the SN and VTA respond to unexpected appetitive stimuli
(Romo & Schultz, 1990; Figure 1.5). However, subsequent studies showed that if the
reward was repeatedly paired with a predictive cue, the dopaminergic response
gradually transferred to this earlier predictor of reward (Mirenowicz & Schultz,
1994). As the time of reward delivery became more predictable due to associative
pairing, response to the reward itself was reduced or absent. If the reward was omitted
at the normal time, dopamine responses were depressed below their basal level of
activity (Schultz, Dayan, & Montague, 1997). Thus, these response dynamics are
fundamentally sensitive to the expected time of reward delivery (Hollerman &
Schultz, 1998). This collection of findings implicated the dopamine response as
approximating a temporal difference reinforcement learning signal known as the
reward prediction error (Schultz et al., 1997) and this has been the successful basis of
many computational models of cortical learning (Montague, Daya, & Sejnowski,
1996; for a detailed review of the reward prediction error hypothesis, see Schultz,
2002, and Schultz, 1998). These findings have all been corroborated in humans using
fMRI imaging of the striatum (Berns, McClure, Pagnoni, & Montague, 2001;
McClure, Berns, & Montague, 2003; Pagnoni, Zink, Montague, & Berns, 2002).
Figure 1.5. Reward prediction error. Single neuron recordings from dopamine neurons in the substantia nigra in response to an unexpected reward, a reward predicted by a cue (CS), and the omission of reward after a previously learnt reward-predicting cue. Adapted from Schultz, Dayan, & Montague (1997).

Importantly, if different cues signal that the rewards will be delivered at different times, the responses of dopamine neurons to these cue depend on the anticipated delays (Kobayashi & Schultz, 2008; Gregorios-Pippas, Tobler, & Schultz, 2009; as well as reward probability, magnitude and type, Lak, Stauffer, & Schultz, 2014; Stauffer, Lak, & Schultz, 2014). This decreased response to longer reward delays typifies the economic principle of temporal discounting: rewards are devalued as a function of delay until their receipt (Chapter 2). In fact, the decrease in activity approximates a hyperbolic discounting function that corresponds to that observed for human temporal discounting choice data (Mazur, 1987). Dopamine neuron responses to the predicted rewards themselves are larger when delays are longer (Fiorillo, Newsome, & Schultz, 2008), which has been assumed to reflect increasingly uncertain temporal precision (i.e. the scalar property) and reduced associative learning (Fiorillo, Tobler, & Schultz, 2005). These characteristics of dopamine responses demonstrate that they are highly sensitive to timing and appear to encode the intervals between cues and rewards. This suggests that timing is an integral aspect of reward processing (Gershman, Moustafa, & Ludvig, 2014; Daw, Courville, & Touretzky, 2006; Kirkpatrick, 2013; and see Bermudez & Schultz, 2014 for review).
Apart from the phasic signals discussed above, striatal dopamine neurons also exhibit “quasi-phasic” responses (Lloyd & Dayan, 2015), as well as tonic responses. The quasi-phasic responses manifest as a ramping up of activity as reward approaches — evidently an anticipatory signal that may be involved in motivation and persistence (Bromberg-Martin, Matsumoto, & Hikosaka, 2010b; Howe, Tierney, Sandberg, Phillips, & Graybiel, 2013). Similar anticipatory signals have also been observed in human BOLD imaging studies in striatum (Jimura, Chushak, & Braver, 2013), as well as in other areas sensitive to subjective value, such as medial prefrontal cortex (McGuire & Kable, 2015). Notably, the persistence of these dynamics after learning do not fit neatly into the reward prediction error theory that the phasic activity of these neurons supports (Niv, 2013)\(^\text{10}\). The tonic activity of dopamine neurons in the striatum takes place over a longer time scale (seconds to minutes) and is thought to be related to the calibration of the vigour of actions (Niv, Daw, & Dayan, 2005; Niv, Daw, Joel, & Dayan, 2007; see Chapter 6). However, earlier suggestions have associated the basal firing rates of dopaminergic neurons in the striatum to the rate of the pacemaker in pacemaker-accumulator models (Meck, 1988). Given the principle pharmacological role of dopamine in affecting the pacemaker (Section 1.3.4), the intimate relationship between dopamine and reward clearly suggests that reward (as a psychological construct) may also affect time perception.

1.4.4 Reward and time perception. A number of researchers have previously noted that time perception is an integral aspect of reward seeking. For example, Meck (1988) has suggested the existence of a general brain mechanism that subserves both the quantification of brain-stimulation reward and duration, evidenced by an experiment showing that the stimulation of the medial forebrain bundle (which consists of ascending dopaminergic fibres from the ventral tegmental area; VTA) can...
cause leftward shifts in the psychometric function for temporal bisection (Meck, 1988). This comes in addition to models such as BeT, a main principle of which is that the rate of a hypothetical pacemaker is proportional to reinforcement rate (Section 1.2.2). However, despite these suggestions, only very few studies have actually provided direct empirical data on this relationship.

For example, building on anecdotal and experiential evidence, an early study suggested that the duration of a successfully completed task is underestimated relative to a failed task of an identical duration (Harton, 1939). To add to the idea that rewarding experiences can influence time perception, individuals may also use time cues to evaluate how rewarding their experience is. This has been suggested by William James, who described the experience of time awareness as “odious” and “insipid” (James, 1890). By manipulating the time displayed on clocks during the completion of a task, a study showed that individuals who thought less time had passed rated the task as more boring than those who thought more time had passed (London & Monello, 1974). A more recent series of experiments also used similar methodology to create the illusion of slow or fast time progression and showed that ratings of hedonic experience are higher when time is thought to have passed more quickly (Sackett, Meyvis, Nelson, Converse, & Sackett, 2010). Thus, while many studies implicitly assume that time experience is a function of reward, the relationship between time perception and reward may be bidirectional.

However, contemporary empirical investigations that have both explicitly acknowledged the dopamine clock hypothesis and drawn a distinction between motivation and reward are lacking. Instead, studies have examined other factors related to reward. For example, one study examined the impact of reward priming (which is arguably closer to the experience of reward) on temporal binding (or intentional binding, Aarts et al., 2012). Temporal binding refers to the perceived
compression of time between an action and its outcome (Moore & Obhi, 2012). While often used as a proxy to assess the sense of agency, it has also been suggested that this effect is due to a transient slowing of the rate of the hypothetical pacemaker, as sensory discrimination performance is decreased during these intervals (Wenke & Haggard, 2009). Aarts et al. (2012) showed that participants primed with images with positive valence experienced more compression between actions and outcomes (i.e. they underestimated the interval to a greater degree). Notably, this effect was primarily driven by individuals with higher spontaneous blink rates, which may indicate higher levels of tonic dopamine in the striatum (Karson, 1983; Taylor, 1999). Similar results have been observed when the actions are paired with monetary rewards, particularly in individuals with high trait sensitivity to reward (Muhle-Karbe & Krebs, 2012). This suggests that, especially in individuals with higher levels of tonic striatal dopamine, reward can lead to underestimations of time. One study also found that punishment can also affect temporal binding (Takahata et al., 2012). This effect appeared to occur postdictively: when the outcome of the action indicated a loss of money, temporal binding was attenuated (Takahata et al., 2012). This suggests that reward could alternatively affect the memory representation of duration rather than pacemaker rate.

Although images with positive valence may constitute rewarding stimuli (see Gable & Poole, 2012 in Section 1.4.2 above), in the above studies the rewarding characteristics are not a direct feature of the target stimulus for which a time estimate must be made. However, a study by Failing and Theeuwes (2016) directly assessed the temporal perception of a stimulus which itself signalled reward using a temporal oddball paradigm. Stimuli that provide advance information about the receipt of rewards appear to have the same effects on midbrain dopamine neurons (Bromberg-Martin & Hikosaka, 2009). Thus, at least neurobiologically, these stimuli may be
equated to an actual rewarding experience. In their first experiment, the authors used an oddball paradigm (described in Section 1.3.1), with an oddball stimulus that also signalled whether a correct response would be rewarded or not. In essence, this signal should act as a predictive cue for reward and should theoretically lead to a phasic dopamine signal. The results showed that the point of subjective equality (PSE) was shifted to the left in the reward condition, indicating that when the oddball signalled reward its duration was overestimated. In a second experiment, the sequence of standard stimuli instead signalled reward availability. In this case, there was no effect on PSE, but the precision of judgements increased. A third experiment, nearly identical to the first, compared two oddball stimuli that signalled either low or high rewards. The results of this experiment showed that the perceived duration of the oddball was longer for the high reward oddball than the low reward oddball, suggesting a parametric effect (Failing & Theeuwes, 2016). In summary, this study appeared to show a dissociation between motivational effects and actual reward receipt: reward receipt affected the pacemaker rate, whereas motivational differences only affected judgement sensitivity.

This is the only human study to explicitly test the effect of reward experience, rather than differences in prospective reward, on time perception. However, there is at least one non-human animal study that investigated whether the consumption of a range of different primary rewards would change timing behaviour. Meck and Church (1987) trained rats on a peak-interval procedure and then pre-fed them with specific nutrients to see whether this would affect performance. The rats received either lecithin, casein, sucrose, or a saccharine control. Lecithin is found in egg yolks, liver, and soybeans, and contains choline, a precursor to acetylcholine. Casein is a protein found in milk, and contains tyrosine, a catecholamine precursor. High carbohydrate foods lead to an increase in brain tryptophan, the precursor to serotonin (Wurtman &
Fernstrom, 1976). Thus, each of these three nutrients exert natural effects on neurotransmitter systems (Wurtman, Hefti, & Melamed, 1980). Importantly, these nutritive primary rewards are inherent in naturally occurring foods and thus any effects observed are more likely to be ecologically valid than either money or drugs. The results showed that lecithin shifted the response curves to the left, although slowly, across a span of days. Casein also shifted the response curve to the left, but this was more abrupt and the responses eventually normalised during this testing period. In a post-test phase without casein, the response curve appeared to overcompensate and shift rightward before normalising. In the sucrose group, the pattern of results was dynamically similar to that of protein, but in the opposite direction. The researchers went further than ascribing the observed effects to “reward” or lack of motivation due to pre-feeding, and instead used existing research to evaluate how these nutrients specifically act on brain chemistry (Wurtman et al., 1980). Their interpretation was that acetylcholine (lecithin) acted slowly on memory processes, dopamine (casein) increased the rate of the pacemaker, and serotonin (sucrose) decreased the rate of the pacemaker. Crucially, this study shows that naturally occurring rewards do not all act on time perception in the same way (Meck & Church, 1987). Thus, it is unlikely that the effect of all rewards on time perception can be attributed solely to dopamine.

Relevant to the idea that different nutrients affect time perception in different ways, metabolic hormones have also been shown to affect time perception. For example, circulatory levels of the “hunger hormone” ghrelin increase during fasting. When injected with ghrelin, rats previously trained on a 20 s fixed-interval procedure made more early responses (Anderberg et al., 2016). On the other hand, when central ghrelin receptors were blocked, rats made more efficient responses, not wasting energy with responses earlier than the target time (Anderberg et al., 2016). Overall
this suggests that circulating ghrelin has a role in modulating the timing of behaviour. Notably, ghrelin receptors frequently co-localise with dopamine receptors (Dickson et al., 2011).

Relationships between metabolic factors and time perception have also been observed in humans. By artificially manipulating perceived time by making a wall-mounted clock run either faster or slower, one study showed that the rate of blood-glucose decrease in diabetic subjects was a function of perceived time, rather than standard clock time (Park, Pagnini, Reece, Phillips, & Langer, 2016). In other words, blood-glucose levels fell faster if the clock was manipulated to run faster. This counter-intuitive finding demonstrates that psychophysiological relationships can be bidirectional and that in this specific case, the psychological perception of duration appeared to be capable of impacting metabolism.

In summary, similar to the more direct effects of dopamine on time perception, the literature relating psychologically rewarding factors to time perception is unequivocal. Many of the directional effects that increased reward magnitude can have on timing behaviour in the non-human animal literature may be accounted for by motivational effects (Balcı, 2014), which may be distinct from an effect on the perception of time itself. There is also considerable evidence that physiological and metabolic factors are important to time perception, which raises the question of whether different types of rewards (i.e. primary versus secondary) could affect time perception in different ways. The association with physiological and metabolic factors can be explained from the perspective outlined in the previous section: that homeostatic processes may constitute part of a timing mechanism. This also makes sense from the perspective that animals have a fundamental requirement for energy. Thus, if they use energy state
to inform their sense of urgency, they can act to consume energy in an optimal way. This latter point anticipates the discussion of temporal decision making models in Chapter 2.
1.5 SUMMARY AND RESEARCH QUESTION

1.5.1 Summary of Chapter 1. This chapter discussed some background literature relating to time perception, including methodology and some of the characteristic measurement features of timing behaviour. It also outlined how timing behaviour in a variety of tasks can be related back to the concept of a hypothetical pacemaker, the rate of which can vary. A review of the literature identified some candidate physiological and neurophysiological substrates of time perception, which may fulfil the role of a pacemaker. In particular, dopaminergic neurons in basal ganglia and the striatum have been shown to encode representations of time. This chapter also summarised evidence that dopamine itself plays a critical role in time perception, although its precise effect on hypothetical pacemaker rate has not been fully resolved. Finally, this chapter explained the relationship between dopamine and psychological factors, and summarised findings showing that both reward and motivation affect timing behaviour. Notably, “reward” is not a unitary construct and the literature suggests that different types of primary rewards can affect time perception in different ways.

1.5.2 Research question. The perception of time is extremely critical to behaviour and decision making. Thus, a research agenda that seeks to characterise factors that alter time perception is of great significance. As discussed in the preceding sections, there is considerable evidence to suggest that rewarding factors affect time perception in humans. However, many of the existing studies have not isolated the effects of motivation from the effects of experienced reward (e.g. Balci, Wiener, Çavdaroğlu, & Coslett, 2013; Gable & Poole, 2012). Only one study has directly tested time estimates of rewarding stimuli in humans (Failing & Theeuwes, 2016) and this was implemented in a paradigm that already elicits changes in time perception at baseline
(also see Aarts et al., 2012). Furthermore, it is arguable that the way this study was implemented — using information about possible upcoming reward rather than the actualised consumption of reward — constitutes a motivational manipulation. If this is the case, then no study has addressed the question of whether reward consumption can affect time perception in humans. This first research question presented an opportunity to fill an existing gap in the literature and to characterise a novel but theoretically justified effect on time perception.

Because early animal studies found differential effects of different primary rewards (Meck & Church, 1987), the choice of the specific reward was important. Given that researchers have previously proposed a physiological basis for the hypothetical pacemaker (Craig, 2009a) and that metabolic factors have been related to time perception (e.g. Anderberg et al., 2016; Park, Pagnini, Reece, Phillips, & Langer, 2016), an appropriate choice would be a primary reward with inherent metabolic value. Chapter 3 presents a series of experiments that explicitly address this research question.

Importantly, if reward affects time perception, this may more widely affect behaviours that involve time. Chapter 2 will subsequently present some background information on these types of behaviours (i.e. temporal decision making), which will lead to the derivation of the second and third major research questions of this thesis and the theoretical justification for the studies reported in Chapter 4 and Chapter 5.
As mentioned at the start of this document, timing is implicit in almost all behaviours and cognitive processes (Marshall & Kirkpatrick, 2015). Some behaviours explicitly involve time perception, as in the standard time measurement procedures discussed in Chapter 1. These seek to measure time perception, unaffected by other factors. However, time perception and representation are also an important element of many everyday decision-making processes and an approach that investigates these processes might constitute a more ecological investigation of time perception as it is in naturalistic contexts.

There are a number of models of temporal decision making which necessitate a representation of time. This thesis specifically relies on two canonical examples. One is intertemporal choice, a behavioural model that addresses the fact that organisms prefer immediately available rewards to those whose acquisition is delayed (Loewenstein, Read, & Baumeister, 2003). This preference for immediacy clearly necessitates that the decision maker has a representation of time in order to appropriately evaluate the future reward. The other model of temporal decision making comes from the foraging literature, where temporal preferences are described from the perspective of a decision maker balancing the potential rewards and costs of the current environment versus a different environment (Stephens & Krebs, 1986). Given that most organisms have continuous metabolic activity, time is a crucial determinant of the potential costs in these decisions as well as a necessary aspect of
estimating the average reward rate of any given environment. These two models are relevant to Chapter 4 and Chapter 5 respectively, and will be discussed in greater detail in the subsequent sections.

Different models of temporal decision making can be unified in their relationship to impulsivity (Ainslie, 1975). Impulsivity is a multifaceted construct, but all of these facets tend to describe a reduced capacity for deliberation and inhibition — the inverse of self-control (Evenden, 1999). Importantly, it has been suggested that impulsive individuals have chronic deficits in time perception. A commonly accepted theory is that impulsive individuals overestimate durations and therefore are more averse to delay (Barratt & Patton, 1983; Glicksohn, Leshem, & Aharoni, 2006; Havik et al., 2012; Rubia, Halari, Christakou, & Taylor, 2009; Schulreich, Pfabigan, Derntl, & Sailer, 2013; van den Broek, Bradshaw, & Szabadi, 1992; Wittmann & Paulus, 2008; Wittmann, Leland, Churan, & Paulus, 2007; and for review, see Moreira, Pinto, Almeida, & Barbosa, 2016). In terms of the hypothetical pacemaker-accumulator model explained in Chapter 1, this would manifest as a chronically increased pacemaker rate. Impulsivity thereby unifies temporal decision making and time perception on a single axis, where at one extreme, subjects with slow pacemakers are relatively patient (delay-prone), whereas at the other extreme, subjects with fast pacemakers are relatively impatient (delay-averse).

One conceptual dichotomy divides impulsivity into ‘decision’ impulsivity, which relates to deliberative decisions about future consequences, and ‘action’ impulsivity, which is required for appropriately timing or inhibiting actions (MacKillop et al., 2016). This can be rephrased in terms of the exemplar decision models above: in intertemporal choice, time guides which decisions to make, whereas in many foraging scenarios, it is important to decide when to act. Thus, both of these
models provide complementary information in terms of these two aspects of impulsivity and in terms of the different ways time can be conceptualised in decision making.

This chapter will proceed with a similar structure to Chapter 1. Firstly, it will outline the standard terminology and typical procedures used in both intertemporal choice and foraging, and how these relate to one another. Notably, variants of both of these procedures are operationalised in the empirical chapters of this thesis. Subsequently, it will delineate the variants of the models used in each of these domains and specifically highlight how these models rely on time perception. It will then discuss some of the neurophysiological factors that are involved in both of these temporal decision making processes. Finally, this chapter discusses the existing factors known to influence temporal decision making. This review will be the basis for the second and third research questions of this thesis.
2.1 THE MEASUREMENT OF TEMPORAL DECISION MAKING

2.1.1 Intertemporal choice. Historically, it has been the domain of economics that has sought to explain intertemporal choice. This economic literature has provided a framework which describes how rewards are devalued over time, using the model of temporal discounting (Samuelson, 1937). A typical example of temporal discounting is that I may prefer to be given $10 now, over $12 dollars that I must wait a year for. However, I may be indifferent between having $10 now and $20 in a year. From an economic perspective, my indifference in the latter scenario reveals the present value of the delayed option. In the standard version of a temporal discounting procedure, subjects are presented with a series of these smaller-sooner/larger-later options (Hardisty, Thompson, Krantz, & Weber, 2013; Figure 2.1).
**Figure 2.1.** Temporal discounting task. The beginning of a trial is marked with an open circle. After an inter-trial interval (ITI), participants are presented with a choice (filled circle) between a small reward ($R_S$) delivered after a short delay ($D_S$), and a large reward ($R_L$) delivered after a long delay ($D_L$). Adapted from Stephens, Kerr, & Fernandez-Juricic (2004).

With a sufficient amount of choices, indifference points for different rewards at different delays can be derived as in the example above. In combination, these yield a discount function (Figure 2.2), the steepness of which can be characterised with a single statistic known as the discount rate ($k$, Rachlin, 2006).
Figure 2.2. Temporal discounting function. The value of rewards declines as a function of their delay. Adapted from Kable and Glimcher (2007).

The discount rate (and the corresponding steepness of the discount function) is the empirical measure of impulsivity; steeper discounters (larger $k$) value delayed rewards less and vice versa. Despite there being significant variability in discount rates between individuals (Peters & Büchel, 2011), this measure has been shown to be at least partly heritable (Anokhin, Grant, Mulligan, & Heath, 2015) and temporal discounting has therefore suggested to be an endophenotype (Bickel, 2015). Temporal discounting has also been used as a marker for clinically recognised disorders of
impulsivity and is affected by substance abuse, pathological gambling, attention deficit hyperactive disorder, schizophrenia, and depression (Bickel, Jarmolowicz, Mueller, Koffarnus, & Gatchalian, 2012; Bickel, Koffarnus, Moody, & Wilson, 2014; Miedl, Peters, & Büchel, 2012; Peters, Miedl, & Büchel, 2012). Intertemporal preferences are also able to discriminate between individuals with nicotine dependence (e.g. Amlung & MacKillop, 2014), obesity (e.g. Amlung, Petker, Jackson, Balodis, & MacKillop, 2016), and can be predictive of smoking relapse (e.g. Sheffer et al., 2014), as well as general health behaviours (e.g. Bradford, 2010) and outcomes (e.g. BMI and exercise, Sweeney & Culcea, 2017; but see Arfer & Luhmann, 2017 for an example of the limits of temporal discounting as a marker for real-world self-control). Notably, a standard discounting task (as explained above) is implemented in Study 2.

One straightforward psychological interpretation of the devaluation of delayed reward is one that treats time as an investment cost (Loewenstein, Read, & Baumeister, 2003). That is to say that a delay to a reward is time during which the alternative immediate reward cannot be used or invested, or even time that cannot be spent engaging in other, potentially rewarding behaviours. However, in many studies that employ temporal discounting, the consequences of participants’ decisions are hypothetical (delivering rewards to participants in the distant future can be difficult). This means that intertemporal choice rarely engender actual opportunity costs (subjects do not actually have to wait throughout the delay to receive a reward), which may make potential delays more abstract and less aversive. In addition to the fact that the choice options are often hypothetical in nature, subjects are frequently asked to treat the trials as if they were independent from one another (in line with the
assumption of consumption independence in discounted utility theory, Frederick, Loewenstein, & O'Donoghue, 2002). In other words, the consequences of each decision should not interfere with any other decision.

A number of studies have tried to more closely relate the canonical temporal discounting paradigm to more consequential outcomes by creating “experiential” intertemporal choice tasks. These primarily entail real delays, which mean that subjects experience the temporal cost of their choices (Bixter & Luhmann, 2013; Horan, Johnson, & Green, 2017; Reynolds & Schiffbauer, 2004; Schweighofer et al., 2006; Smits, Stein, Johnson, Odum, & Madden, 2013). Given that primary rewards have been found to be discounted significantly more steeply (even when hypothetical) compared to secondary rewards like money (Estle, Green, Myerson, & Holt, 2007; Forzano & Logue, 1992), some experiential discounting tasks also entail consumable primary rewards (e.g. Gregorios-Pippas, Tobler, & Schultz, 2009; Jimura, Myerson, Hilgard, Braver, & Green, 2009). Subjects in these studies are typically required to fast prior to experimentation, as overexposure can devalue primary rewards via satiety (e.g. Minamimoto, La Camera, & Richmond, 2009; Valentin, Dickinson, & O'Doherty, 2007). It has not been investigated whether varying the nutritional content of primary rewards affect discounting behaviour differently, as in the time perception study with rats in Section 1.4.4. In general however, subjects exhibit typical discounting behaviour in experiential discounting tasks, regardless of whether the rewards are hypothetical or monetary (Bixter & Luhmann, 2013; Gregorios-Pippas et al., 2009; Horan et al., 2017; Jimura et al., 2009; Jimura, Chushak, & Braver, 2013; Reynolds & Schiffbauer, 2004; Schweighofer et al., 2006). These experiential procedures ultimately end up being very similar to the patch-leaving paradigm (described below) and other foraging paradigms.
Foraging theory is derived from the study of behavioural ecology and can be seen as a model of time preference that predates the human-focused domain of temporal discounting. In canonical foraging theory, time preferences are conceptualised as a tradeoff between the resources available in the current “patch” of the environment and the time/energy taken to travel to a new resource patch. Unlike temporal discounting, which can be characterised as a descriptive model of choice, foraging models tend to be prescriptive and aim to show how animals can optimise their behaviour given different environmental contingencies. The typical measurement procedure for foraging is known as the patch-leaving task (Figure 2.3).
Figure 2.3. Patch-leaving task. The beginning of a trial is marked with an open circle. After an inter-trial interval (ITI), participants spend a short duration ($D_S$) accumulating a small reward ($R_S$). After this, participants are presented with a choice (filled circle) to move to a new patch (restart the trial) or to spend extra time ($D_L - D_S$) accumulating additional reward ($R_L - R_S$). Note that in this scenario the inter-trial interval represents the time required to travel to a new patch. Adapted from Stephens, Kerr, & Fernandez-Juricic (2004).

Foraging paradigms are often said to be similar (if not formally equivalent) to standard intertemporal choice tasks but within a dynamic and ecological context (Bourgeois-Gironde, 2012; Stephens et al., 2004; Stephens & Anderson, 2001). To see why this is the case, one can compare reformulations of each paradigm that have been
standardised so that they proceed from choice-point-to-choice-point. For the temporal
dISCOUNTING paradigm, this simply means appending the inter-trial interval as an
equivalent cost for each choice option (Figure 2.4).

Figure 2.4. Standardised temporal discounting task. This task is the same as
that presented in Figure 2.1, but from a choice-point-to-choice-point perspective.

However, for the patch-leaving paradigm, this reframes the task as a choice between a
smaller reward delivered after an inter-trial interval (travel time) and a short time
gathering reward, or a marginally larger total reward delivered after a marginally
larger delay (Figure 2.5). In other words, this recontextualises the patch-leaving
paradigm as a choice between a smaller/sooner reward and a larger/later reward.
Crucially, the choice options maintain the same overall reward rates.
An important variant of the patch-leaving paradigm does not constrain decision makers to a single choice-point and instead simulates a continuous and dynamic accumulation of resources while allowing subjects to travel to a new patch (‘restart’ the trial) at any time. Thus, this version of the task requires sustained commitment to a course of action, rather than a one-off choice. Apart from more accurately representing naturalistic foraging scenarios, this variant also better complements the typical temporal discounting paradigm in terms of how time is treated. In temporal discounting, time guides *which* decisions to make, whereas in a continuous-time variant of the patch-leaving paradigm, agents much decide *when* to leave. In other words, the former is a decision *about* time, while the latter is a decision *in* time. A version of this continuous-time patch-leaving task is implemented in Study 3.
The continuous-time variant also maintains its formal similarity to temporal discounting. To illustrate, one can imagine the patch-leaving task as a series of intertemporal choices where the value of the sooner reward option decreases each time it is chosen, while the delayed option “resets” the sooner reward option to its original value. At some point, the time cost of choosing the delayed option will outweigh the reduced value of sooner reward and a decision maker will shift their preference to the delayed option (Stephens, 2008). Indeed, this is the principle behind the marginal value theorem (MTV), which states that an animal should leave a resource patch when the marginal reward rate falls below that of the environment at large (Charnov, 1976). Thus, from a foraging perspective, the value of a reward is determined by its contrast in relation to the background environment (i.e. the opportunity cost).

2.1.3 Differences between intertemporal choice and foraging. There are a number of key differences between standard intertemporal choice tasks and foraging tasks. For example, in temporal discounting tasks, binary choices are typically presented simultaneously\textsuperscript{12}, whereas patch-leaving decisions occur sequentially. This means that there is a direct comparative valuation of the choice options in temporal discounting but a serial “accept-or-reject” process in patch-leaving.

A second difference between intertemporal choice and foraging is how each tasks reflects preference reversals. In many real-world scenarios, agents initially make a commitment to a long-term goal (e.g. dieting, smoking cessation) but face continuous opportunities to renege on that commitment. From the perspective of intertemporal choice, if this happens, it can be interpreted as a preference reversal from the later option to the sooner option. In temporal discounting, the act of a preference reversal is not usually observed, as experimenters only provide a one-shot
decision between choice options and do not observe subjects throughout the waiting period. (However, preference reversals can be inferred from the hyperbolic fit of data from a temporal discounting paradigm; see Section 2.2.1.) However, in foraging tasks (specifically the continuous patch-leaving task), agents have the opportunity to “give up” at any point after an initial commitment to a delay period (see Ainslie, 1975). Thus, foraging tasks may better capture the effects of any phenomenological urgency that might facilitate preference reversals.

While these two differences set a contrast between the two paradigms, the most important difference between intertemporal choice and foraging is what kind of cost the time delays in each paradigm carry and, as a consequence, how each treats the potential rate of reward that can be earned (Fawcett, McNamara, & Houston, 2012). To be specific, time delays in both paradigms present three types of costs: collection risk (e.g. when something interrupts the possibility of acquiring the reward during the delay, see Bixter & Luhmann, 2015; Weber & Chapman, 2005), metabolic cost (e.g. the cost of passive, baseline homeostasis), and investment cost, which is the cost of forgone potential reward (i.e. opportunity cost, Stephens, 2002). Because trials in temporal discounting are treated as independent from one another (each choice is “one-shot”), all trials are of equal duration, regardless of choice (this is also the case in non-human animal studies, where a post-reward buffer interval is added to equate trial durations). Thus, the investment cost of delay in temporal discounting entails little more than a forgone chance for financial investment (perhaps akin to compounding interest). However, in foraging, different choices consequentially prevent further decisions and potential reward gain, as the time delays represent “travel time”. This means delays in foraging scenarios not only carry investment cost but also entail additional opportunity cost. This is a critical difference, as in the foraging case, one may be able to make a higher long-term gain by making an initially
“impulsive” decision that may expedite future rewards. Likewise, one might be able to earn multiple immediate rewards in the time it would take to earn a delayed reward of lesser total value. From the perspective of a native foraging agent (with a goal of reward rate maximisation), impulsive choices in temporal discounting are suboptimal because trial length is constant regardless of choice. Of course, many non-human animals are not explicitly made aware of this and, as a result, non-human animals might appear to display discounting in temporal discounting tasks when they are actually following the reward maximising strategy under the misguided assumption that trial lengths are different. This possibility has received some empirical support, as when post-reward delays for either choice have been explicitly cued with an adjunctive small reward, non-human primates have been shown to reduce their discounting, which is not accounted for by the discounting perspective (Blanchard, Pearson, & Hayden, 2013; Pearson, Hayden, & Platt, 2010).

Ultimately, despite their superficial similarity, behaviour in temporal discounting tasks and foraging tasks is often different by mere nature of how the tasks are framed, even when the tasks are equivalent in overall rate of reward and effort. For example, Carter et al. (2015) tested human participants on both a delay discounting task and a patch-style foraging task. Each of the tasks involved choices between two rewards delivered at different times; the delay to the sooner reward was either 5 or 50 s and the delay to the later reward was either 60 or 90 s. In the delay discounting scenario, participants were presented with both choice options simultaneously. In the foraging scenario, participants were initially forced to choose the sooner reward and after waiting for the appropriate delay and receiving the reward, were then given a choice to continue waiting for the large reward. It was found that participants were significantly more likely to adopt a long-term reward rate maximising strategy by waiting for the large rewards in the foraging scenario (Carter
et al., 2015). This reflects the general consensus in the literature: behaviour in patch-leaving scenarios is less impulsive compared to temporal discounting scenarios, across a range of species (blue jays, Stephens & Anderson, 2001; rats, Carter & Redish, 2016; non-human primates, Blanchard & Hayden, 2015; and humans, Carter et al., 2015).

In summary, both the intertemporal choice and foraging literatures provide well established frameworks with which to view time preferences. Foraging complements intertemporal choice in that it views temporal decision making as a dynamic processes that includes choices regarding when to act, rather than just which choice to make. In this regard, foraging paradigms capture an aspect of behaviour that is absent in temporal discounting by further emphasising the opportunity cost of time, and by recontextualising the goal of behaviour as maximising reward over a series of decisions. While some have questioned the ecological validity of temporal discounting paradigms for these reasons (e.g. Blanchard & Hayden, 2015; Fawcett et al., 2012; Hayden, 2016; Stephens, 2008), temporal discounting arguably captures an important aspect of impulsivity that is separate from that assessed in foraging scenarios (Frederick, Loewenstein, & O’Donoghue, 2002). Moreover, while they may not occur frequently in ecological contexts, simultaneous choices with multiple alternatives are relatively commonplace in modern society, and temporal discounting is empirically related to many relevant behaviours (Anokhin et al., 2015; Bickel, 2015; Peters & Büchel, 2011). Indeed, simultaneous choices involve different neural areas compared to foraging decisions (Kolling, Behrens, Mars, & Rushworth, 2012). Thus, it is possible that modern humans have evolved different cognitive strategies to deal with these two different types of decision processes.
The remainder of this chapter will adhere to the following terminology: ‘temporal discounting’ refers to the standard, simultaneous choice paradigm typically used in the intertemporal choice literature; ‘patch-leaving’ refers to the sequential choice paradigm typically used in the foraging literature; and ‘time preference’ refers broadly to behaviours in both of these tasks.
2.2 MODELS OF TEMPORAL DECISION MAKING

The previous section described the typical paradigms used in intertemporal choice and foraging, as well as some key differences between them. The current section will describe extant models of intertemporal choice and foraging. For the most part, these models implicitly assume that a decision maker’s representation of time / delay is veridical. However, as demonstrated in Chapter 1, time perception is labile to a host of internal and external factors, as well as having systematic biases. Some theoretical studies have, however, made attempts to accommodate inexact representations of time in models of intertemporal choice and foraging. In addition to describing the canonical “objective” time models, this section will also discuss existing research that has attempted to address the possibility of non-veridical time perception in each of these models. This section ends with a discussion of two models which attempt to unify intertemporal choice and foraging, and which also claim that decision makers representation of time is non-veridical.

2.2.1 Intertemporal choice. As mentioned in the previous section, by eliciting intertemporal choices from subjects in a temporal discounting task, one can derive a discount function (Figure 2.2). There are two common, core models used to describe the discount function and recover the discount rate. The exponential model represents ‘rational’ discounting and reflects the classic economic ideal of value maximisation when taking into account compounding interest (Samuelson, 1937)

\[ V = R \cdot e^{-kD} \]

where \( V \) is subjective value, \( R \) is the objective reward amount, \( k \) is the discount rate and \( D \) is the delay to the reward. There are a number of assumptions in this model (Frederick, Loewenstein, & O’Donoghue, 2002), a key one being dynamic
consistency: if an agent prefers reward 1 at time $x$ compared to reward 2 at time $y$, then that preference should not change with any proportional change to delays $x$ and $y$.

However, empirical data from both humans and animals have suggested that the rate of devaluation diminishes with the size of delay (Rachlin, Raineri, & Cross, 1991) which can lead to preference reversals and a violation of dynamic consistency$^{13}$. This has lead to the more common practice of fitting intertemporal choice data with the hyperbolic function (Mazur, 1987) which allows for preference reversals as explained above. The hyperbolic mode is

$$V = R \cdot \frac{1}{1 + kD}$$

where the variables are the same as above. Another popular elaboration of hyperbolic model is often referred to as the quasi-hyperbolic model (Laibson, 1997), which is formulated as

$$V = R + \beta \sum_{D=1}^{\infty} \delta^D R_D$$

where $V$ is the subjective value of a stream of consumption, and the parameters $\delta$ and $\beta$ are discount parameters. This model can be conceptually decomposed into two subsystems: an exponential system with a discount rate of $\delta$, and the ‘impatient’ $\beta$ system which captures additional weight given to immediately available rewards. While there is some evidence that these two subsystems are represented in different brain areas (McClure, 2004; McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007), these claims have been contested on the basis of errors in statistical inference (Kable & Glimcher, 2010). Modelling choice using these types of discount functions
has lead to several neuroeconomic investigations showing that parameters from the models are correlated with activity in brain regions canonically associated with subjective value (Kable & Glimcher, 2007; McClure, 2004). These representations are robust enough that an individual’s discount rate can be recovered from BOLD activity in these regions (Kable & Glimcher, 2007). Importantly, these functions implicitly assume that individuals incorporate an objective representation of delay into their decisions — that is, they assume that people have precise knowledge about the duration of intervals.

One stream of research has recently attempted to attribute some of the “anomalous” features of discounting behaviour — most commonly the hyperbolicity of the discount function — to biases of human time perception. The first articles to formally suggest that non-linearities in time perception could result in hyperbolic discounting were those by Takai Takahashi and colleagues (Takahashi, 2005; 2006; 2009; 2011; Takahashi, Ikeda, & Hasegawa, 2007; Takahashi, Oono, & Radford, 2008), in what has now been termed the “tempospect” theory of intertemporal choice (Takahashi & Han, 2012). In essence, these accounts alter the standard discounting functions by incorporating either the Weber-Fechner law, or Steven’s Power law into the representation of delay (Section 1.1). However, many of the above articles were theory driven, with little empirical data to support the hypothesis.

One of the first empirical papers to provide support for this idea was by Zauberman et al. (2009), who separately measured discount rates as well as the non-linearities of participants’ subjective time horizons (estimates of how far away delays appear on a visual analog scale; also see Bradford, Dolan, & Galizzi, 2013). When these non-linearities were taken into account, participants’ intertemporal preferences conformed to the “rational” exponential model rather than the hyperbolic model. In essence, this meant that participants’ subjective judgements about prospective delays
were correlated with their discount rates (Kim & Zauberman, 2009). A follow-up study using fMRI demonstrated that discount rates could be recovered from the BOLD activity in ventral striatum and ventromedial prefrontal cortex when participants were merely thinking about the future at specific time scales (Cooper, Kable, Kim, & Zauberman, 2013). Specifically, steep discounters had higher BOLD activity in these areas in response to shorter time scales and lower BOLD activity in response to longer time scales, while shallow discounters showed the opposite pattern. The above findings were strongly suggestive that hyperbolic discounting was due to biases in prospective time perception (but see Wiehler, Bromberg, & Peters, 2015 for a null finding using a similar experimental design).

The studies above constitute the main empirical findings in regard to subjective time perception in temporal discounting. However, since that time, a number of other researchers have proposed similar theoretical accounts of subjective time perception in temporal discounting. For example, Ray & Bossaerts (2011) provided analytical evidence that hyperbolic discounting can arise if the rate of the hypothetical pacemaker is autocorrelated. Similarly, Cui (2011) demonstrated that hyperbolic discounting may simply be a result of the scalar property of time perception alone.

Despite the evidence that time horizons have been shown to be correlated with discount rates, and the implication that time perception may be partly responsible for temporal discounting, there have been few direct empirical tests of this relationship. A single study tested the relationship between performance in a temporal bisection task (target times of 2-4 s) and discount rates, finding correlations between the two tasks (Baumann & Odum, 2012). Specifically, individuals in this study who overestimated time also tended to have steeper discount functions, supporting the general idea that time overestimation is related to impulsivity. However, a number of
similar studies have shown null findings. For example, one study trained participants to estimate a “20 s” interval with a metronome that ran either fast or slow (Berman, 2013). The trained participants subsequently underestimated or overestimated this 20 s interval, respectively. However, this recalibration effect did not generalise to an estimate of the length of the entire experiment and did not affect a subsequent temporal discounting task (Berman, 2013). One possible reason for this is the timescales involved in the behavioural tasks: interval timing tasks usually assess timing in the range of seconds, while temporal discounting tasks tend to measure preferences over days or months. There is also an apparent disconnect between concurrent timing behaviour and the kind of prospective, projected representation of time that is important in intertemporal choice. Thus, while time perception may be related to impulsivity more generally, given the lack of empirical support, it seems unlikely to be specifically involved in temporal discounting as measured using standard intertemporal choice tasks. However, further tests using a variety of measurement procedures may be helpful in clarifying whether or not this relationship exists.

2.2.2 Foraging. Most models of foraging behaviour appeal to the idea that in order to maximise total reward, organisms should maximise the rate of reward over an indefinite period. (In classical foraging theory, the reward is energy intake. Thus, the objective is to maximise the net rate of energy intake, Schoener, 1971.) This concept is captured by optimal foraging theory (Stephens & Krebs, 1986), according to which decision makers should act as to maximise their long-term reward rate $R_l$

$$R_l = \frac{\sum_{i=1}^{\infty} r_i}{\sum_{i=1}^{\infty} t_i}$$
where $r_i$ is a reward, $t_i$ is delay associated with reward $r_i$, and $i$ is any given “trial”. Notably, by maximising this ratio, organisms who reach a sufficient energy intake level will have more time available for other important behaviours like reproduction. This means that the process of maximising reward rate also minimises opportunity cost. However, there are two biological constraints that make this decision process infeasible. Firstly, the assumption that organisms have knowledge of all future rewards and delays is not plausible. Secondly, organisms have metabolic constraints and thus cannot endure low reward rates in the short-term without risking death, even if this maximises reward in the long-term. Thus, a simpler version of optimal foraging theory — the ecological rationality theory — simply maximises the expected reward for a single “trial”, and ignores any delays that occur after the delivery of reward (Stephens, Kerr, & Fernandez-Juricic, 2004; see Table 2). Maximising this short-term reward rate ($R_s$) approximates long-term reward rate maximisation.

One may notice that optimal foraging theory is a prescriptive ideal of how organisms should forage over time, but it does not describe how organisms develop expectations of rewards and delays, nor when organisms will actually make a decision to reject the current resource patch and move to a new patch. This can be clarified by the marginal value theorem (MTV), which states that an organism should leave a resource patch when the marginal reward rate falls below that of the environment at large (Charnov, 1976). This is based on the relatively uncontroversial assumption that organisms can estimate and represent both a long-term (the average rate of the environment) and a short-term (the average rate of the current patch) rate of reward. The marginal value theorem received empirical support rapidly after its development.
(e.g. Krebs, Ryan, & Charnov, 1974) and is still considered the dominant foraging algorithm for optimal allocation of time to resource patches (e.g. Bettinger & Grote, 2016; Nonacs, 2001).

There are a number of accounts that have noted the relevance of time perception to foraging behaviour (e.g. Balci et al., 2011; Bateson, 2003; Hills & Adler, 2002). In general, foraging requires at least two different representations of time (Gibbon & Church, 1990). Firstly, organisms must have a representation of the time it takes to travel between patches. Given that there might be different travel times, this may amount to an averaged internal reference. Secondly, organisms must also be able to measure the reward gained in each patch and when the rate of gained reward no longer has relative utility. Organisms therefore require a representation of reward relative to how long they have spent in the patch.

As discussed in Chapter 1, the behavioural theory of timing (BeT) proposes that the rate of the hypothetical pacemaker is proportional to rate of reinforcement (Bizo & White, 1994; 1995; Fetterman & Killeen, 1991; Killeen & Fetterman, 1988). If this assumption is true, and animals incorporate this time representation into a foraging decision rule, then their own decision behaviour may be biased by their foraging success. This proposal was theoretically explored by Hills & Alder (2002), who characterised the effect of rate-biased time perception on the marginal value theorem. The authors first noted that it is unclear whether a non-veridical pacemaker would affect the representation of travel time ($P_t$), or the representation of time spent in the resource patch ($P_r$), or both. However, they provided analytical evidence for each scenario, under the assumption that the rate of the pacemaker is an instantaneous linear function of reinforcement rate. If $P_t = P_r$, the animal’s behaviour should remain optimal. If $P_t < P_r$, animals should leave the patch earlier than dictated by the marginal value theorem, whereas if $P_t > P_r$, they should leave later. A survey of 26
patch-leaving studies has shown that foraging agents more often stay longer in patches than dictated by the marginal value theorem (Nonacs, 2001), which lends some supports to the latter possibility. However, these predictions of Hills and Alder (2002) do not factor in non-linearities in the relationship between reinforcement rate and pacemaker rate, nor do they account for lags in the effect (although they discuss these possibilities). Similarly, uncertainty in timing, i.e. the scalar property, is not taken into account here. Despite this, this analysis still provides rudimentary predictions of how time perception should affect temporal decision making.

Other researchers have accounted for how uncertainty and the scalar property of timing might effect foraging behaviour (Bateson, 2003). However, given that this thesis is principally concerned with non-veridical time perception in terms of pacemaker rate, rather than timing uncertainty, this review will be somewhat abridged. Balcı et al. (2011) reviewed a number of studies providing evidence that animals and humans take into account their timing uncertainty during decision making. For example, in a modified temporal bisection task, rats have been shown to settle with a smaller, certain reward when the target interval lies intermediate to the short and long references (Foote & Crystal, 2007). Balcı et al. (2011) also reviewed literature explicitly relating timing uncertainty to a patch-leaving scenario, where rewards are delivered on a fixed interval schedule before becoming suddenly unavailable. After the sudden depletion of a patch, starlings have been shown to wait for a constant proportion of the normal target time, and this waiting interval approximates 95% of the cumulative distribution function of the certainty of the target time (if the CV is at an empirically validated value of 0.25, Brunner, Kacelnik, & Gibbon, 1992). This provides evidence that patch-departure times in foraging tasks account for endogenous timing uncertainty, as a form of metacognition.
In summary, foraging models provide another framework to investigate how non-veridical time perception can affect temporal decision making. Notably, articles that have explored how variable pacemaker rates might affect foraging behaviour have been entirely theoretical (Hills & Adler, 2002), and no explicit empirical tests of the predictions from these accounts have been made in humans or non-human animals.

2.2.3 Unified models. A number of efforts have been made to consolidate intertemporal choice and foraging into a unified model. Two of these accounts also explicitly address non-veridical time perception as it relates to these decision processes. Given the relevance of the latter point to the second theme of this thesis, these models will be discussed in detail below.

The first of these models stems from the idea that non-human animals do not incorporate post-reward delays into temporal discounting decision processes (Kacelnik & Bateson, 1996). This has been theoretically justified on the basis that animals are unlikely to encounter variable post-reward delays in nature, and that associating rewards with subsequent delays presents a credit assignment problem that impedes the learning of this relationship (animals learn better from events that precede rewards rather than events that follow rewards, Kacelnik, 2003). As mentioned in the previous section, discount rates in non-human primates have been shown to be reduced when post-reward delays are more explicitly cued (Blanchard, Pearson, & Hayden, 2013; Pearson, Hayden, & Platt, 2010) which lends this idea empirical support. The Bounded Rationality model of Blanchard et al. (2013) took this feature into account and proposed a model whereby decision makers evaluate simultaneously presented choices as a ratio of reward and delay, but have a biased representation of the post-reward delay. This biased representation is reflected in a
free parameter ($\omega$). Thus, this heuristic rule chooses the option that maximises the short-term reward rate

$$\tilde{R}_s = \frac{R}{D + \omega}$$

This model was shown to fit temporal discounting data from non-human primates, as long as $\omega$ was a smaller, constant ratio of the actual delay. This shortened representation of delay is approximately consistent with the systemic underestimation of delays noted in the time perception literature (Eisler, 2003; Riemer, Rhodes, & Wolbers, 2016; Riemer, Trojan, Kleinböhle, & Hörlzl, 2012; Wackermann & Ehm, 2006), as well as the underestimation of delays that occurs when attention is not focused on temporal information (Alonso, Brocas, & Carrillo, 2014; Buhusi & Meck, 2009; Zakay & Block, 1995, see Section 1.4.2). Notably, this model is almost identical to the hyperbolic discount function above, in that it has a single free parameter. However, instead of implying a psychological discounting process per se, the prime mover of the devaluation of delayed reward is the $\omega$ parameter: a bias in time representation.

The second model is rather unique in that it places emphasis on the primacy of reward-seeking compared to time perception, and proposes that non-veridical time perception is a result of optimal, reward-maximising decision processes (Namboodiri & Shuler, 2016). This is in contrast to most other accounts presented in this document, which make the more intuitive assumption that time perception is more fundamental than decision processes. The training-integrated maximized estimation of reinforcement rate (TIMERR) model of Namboodiri et al. (2014) is a more general account of time perception and intertemporal decision making which draws heavily on optimal foraging algorithms\textsuperscript{14}. In their model, agents use their recent
reinforcement rate to predict their future expected reward rate, and then use this expected rate to devalue future delays (Namboodiri et al., 2014). A modified discount function for this model is

\[
V = R - \frac{R^* \cdot D}{1 + (D/T)}
\]

where \( R^* \) is the estimated reinforcement rate over the past time window \( T \). In essence, the fraction term acts as a penalty that is equal to the predicted reward lost as a result of waiting: the opportunity cost of time. The critical parameter of this model is how far back agents integrate their previous reward experience (given the biological implausibility of maintaining an unlimited reward history)\(^{15} \).

If \( T \) is relatively longer, agents will have lower perceived opportunity costs and a higher tolerance to future delays, whereas if \( T \) is relatively shorter, agents will have higher perceived opportunity costs and a lower tolerance to future delays. Notionally, \( T \) should be a tradeoff between an accurate representation of reward rate (given a dynamic environment) and the metabolic/cognitive costs of having a longer window of remembered reinforcement history (Namboodiri et al., 2014). Interestingly, the model allows for the possibility of negative values of \( V \). In this case, an agent should forgo either option with the expectation that better, alternative options may become available. In this way, the model simultaneously captures the “accept-reject” serial decision process inherent in patch-leaving tasks.

The TIMERR model also predicts non-veridical time perception as a result of reward-maximisation (Namboodiri et al., 2014). Put differently, TIMERR represents subjective duration such that it is optimised for detecting changes in reward rates: perceived reward rate equals the actual reward rate minus the expected (recently
experienced) reward rate (in this sense, time perception is a function of a “prediction error” in reward rate). Identified formally, subjective reward rate \( R^* \) can be decomposed into subjective value \( V \) (itself a function of reward and delay) and subjective time \( \psi \), and thus

\[
\frac{V(r_i, t_i)}{\psi(t_i)} = \frac{r_i}{t_i - \frac{R_T}{T}}
\]

where \( R_T \) is the experienced cumulative reward over the past time window \( T \). In combination with the previous equation, this gives

\[
\psi(t_i) = \frac{t_i}{1 + t_i/T}
\]

Given this formulation, time will be overestimated with smaller values of \( T \), and underestimated with larger values of \( T \). The authors do not confer much specificity to \( T \) (the past time over which experienced reward is integrated), other than to constrain it to be biologically plausible, and thus finite \( (\psi(\infty) = T) \). However, they do suggest that \( T \) could be adaptively calibrated depending on an animal’s metabolic requirements and the volatility of the environment (see appendix of Namboodiri et al., 2014).

However, overall, TIMERR is valuable in that it formally unifies intertemporal choice and foraging and additionally predicts features of time perception that are consistent with a relationship between pacemaker rate and reinforcement rate.

A complete list of the models of intertemporal preferences noted in this section of some models of temporal preferences is displayed in Table 2 below.
Table 2. Theories of intertemporal preference (adapted from Namboodiri & Shuler, 2016).

<table>
<thead>
<tr>
<th>Theory</th>
<th>Principle</th>
<th>Algorithm</th>
<th>Key parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Discounted utility</td>
<td>Stationary compounding interest</td>
<td>$V = R \cdot e^{-kD}$</td>
<td>Fitted discount rate</td>
</tr>
<tr>
<td>Discounted utility</td>
<td>Non-stationary discounting</td>
<td>$V = R \cdot \frac{1}{1+kD}$</td>
<td>Fitted discount rate</td>
</tr>
<tr>
<td>(hyperbolic)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Optimal foraging</td>
<td>Long-term reward rate maximisation</td>
<td>$\tilde{R} = \frac{\sum_{i=1}^{\infty} r_i}{\sum_{i=1}^{\infty} t_i}$</td>
<td>Inter-trial interval</td>
</tr>
<tr>
<td>Ecological rationality</td>
<td>Short-term reward rate maximisation</td>
<td>$\tilde{R} = \frac{r_i}{t_i}$</td>
<td>None</td>
</tr>
<tr>
<td>Bounded rationality</td>
<td>Short-term reward rate maximisation</td>
<td>$\tilde{R} = \frac{R}{D + \omega}$</td>
<td>Biased post-reward interval</td>
</tr>
<tr>
<td>TIMERR</td>
<td>Experientially-bounded reward rate</td>
<td>$V = R - \tilde{R} \cdot \frac{D}{(D/T)}$</td>
<td>Past reward integration interval</td>
</tr>
</tbody>
</table>
2.3 FACTORS THAT INFLUENCE TEMPORAL DECISION MAKING

Having previously described the typical measurement procedures and models of temporal decision making behaviour, this section will outline some physiological and pharmacological factors that affect temporal preferences. The purpose of this is twofold. Firstly, it will draw a similarity between these factors and the factors that have been shown to affect time perception (discussed in Chapter 1), supporting the argument that time perception may underlie temporal decision making. Secondly, it provides some background literature that informs how specific types of reward might affect temporal decision making. It begins with a short review of how temporal decision making can be affected by brain pathology. It then discusses pharmacological manipulations of temporal decision making in healthy individuals. Finally, this section discusses how physiological factors can affect temporal decision making. Notably, the former two parts of this section focus on human intertemporal choice, whereas the latter part focuses more on animal foraging. This reflects the relative emphasis of ecological factors in the foraging literature.

2.3.1 Pathology. Impulsivity, and intertemporal choice in particular, have been closely examined in relation to brain pathology and disease. In the case of synthetic causes of brain injury, patients with orbitofrontal cortex lesions have been reported to exhibit increased impulsivity as measured by personality questionnaires (Berlin, Rolls, & Kischka, 2004) and temporal discounting (Peters, 2011; Sellitto, Ciaramelli, & di Pellegrino, 2010). Notably, these patients have also been shown to overestimate and underproduce intervals in estimation and production tasks, respectively (Berlin et al., 2004).
Impulsivity and time perception deficits are also both behavioural identifiers present in the case of several neurological diseases. For example, individuals with ADHD (Barkley, Edwards, Laneri, Fletcher, & Metevia, 2001) have been shown to display higher impulsivity as measured by temporal discounting, as well as overestimations and under-reproductions of time (Barkley et al., 2001; Barkley, Murphy, & Bush, 2001). Relative to healthy individuals, individuals with schizophrenia have also been shown to exhibit increased temporal discounting, in standard temporal discounting tasks (Weller et al., 2014) and experiential discounting tasks (Horan, Johnson, & Green, 2017).

In addition to time perception deficits (Section 1.3.2), Parkinson’s patients have also been shown to display more impulsive choices in temporal discounting tasks, relative to healthy controls (Clark & Dagher, 2014; Milenkova et al., 2011). However, impulsivity in Parkinson’s patients can vary depending on whether they are medicated with dopaminergic treatments (typically L-DOPA) or not. For example, a subset of Parkinson’s patients who are medicated, and thus have higher levels of dopamine, have been shown to have reduced discount rates, compared to non-medicated states and healthy controls (Foerde et al., 2016). Temporal discounting behaviour has also been shown to depend on whether the individuals with Parkinson’s have comorbid impulse control disorders or not (Leroi et al., 2013). Given these findings, it has been suggested that dopaminergic dysfunction has a general role in impulsive behaviour (Frank, Samanta, Moustafa, & Sherman, 2007). However, the idea that impulsivity is directly and linearly related to dopamine levels is likely to be an oversimplification in Parkinson’s, especially as other comorbidities may cloud such a relationship (Sinha, Manohar, & Husain, 2013).
More generally, brain regions involved in time perception have also been shown to be involved in intertemporal choice (e.g. anterior insula cortex, striatum, Wittmann, Leland, & Paulus, 2007; Wittmann, Lovero, Lane, & Paulus, 2010), which may explain why pathology affecting these regions is linked to behavioural deficits in both timing and temporal decision making.

2.3.2 Pharmacology. To overcome potential issues with comorbidity and non-specificity in pathology, we can turn to studies that have examined the pharmacological effects of neurotransmitters on intertemporal choice in healthy individuals (for review see Peters & Büchel, 2011). Experiments that have manipulated dopamine have revealed mixed effects. One study found that the dopamine precursor L-DOPA increased discount rates, commensurate with an increase in BOLD activity in brain regions that encode subjective value (e.g. striatum, insula and orbitofrontal cortex, Pine, Shiner, Seymour, & Dolan, 2010). However, another study that used the Catechol-O-methyl transferase (COMT) inhibitor tolcapone to increase dopamine found that this lead to decreased discount rates and increased BOLD activity in striatum and insula (Kayser, Allen, Navarro-Cebrian, Mitchell, & Fields, 2012). The discrepancy of these results is likely to be due to variations in the mechanism of each drug, L-DOPA principally boosts dopamine synthesis in the striatum, while COMT primarily degrades dopamine in prefrontal areas. The differential effects of dopamine in striatum and prefrontal cortex on discounting have been supported by studies that have associated discount rates with genetic polymorphisms related to dopamine function. Specifically, individuals with the A1+ genotype at the DRD2/ANKK1-Taq1a locus (which indicates lower striatal $D_2$ receptor density) and carriers of the 158Val allele at the COMT-Val158Met gene (which indicates more enzymatically active COMT and relatively low prefrontal
dopamine) have relatively higher discount rates (Boettiger et al., 2007; Eisenberg, MacKillop, & Modi, 2007; Gianotti, 2012). The disassociation between the effects of dopamine in the striatum and in the prefrontal cortex mirrors that found in the effect of methamphetamine on time perception (Balci, Wiener, Cavdaroglu, & Coslett, 2013; Section 1.3.4).

In addition to the effects of dopamine, a number of studies have also demonstrated robust effects of serotonin on intertemporal choice and impulsivity in general (Dougherty, Richard, James, & Mathias, 2010; Winstanley, 2011; Worbe, Savulich, Voon, Fernandez-Egea, & Robbins, 2014). For instance, it has been shown that inhibition of dorsal raphe nucleus serotonin neurons reduces rats’ capacity to wait for delayed rewards (Miyazaki, Miyazaki, & Doya, 2012), while optogenetic activation of these neurons enhances patience (Miyazaki et al., 2014; Miyazaki, Miyazaki, & Doya, 2017). In humans, tryptophan depletion (which decreases serotonin synthesis) has been shown to increase impulsive choices in a variant of a discounting task (Schweighofer et al., 2008). A fMRI study using the same procedure showed that this effect was reflected in the differential activity of the ventral and dorsal striatum: ventral striatal activation was more strongly correlated with rewards at short time scales when serotonin was lower, whereas dorsal striatal activity was more strongly correlated with rewards at long time scales when serotonin was higher (Tanaka et al., 2007). This has led to a view that proposes opponent functions of striatal dopamine and serotonin in impulsive behaviour (Daw, Kakade, & Dayan, 2002; Schweighofer, Tanaka, & Doya, 2007).

Another experiment examined the effects of both dopaminergic and serotonergic manipulations, while simultaneously measuring both time perception and impulsivity in rats (Heilbronner & Meck, 2014). To do this, they trained rats on a peak-interval procedure with target times of 10 and 40 s, but also allowed the rats to
“defect” by pressing an independent lever, which ended the trial and resulted in a 20% chance of a small reward. The probability of a response to this “defect” lever was taken as a measure of impulsivity. The experimenters found that rats with later peak times were less likely to defect, suggesting that these rats had both slower pacemaker rates (evident in their peak times) and were also more patient (although this only held for a 10 s target time, and not for a 40 s target time). The administration of fluoxetine (a serotonin re-uptake inhibitor) reduced defect probability, but did not have an effect on peak times, suggesting that increased serotonin decreased impulsivity but did not alter pacemaker rate. In contrast, the administration of both cocaine and methamphetamine increased defection probability and decreased peak times, suggesting that increases in dopamine increase impulsivity as well as pacemaker rate (Heilbrunner & Meck, 2014).

Overall, dopaminergic manipulations in healthy individuals — both human and non-human animals — appear to affect impulsivity and temporal discounting in a fairly characterised manner. This provides further neurobiological evidence of a commonality between temporal decision making and time perception.

2.3.3 Physiology. The low-arousal theory of impulsivity is one of the earlier biological theories of personality (Eysenck, 1967; 1993). This theory proposes that impulsive behaviour stimulates arousal as a compensatory mechanism for those with chronically low baseline levels of arousal. While this theory has attracted criticism (e.g. Gray, 1981), it has also received some contemporary empirical support (Allen, Hogan, & Laird, 2009; Lempert, Johnson, & Phelps, 2016; Mathias & Stanford, 2003; Portnoy et al., 2014; Takahashi, Ikeda, Fukushima, & Hasegawa, 2007; Wilson & Scarpa, 2014). For example, individuals with low resting heart rates have been reported to be more likely to make impulsive risky gambles (Schmidt, Mussel, &
More relevant to time-related impulsivity, males with slower resting heart rates have been shown to have higher impulsive traits as measured by an impulsivity questionnaire (Mathias & Stanford, 2003). This is consistent with a negative correlation reported between discount rates and salivary alpha-amylase levels (another measure of physiological arousal, Takahashi et al., 2007; 2010). The low-arousal theory also suggests that while they have low baseline arousal, impulsive individuals should have higher arousal reactivity. This is also reasonably well supported, as the study above found that impulsive individuals exhibited relatively increased heart rate during a serial attention addition task, compared to low impulsivity individuals (Mathias & Stanford, 2003). This is also consistent with other studies showing that arousal reactivity (measured via pupil dilation) can predict intertemporal choices (Lempert et al., 2016). Likewise, choices toward immediate rewards in temporal discounting tasks have been shown to increase after exposure to emotionally arousing images, relative to neutral stimuli (Sohn et al., 2015), similar to the increase in pacemaker rate observed in arousal-based manipulations of time perception (Section 1.3.1). Thus, there is some evidence to suggest that sympathetic arousal has an association with impulsivity. However, this is not overwhelming evidence that it is specifically associated with temporal decision making, and there are issues with different measures of sympathetic arousal that make this potential relationship somewhat opaque (Picard, Fedor, & Ayzenberg, 2015). Chapter 4 presents a study that is highly relevant to this literature, and contributes to the idea that sympathetic arousal is related to temporal discounting.

The low-arousal theory of impulsivity is also particularly relevant here, as Chapter 1 highlighted findings showing that time perception is also related to arousal. However, on the basis of this literature, in terms of a pacemaker-accumulator model, low arousal would be associated with a lower pacemaker rate. This would predict
underestimations of time, and presumably lower rather than higher impulsivity due to arousal. One possibility is that impulsive individuals have a relatively slower pacemaker at rest and a relatively faster pacemaker during arousal reactivity. In aggregate, the literature cited above provides additional evidence for a commonality between time perception and impulsivity.

The impact of physiological factors on behaviour has had a much longer historical treatment within the foraging literature. This stems from organisms' absolute ecological requirement for energy, which generally implies that animals' behaviour and valuation of rewards should be sensitive to environmental and metabolic context (e.g. Marsh, Schuck-Paim, & Kacelnik, 2004; Pompilio & Kacelnik, 2010; Pompilio, Kacelnik, & Behmer, 2006; Vasconcelos & Urcuioli, 2008). The exemplar here is risk-sensitive foraging theory, which attempts to describe how animals should alter their tolerance to uncertainty as a function of their current homeostatic state (McNamara & Houston, 1992; Stephens, 1981). Consider for example a bird that has not fed for days and is on the brink of starvation. This animal is given a choice between pursuing a small meal that can be acquired with certainty, or the acquisition of a large, sustaining meal that has a chance of failure. Given the energy requirements of pursuit, and the uncertainty of subsequent reward in both cases, there are circumstances in which the certain, small reward will not provide sufficient sustenance for survival. Thus, in these circumstances, the bird ought to be risk-tolerant and gamble on the large reward. This is known as the energy-budget rule of risk-sensitive foraging: individuals with positive energy-budgets ought to be risk-averse, while those with negative energy-budgets ought to be risk prone (Stephens, 1981).
For simultaneously presented reward options that differ in their variability, this rule has received considerable empirical support in a variety of animals (including bees, fish, rats, birds and chimpanzees; Bacon, Hurly, & Healy, 2010; Caraco, 1981; Caraco et al., 1990; Caraco, Martindale, & Whittam, 1980; Gilby & Wramgham, 2007; Kirshenbaum, Szalda-Petree, & Haddad, 2000; Mayack & Naug, 2011; Young, Clayton, & Barnard, 1990; and for reviews see Bateson, 2002; Bateson & Kacelnik, 1998; Kacelnik & Bateson, 1996), although it is worth noting that the results of some studies have not been entirely unequivocal (Banschbach & Waddington, 1994; Orduña & Bouzas, 2004). Studies that test the energy-budget rule usually employ pre-experimental deprivation and pre-feeding to manipulate energy-budget. However, one study manipulated ambient temperature to change expected energy levels, as colder temperatures require more energy for homeostatic stability (Caraco et al., 1990; Houston & McNamara, 1990). This study found the same results: warmer ambient temperatures lead to relative risk-aversion and choices to a certain but smaller reward. There have also been studies that have demonstrated an effect similar to the energy-budget rule in humans, but instead used monetary earnings to simulate an energy budget (Pietras & Hackenberg, 2001; Pietras, Locey, & Hackenberg, 2003; Pietras, Searcy, Huisema, & Brandt, 2008; Rode, Cosmides, Hell, & Tooby, 1999). For example, Pietras et al. (2008) recorded subjects’ choices between a certain, small reward (e.g. $0.01) or a probabilistic, but larger reward (e.g. $0.05 with a probability of .5). Subjects had to earn a certain total amount of money to be able to keep the money and the researchers varied the amount that subjects started with in order to simulate different energy reserves. The results showed that with positive energy-budgets, individuals were risk-averse, and chose the certain option more frequently, whereas with negative energy-budgets, individuals were risk-prone. In general, this finding seems to be consistent in the human literature (Pietras et al., 2003; 2008;
Pietras & Hackenberc, 2001; Rode et al., 1999). Further to these findings, when actual energy levels are manipulated via food deprivation, sated human participants have been shown to be more risk-averse toward both monetary rewards (Symmonds, Emmanuel, Drew, Batterham, & Dolan, 2010), as well as physiological rewards (Levy, Thavikulwat, & Glimcher, 2013), compared with their hungry counterparts. Thus, the energy budget rule has considerable explanatory power, and in particular appears to be a robust effect in humans as well as non-human animals.

Despite the attention given to risk-sensitive preferences in foraging scenarios, no similar treatment has been given to tolerance for delay in these tasks, which is of more relevance to this thesis (although it should be noted that there is a substantial literature examining behavioural preferences for variability in delay, e.g. Bateson, 1995; and for reviews see Bateson, 2002; Bateson & Kacelnik, 1998; Kacelnik & Bateson, 1996). However, while the foraging literature has not investigated whether homeostatic factors can influence temporal decision making, there are a number of intertemporal choice studies that speak to this question. Firstly, compared with an artificially sweetened placebo, the ingestion of glucose has been shown to reduce temporal discounting (Wang & Huangfu, 2017; Wang & Dvorak, 2010; but also see Lange & Eggert, 2014). This effect has been reported to be specific to glucose rather than isocaloric sugars (Wang & Huangfu, 2017) or fructose (Luo, Monterosso, Sarpelleh, & Page, 2015), which are both processed outside of the insulin pathway. Similarly, endogenous levels of the “hunger hormone” ghrelin modulate discounting, such that higher levels of ghrelin increase discount rates (Anderberg et al., 2016). A meta analysis of 11 other studies that tested blood-glucose sensitive differences in temporal discounting supports the idea that individuals with low blood glucose are more impatient (Orquin & Kurzban, 2016). These findings support the informal notion that animals should be more patient when sated, as the urgency of acquiring
food is lower. However, findings that conflict with the results of these studies should be noted. Firstly, in addition to replicating the finding that hunger increases risk-proneness (see above), one study has also found that hunger decreases the temporal discounting of larger monetary rewards (de Ridder, Kroese, Adriaanse, & Evers, 2014). Another recent study has found that ingestion of a sweetened placebo can also reduce temporal discounting, demonstrating that perceptual cues for nutrition may be important in addition to actual energy content (Kuhn, Kuhn, & Villeval, 2017). To summarise these findings, intertemporal choice appears to be sensitive to homeostatic factors. However, there is no formal consensus regarding how energy sensing and hunger should affect discount rates and there is incomplete unanimity in terms of the empirical results of experiments that have specifically investigated this.

Apart from the notion that satiation should lead to patience (e.g. Peters & Büchel, 2011), there is another theoretical perspective that provides a contrasting prediction of how energy-budget could affect intertemporal choice. Some researchers have noted that risk is implicit in delay (i.e. collection risk; the possibility of an interruption that prevents reward acquisition) and that uncertainty about reward delivery may account for some of the devaluation normally attributed to impatience (Benzion, Rapoport, & Yagil, 1989; Bixter & Luhmann, 2015; Hayden & Platt, 2007; Kalenscher, 2007; Dasgupta & Maskin, 2005; Sozou, 1998; Stevenson, 1986; Weber & Chapman, 2005). Indeed, there is considerable evidence for this implicit risk hypothesis. Firstly, humans explicitly rate delayed rewards as less certain (Patak & Reynolds, 2007). Secondly, the magnitude of discounting strongly correlates with these uncertainty ratings in humans (Patak & Reynolds, 2007), and also uncertainty as measured by risk-aversion in rhesus macaques (Hayden & Platt, 2007; Kalenscher, 2007). In standard temporal discounting tasks, adding uncertainty to immediate choice options or adding delay to certain choice options has been shown to alleviate the
discounting normally attributed to delay or risk, respectively (Weber & Chapman, 2005). Similarly, individuals have been shown to be less patient when first presented with a risky choice, relative to when an intertemporal choice is presented prior to a risky choice (Bixter & Luhmann, 2015). However, while the rate of increase in uncertainty over time has been shown to be related to individuals’ discount rates, the functional form of probability discounting differs from that of temporal discounting (Takahashi, Ikeda, & Hasegawa, 2007). In sum, this suggests that while delay and risk are not treated as absolutely psychologically equivalent, there is considerable correspondence between the two. Thus, given that risk is somewhat implicit in delay, risk-sensitive foraging theory would predict that lower energy-budgets should lead to a greater tolerance for delay due to increased risk tolerance.

Thus, there are two different perspectives on how relative energy state should affect temporal decision making. On one hand, organisms should be more patient when they have a positive energy-budget, as their requirement for nutrition is less urgent. On the other hand, organisms with positive-energy budgets are risk-averse, which may also entail aversion to delay. Both of these perspectives have received some support in studies of intertemporal choice, despite their incompatible predictions. However, the effect of energy-budget on delay tolerance in foraging tasks has not yet been tested. Chapter 5 presents a study that explicitly addresses this question.
2.4 Summary and Research Questions

2.4.1 Summary of Chapter 2. In the preceding sections, two dominant models of temporal decision making — intertemporal choice and foraging — were discussed. The behaviours described by these models both appear to necessitate some representation of time and some theoretical models have shown that many characteristics of these behaviours may result from the biases inherent in non-veridical temporal representations (Balcı et al., 2011; Bateson, 2003; Cooper, Kable, Kim, & Zauberman, 2013; Cui, 2011; Gibbon & Church, 1990; Hills & Adler, 2002; Kim & Zauberman, 2009; Namboodiri & Shuler, 2016; Ray & Bossaerts, 2011; Takahashi & Han, 2012; Zauberman, Kim, Malkoc, & Bettman, 2009).

Chapter 1 provided evidence that time perception is labile to a number of factors, including pharmacological factors and physiological factors. Temporal decision making behaviour appears to be affected by similar factors, suggesting that these effects may be an indirect result of changes in time perception. However, the few studies that have directly tested a relationship between time perception tasks and temporal decision making tasks have shown mixed results (Baumann & Odum, 2012; Berman, 2013).

2.4.2 Research questions. Given the conceptual and theoretical links between time perception and temporal decision making, as well as the empirical commonalities between the two, this part of the thesis postulates that there is a more fundamental association between time perception and temporal decision making. An alternative (null) explanation is that time perception is distinct from temporal decision making (which may use a different representation of time) and thus time perception and temporal decision making will not be systematically related.
For the purposes of this thesis, the above hypothesis can be divided into two research questions which address the hypothesis from different perspectives. It has previously been shown that impulsive individuals under-reproduce time intervals (Moreira, Pinto, Almeida, & Barbosa, 2016; van den Broek, Bradshaw, & Szabadi, 1992), which suggests that there may be a common mechanism that subserves both time perception and temporal decision making, and that this varies between individuals. Accordingly, the first research question asks: are individual differences in time perception related to individual differences in temporal decision making? Given that time perception and temporal decision making have both been linked back to physiological factors, then, if there is a common mechanism subserving both, this may be reflected physiologically. It is also possible that this hypothetical common mechanism is sensitive to various external factors which would affect both time perception and temporal decision making. Thus, the second research question asks: can factors known to influence time perception also affect temporal decision making? Chapter 4 and Chapter 5 investigate these two questions, respectively, and make relevant contributions to the literature reviewed in this chapter.
Chapter 3: Consumption of caloric reward systematically biases time perception

3.1 AIMS OF STUDY 1

Chapter 1 provided an examination of the models of time perception and explored the idea that human time perception may rely on a physiological pacemaker. It also surveyed literature suggesting that factors related to reward (e.g. arousal, motivation, and dopamine) could systematically affect the rate of this pacemaker. While arousal, motivation and dopamine have all previously been found to affect the pacemaker (Buhusi & Meck, 2002; Gable & Poole, 2012; Gil & Droit-Volet, 2012), the experience of reward consumption itself (the hedonic experience of consumption) has not been investigated in sufficient detail in humans. Similarly, the effect of reward anticipation on time perception has not been tested without the potential confound of motivation. Thus, the primary aim of Study 1 was to address the first main theme of this thesis: whether reward anticipation or consumption would affect human time perception.

Previous animal studies have reported differential effects of the consumption of different primary rewards (Meck & Church, 1987) and therefore the nature of the reward used in this study was likely to be an important variable. As physiological and metabolic factors have been suggested to alter the rate of the hypothetical pacemaker (Anderberg et al., 2016; Craig, 2009a; Park, Pagnini, Reece, Phillips, & Langer, 2016), a primary reward with inherent metabolic value would be a good candidate, with broad ecological relevance. Thus, if reward was found to affect time perception, a secondary aim of this study was to assess what characteristics of reward were necessary to elicit this effect.
In each experiment reported in Study 1, fasted subjects performed a temporal production paradigm in which they made time estimations while waiting for the delivery of rewards. In each trial, subjects were cued to the volume of an upcoming liquid primary reward, as well as the delay to the delivery of the reward (4, 6, 8 or 10 s). Participants were asked to make a response at a target time that was half the duration of these reward delays (2, 3, 4 or 5 s). After the full delay, participants received the appropriate reward.

This same paradigm was used in a series of five experiments which tested five different types of rewards in order to identify the characteristics necessary to elicit changes in temporal production. These rewards were fruit juice (a sweet, caloric reward), money (a secondary reward), water (a tasteless, noncaloric reward), aspartame (a sweet, noncaloric reward), and maltodextrin (a tasteless, caloric reward). This choice of rewards orthogonalised the hedonic (sweet) and alimentary (caloric) components of these liquids.

Given that motivation has been shown to lead to underestimations of time (Gable & Poole, 2012), it was hypothesised that the anticipation of reward would also lead to underestimations of these intervals (overproductions). On the other hand, reward receipt has previously been associated with a phasic dopamine response (Romo & Schultz, 1990), and increases in dopamine have been predominantly related to overestimations of time (e.g. Buhusi & Meck, 2002). Therefore, it was also hypothesised that reward consumption would lead to overestimations of time (underproductions). It was also hypothesised that both of these effects would increase with increasing magnitudes of reward.

To test the first hypotheses that anticipated reward, or reward consumed on the previous trial would affect time estimates, subjects time estimates were collapsed and analysed with repeated measures analysis of variance. Mixed effects regression
modelling was then employed to assess whether time estimates varied as a function of the magnitude of the anticipated or consumed rewards. These models additionally controlled for other potential confounds (e.g. carry-over effects).

3.1.1 A note on motivation and time estimates. As noted in Chapter 1, the behavioural consequences of experimental manipulations of reward on time perception are difficult to disentangle from those of motivation. For example, an animal may be willing to expend more effort in order to ensure that it attains a desired reward. This may either decrease the threshold for response initiation or increase rates of responding, both of which could be incorrectly interpreted as a change in the rate of a hypothetical pacemaker rate. Balcı (2014) provides an excellent evaluation of these issues. To summarise, a number of studies have ostensibly investigated the effect of reward or motivation on time perception using the peak-interval procedure (Balcı, Wiener, Çavdaroğlu, & Coslett, 2013; Galtress & Kirkpatrick, 2009; Galtress, Marshall, & Kirkpatrick, 2012; Ludvig, Balcı, & Spetch, 2011; Ludvig, Conover, & Shizgal, 2007). Upon single trial analysis of response initiation and response termination (e.g. start and stop times; see Section 1.1), these studies have observed a pattern of responses more consistent with strategic changes in decision threshold rather than changes in pacemaker rate.

The experiments in Study 1 were designed in such a way to overcome the potential confounding motivational influences on time estimates which may have affected previous studies. Specifically, the rewards were not contingent on performance and were passively delivered regardless of the subjects’ timing accuracy. This meant that the potential effects of reward related only to the anticipation or consumption of the reward and not to any motivational changes in strategic responding.
The full manuscript for this study was published in *Journal of Experimental Psychology: Human Perception and Performance* (Fung, Murawski, & Bode, 2017) and is presented here in its native format.

3.2 MANUSCRIPT

[Manuscript begins on following page]
Caloric Primary Rewards Systematically Alter Time Perception

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Human time perception can be influenced by contextual factors, such as the presence of reward. Yet, the exact nature of the relationship between time perception and reward has not been conclusively characterized. We implemented a novel experimental paradigm to measure estimations of time across a range of suprasecond intervals, during the anticipation and after the consumption of fruit juice, a physiologically relevant primary reward. We show that average time estimations were systematically affected by the consumption of reward, but not by the anticipation of reward. Compared with baseline estimations of time, reward consumption was associated with subsequent overproductions of time, and this effect increased for larger magnitudes of reward. Additional experiments demonstrated that the effect of consumption did not extend to a secondary reward (money), a tasteless, noncaloric primary reward (water), or a sweet, noncaloric reward (aspartame). However, a tasteless caloric reward (maltodextrin) did induce overproductions of time, although this effect did not scale with reward magnitude. These results suggest that the consumption of caloric primary rewards can alter time perception, which may be a psychophysiological mechanism by which organisms regulate homeostatic balance.

Public Significance Statement
Recent work has suggested that human time perception can be influenced by rewards. We performed a series of experiments to test whether different types of primary rewards, such as fruit juice, could alter time perception. We found that time was systematically underestimated after the consumption of some rewards, but only when they contained calories. This suggests that time perception changes based on our physiological state, which may play a role in the regulation of feeding behavior and decision making.

Keywords: time perception, interval timing, primary reward

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When dining at a restaurant, it can sometimes seem that the hungrier we are, the longer our meals take to arrive. In contrast, once we have eaten, time does not drag on nearly as much—even if our wristwatch measures the durations as equivalent. It seems that our perception of time depends on our physiological state, and in particular, the anticipation and consumption of rewards. Yet, the relationship between the anticipation and consumption of reward and time perception are not very well understood.

Laboratory studies have shown that humans’ perception of time is dynamic—a varying approximation of objective “clock time”—and can be influenced by a range of factors including novelty, stimulus complexity, our actions, and the temporal properties of the environment (Eagleman, 2008; Wenke & Haggard, 2009; Wiener, Thompson, & Coslett, 2014). The dominant “pacemaker-accumulator” models of time perception (Church, 1984) generally seek to explain these effects via arousal (which speeds up the rate of a hypothetical pacemaker; Treisman, 1963) and attention (which restricts the accumulation of the pacemaker’s “pulses”; Zakay & Block, 1998). For example, according to these models, during states of physiological arousal—for instance when body temperature is high (Wearden & Penton-Voak, 1995), or during life threatening situations (Stetson, Fiesta, & Eagleman, 2007)—the...
rate of the pacemaker is increased, and durations are overestimated.

Similar outcomes can also be seen after pharmacological manipulations of arousal, such as noradrenergic blockage (Ramsayer, Hennig, Haag, & Lange, 2001), and dopaminergic stimulation (Meck, 1983). In particular, dopamine agonists cause earlier responding in timing tasks, consistent with an overestimation of duration, while antagonists have the opposite effect (Buhusi & Meck, 2002; Lake & Meck, 2013). Previous research has noted a neurobiological overlap between time processing and reward processing (Bermudez & Schultz, 2014; Meck, 2014), as midbrain dopamine neurons are also well known to respond to reward, and reward expectancy (Schultz, Dayan, & Montague, 1997). The involvement of dopamine in each case suggests that rewards might exert an effect on time perception, either pharmacologically (via dopamine), or psychologically (via arousal).

However, few studies have explicitly investigated the effect of reward on time perception in humans, or have only done so using secondary rewards, like money (Balci, Wiener, Çavdaroğlu, & Branch Coslett, 2013), or food imagery (Gable & Poole, 2012), as opposed to primary rewards, like food or drink. For example, Gable and Poole (2012) found that the duration of images of appetizing food was underestimated compared with control images. They suggested that it may be adaptive for durations to be underestimated when anticipating rewards, as this may prolong reward seeking (Gable & Poole, 2012). From the perspective of a pacemaker-accumulator model, these findings cannot be explained by dopamine or arousal, which would cause the images to be overestimated. They are, however, consistent with an attentional effect: attention toward food-related imagery could restrict the amount of pulses accumulated in memory, resulting in underestimation.

A large body of research has investigated how the actual acquisition or consumption of reward might affect time perception in nonhuman animals, for whom time perception is commonly measured using conditioned responses. However, the overall result of these studies has been ambiguous (Bonem & Crossman, 1988). For instance, it has been reported, variously, that increasing the magnitude of reward causes timed responses to occur earlier (Galtress & Kirkpatrick, 2009), later (Blomeley, Lowe, & Wearden, 2004), or to undergo no change (MacEwen & Killeen, 1991). Others have found differences in the timing of the first response, but not the time of the highest response rate, or the timing of the last response (Ludvig, Conover, & Shizgal, 2007), which could potentially be interpreted as a change in decision criteria (i.e., a motivational change) rather than a change in perceived time. One study that explicitly examined the effects of different nutrients on time perception in rats found that carbohydrates caused later responses, while other nutrient compounds caused earlier responses (Meck & Church, 1987). The ambivalence of results from previous studies may therefore be a consequence of different types of primary reinforcement. Thus, despite considerable evidence that primary rewards can affect time perception, the direction and cause of this effect are unclear. It has also yet to be seen whether primary reward can affect time perception in humans, who can be explicitly asked to estimate time intervals.

Here we present five experiments, which directly tested how different primary and secondary rewards affect time estimation in humans. Our experimental paradigm used a novel variant of a temporal production procedure (Zakay & Block, 1997) in which participants made time estimations of half the duration of the waiting time during a delayed reward delivery. In the first experiment, rewards were different volumes of fruit juice, which constitutes a caloric primary reward with inherent biological value, often used in both human and nonhuman primate studies (McClure, Ericson, Lailson, Loewenstein, & Cohen, 2007; Schultz et al., 1997). Reward magnitude was cued on a trial-by-trial basis and delivered using a syringe pump. This procedure had the advantage that both the size of reward and the timing of reward consumption could be precisely controlled, and we could assess the effect of both previously consumed rewards and anticipated rewards of different magnitudes.

Although it does not provide direct physiological benefit, the rewarding value of money has been suggested to be a modern derivative of that of food (Briers, Pandelaere, Dewitte, & Warlop, 2006). Thus, in a second experiment we investigated whether secondary rewards also have an effect on time perception, using monetary rewards. In a third experiment, we addressed the possibility that orosensory stimulation alone can affect time perception, by using different volumes of calorie-free liquid (water), instead of fruit juice. Finally, the fourth and fifth experiments attempted to identify whether the effect of fruit juice was primarily dependent on its sweet taste or its caloric content. To do this, we used an aspartame solution (a sweet, noncaloric compound) in the fourth experiment, and a maltodextrin solution (a tasteless, caloric compound) in the fifth experiment.

General Method

Participants

All 125 participants were recruited via advertisement at The University of Melbourne, after reporting no dietary restrictions (fructose intolerance, diabetes, phenylketonuria and fluid imbalance). Participants were instructed to refrain from eating or drinking for 4 hours prior to the experiment to decrease satiety. All participants provided written informed consent. The study protocol for all experiments was approved by The University of Melbourne’s Human Research Ethics Committee (no. 1441974).

Stimuli and Apparatus

Time perception was measured using a variant of a temporal production procedure (similar to a peak-interval procedure; Rakitin et al., 1998; Wearden & McShane, 1988; Figure 1b). In each trial, participants were first presented with a reward cue for 3 s that indicated different reward magnitudes, and the delay of reward delivery (either 4, 6, 8, or 10 s; Figure 1a). Following this, a black fixation cross appeared for the duration of the delay. Participants were asked to make a response at a target time that was half of the full delay (i.e., 2, 3, 4, or 5 s). When a response was registered, the fixation cross changed color to orange. Responding at half of the delay meant that the time of the response did not coincide with reward delivery, and ensured that the delivery of reward was precise and valid in respect to the cue. The use of a single response minimized the effect of excessive motor activity that multiple responses may have had on timing processes (Wenke...
may have systematically effected their responses in ways unrelated to their percept of time. After completion of all experimental tasks, participants were debriefed.

**Data Analysis**

In each experiment, trials in which responses were missed, as well as trials with time estimations 2.5 standard deviations from the participants’ mean estimation for that particular delay were excluded. Additionally, participants who missed more than 10% of all trials were excluded from analysis entirely, as we assumed these participants did not pay adequate attention to the task.

For each experiment, we first identified whether potential carry-over effects influenced time estimates on trial-by-trial basis. These included temporal carry-over effects (the influence of the delay experienced on the preceding trial), and decisional carry-over effects (the influence of the response of the previous trial; Wiener et al., 2014). We then identified whether there were general effects of reward, by comparing mean time estimates in the nonrewarded baseline tasks to those in the main experimental task.

Next, we provided a demonstration of the effect of the presence/absence of both anticipated and previously consumed reward independently, and unconditional on any other factors (excluding target time). We had to consider several constraints for this analysis approach. First, a model that coded reward magnitude as a continuous variable would constitute an analysis of covariance model, a key assumption of which is that the regression coefficients for the continuous variable are the same across categorical variables (i.e., target times). As our data exhibited the scalar property (variability that increases with target time), and Vierordt’s law (a central tendency effect), this assumption was violated. We therefore opted to treat reward magnitude as a categorical variable. This also allowed for the detection of any nonlinear effects (in pretesting, we found that individuals valued the liquid as a nonlinear function of its volume). Second, while we may have wished to model both anticipated and previously consumed reward simultaneously, the size of the combinatorial space of a repeated measures analysis of variance (ANOVA) design including both anticipated and previously consumed reward would be very large, and we could not reasonably have a sufficient number of trials to have balanced cells for each participant. This effectively prohibited us from using this approach. (However, the more powerful mixed-effects model below included both anticipated and previously consumed reward, as well as reward magnitude.) Given these constraints, we collapsed our data across reward magnitudes to identify whether the general presence of either anticipated or previously consumed rewards influenced time estimates, using data only from the main experimental task phase.

To determine whether these effects were dose-dependent, and to model both anticipated and previously consumed reward simultaneously, we then estimated a mixed effects panel regression model. This allowed us to assess trial-by-trial time estimates as a function of reward magnitude, and to control for the potentially confounding interplay of other relevant factors, while accounting for unobserved individual heterogeneity.

Where appropriate, Greenhouse–Geisser corrections were performed to account for violations of sphericity, and the correction factors and original degrees of freedom are reported. Eta-squared effect-sizes are reported only for significant analyses. We used the statistical package “plm” for the mixed effects panel
regression model (Croissant & Millo, 2008) in R, which automatically omits variables with high collinearity. The Breusch–Pagan test of heteroskedasticity, and heteroskedasticity-consistent coefficients were also estimated using this package. Differences in all analyses were considered significant if \( p < .05 \).

### Experiment 1 (Fruit Juice)

We first examined the potential effect of reward on time perception, by using an ecologically relevant primary reward. A variety of changes in decision making as a result of glucose consumption have previously been reported (Guillot & Baumeister, 2007; Molden et al., 2012; Orquin & Kurzban, 2016), and previous nonhuman animal studies have found that carbohydrates affect time perception (Meck & Church, 1987). Caloric compounds also activate reward-related dopaminergic midbrain areas (Frank et al., 2008). Thus, we considered a caloric primary reward like fruit juice a likely candidate to affect time perception in humans.

#### Participants and Apparatus

Twenty-five right-handed participants were recruited for the first experiment (mean age, 20.3 years, range = 17–26; 17 female, 8 male). Participants were compensated with AUD 20 for their participation. In Experiment 1, rewards were different volumes of a commercially available apple juice (0.0, 0.5, 1.2, and 2.3 mL). Each combination of delay and reward was presented 10 times in pseudorandom order, resulting in a total of 160 trials. This led to a total consumption of 162 mL of liquid.

#### Results

In Experiment 1, of all trials collected, an average of 5 responses were missed per person (range = 0–26). A further average of 5.16 responses were excluded per person (range = 0–10) due to the standard deviation criterion (2.2% of all trials). No participants were excluded entirely.

**Mean time estimates and time estimate variability.** Time estimates increased monotonically with longer target times—one-way repeated measures ANOVA: \( F(3, 72) = 522.57, p < .001, \ \varepsilon = .43, \ \eta^2 = .77 \)—implying that participants correctly followed the task instructions. The variability of time estimates also increased with target time—one-way repeated measures ANOVA: \( F(3, 72) = 47.36, p < .001, \ \varepsilon = .72, \ \eta^2 = .33 \)—approximating the characteristic scalar property of timing. However, the coefficient of variation (CV; the standard deviation of the estimation divided by the mean estimation; Treisman, 1963) was significantly affected by target time—one-way repeated measures ANOVA, \( F(3, 72) = 23.24, p < .001, \ \varepsilon = .74, \ \eta^2 = .14 \)—suggesting a violation of the scalar property (Lewis & Miall, 2009; Wearden & Lejeune, 2008).

**Carry-over effects.** As time estimates have previously reported to be influenced by both temporal and decisional carry-over effects (Wiener et al., 2014), we sought to identify whether these carry-over effects were present in our data. For each participant, we used linear regression to identify whether the target time or time estimate of the previous trial affected the time estimate of the current trial, while controlling for the target time of the current trial. A one-sample \( t \) test on the resulting individual beta coefficients revealed a significant effect of both previous target time, \( t(24) = 4.33, p = .001, d = .87 \) and previous time estimate, \( t(24) = 6.35, p = .001, d = 1.32 \), suggesting that both carry-over effects were present (see Table 1 for effect estimate).

Previous response ought to be a close function of previous target time, and thus these two variables ought to be correlated. To assess whether this might present an issue of multicollinearity in later analyses, we calculated variance inflation factors (VIF) in a simple linear model of target time, previous target time and previous response. Both previous target time and previous response had a VIF of 2.03, which indicated that multicollinearity was not problematic in terms of model estimation.

### The general influence of reward on mean time estimates.

Next, we tested whether the presence of reward had an effect on mean time estimates across all delays by comparing time estimates in the main reward task phase with time estimates made in the two nonrewarded baseline task phases (Figure 2a). We first standardized time estimates (mean estimate minus target time, divided by the standard deviation for each delay). As there was no significant difference between the first and second baseline task phases, \( t(24) = -0.65, p = .521 \), we averaged the standardized estimates from these. A two-tailed paired-samples \( t \) test revealed that time estimates were significantly overproduced in the main task phase compared with the baseline phases, \( t(24) = 3.62, p = .001, d = .72 \), indicating a general effect of the presence of reward on time estimates.

**Effects of anticipated and previously consumed reward.** We next identified whether rewards influenced time estimates within the main task phase. To do this, we collapsed across reward magnitudes and ran two two-way repeated measures ANOVAs, which included a factor for the target time and a binary factor representing the presence or absence of reward.

For the analysis of the effect of anticipated rewards (whether there was upcoming reward or not), the model revealed a significant effect of target time, \( F(3, 72) = 358.43, p < .001, \ \varepsilon = .48, \ \eta^2 = .74 \) (Figure 2b), but no significant effect of anticipated reward, \( F(1, 24) = 1.46, p = .239 \), nor an interaction of target time and anticipated reward, \( F(3, 72) = .077, p = .514 \).

For the analysis of the effect of previously consumed reward (whether reward was consumed at the end of the previous trial or not), we found a similar effect of target time, \( F(3, 72) = 337.5, p < .001, \ \varepsilon = .46, \ \eta^2 = .73 \), as well as a significant effect of previously consumed reward, \( F(1, 24) = 13.57, p = .001, \ \eta^2 = 0.05 \) (Figure 2c), but no interaction effect, \( F(3, 72) = 1.5, p = .222 \). Overall, this suggested that previously consumed rewards, but not anticipated rewards, was associated with overproduced time estimates within the main task phase.

**Trial-by-trial effects of reward on time estimates.** We next analyzed whether either the magnitude of anticipated reward or previously consumed reward had an effect on time estimates, or whether the observed effect was confounded by other factors. To this end, we estimated a mixed effects panel regression model, which accounted for participant heterogeneity as a random effect, as well as the fixed effects of (a) the target time, (b) temporal carry-over effects (previous delay; Wiener et al., 2014), (c) decisional carry-over effects (previous time estimate; Wiener et al., 2014), (d) anticipated reward magnitude, (v) previous reward magnitude, and (e) possible satiety effects due
to overconsumption (total volume of consumed reward). Given that the data displayed heteroskedasticity, Breush–Pagan test, $BP(14) = 302.89, p < .001$, heteroskedasticity-consistent coefficients were estimated.

The model revealed the expected significant effect of target time, previous delay (8 and 10 s), as well as previous time estimate. It is important to note that even when taking these variables into account, we found significant effects for the small, medium, and large previous reward magnitudes (see Table 1). The marginal effects of consumed rewards on response grew monotonically as their magnitude increased (0.053, 0.09, and 0.1 s, respectively), suggesting the effect was dose-dependent. No significant effects of anticipated reward magnitude were found. Overall, this model accounted for a substantial amount of variance in time estimates, $R^2 = .66, F(14, 3702) = 516.26, p < .001$.

### Discussion

We found that time estimates were overproduced after consuming fruit juice, but that anticipating fruit juice rewards did not systematically affect mean time estimates. Furthermore, this effect was dose-dependent: larger volumes of fruit juice caused larger subsequent overproductions. Notably, we found that fruit juice consumption affected time estimates on a trial-by-trial basis, which suggests that the effect operated on a very short time scale. It is possible that this was due to anticipatory cephalic phase responses triggered by the sensation of nutrients in the mouth (Power & Schulkin, 2008). However, from this experiment alone, we are unable to determine whether this effect was specific to fruit juice, or whether other types of rewards would also be able to elicit changes in time perception.

### Experiment 2 (Money)

In Experiment 2, we addressed the possibility that the effect reported in Experiment 1 would extend to secondary reinforcers (money). Although it does not provide direct physiological benefit, the rewarding value of money has been suggested to be a modern derivative of that of food (Briers, Pandelaere, Dewitte, & Warlop, 2006).

### Participants and Apparatus

An independent sample of 25 participants was recruited (mean age, 21.4 years; range, 18–29; 13 female, 12 male, 2 left-handed). Different monetary amounts were used as rewards (0.0, 5, 15, and 30 cents). To retain incentive compatibility, participants in Experiment 2 were told that they would be paid a random amount up to AUD 20 during the task, but were guaranteed at least AUD 10 for their participation (however, rewards were predetermined such that participants received a minimum of AUD 10).

### Table 1

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* $p < .05$. ** $p < .01$. *** $p < .001$.  

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**Figure 2.** Effects of reward on mean time estimates in Experiment 1 (fruit juice). Figure 2a: Mean time estimates in main task versus baseline tasks. Time estimates are expressed as the difference between mean response and target time. Figure 2b: Effect of anticipated reward within main task phase; differences between reward conditions were nonsignificant (ns; $p > .1$). Figure 2c: Effect of previously consumed reward within main task phase; significant differences based on estimated marginal means of analyses of variance. Time estimates are expressed as standard deviations (the difference between mean response and target time, standardized by target time). Error bars: ± 1 SEM. * $p < .05$. ** $p < .01$.  

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all participants were paid a final amount of AUD 20). Instead of tangible reward delivery, a message was displayed that indicated both monetary amount gained in that trial, and the total money won so far (see Figure S1 in the online supplemental material). All other task components were identical to Experiment 1.

**Results**

In Experiment 2, of all trials collected, an average of 3.2 (range = 0–12) were missed and a further average of 5.6 (range = 1–10) were excluded due to the standard deviation criterion (2.3% of all trials). No participants were excluded entirely.

Mean time estimates revealed the same general pattern of results as in Experiment 1 (for the analysis of carry-over effects, see supplementary information).

**The general influence of reward on mean time estimates.** We tested whether the presence of monetary reward had an effect on standardized time estimates by comparing time estimates in the main reward phase with time estimates made in the two nonrewarded baseline phases, as in Experiment 1. There was no significant difference between the first and second baseline phases, t(24) = −1.22, p = .233, and we averaged the standardized estimates from both baseline phases. A two-tailed paired-samples t test revealed that time estimates were significantly overproduced in the reward phase compared with the baseline phases, t(24) = 2.54, p = .018, d = 0.51, suggesting a possible gross effect of reward on time estimates (see Table S1 in the online supplemental material for summary data).

**Effects of anticipated and previously consumed reward.** We next investigated whether monetary rewards influenced time estimates within the main task phase, using two two-way repeated measures ANOVA analyses identical to that in Experiment 1.

For the analysis of the effect of anticipated rewards, the ANOVA revealed a significant effect of target time, F(3, 72) = 377.83, p < .001, ε = 0.49, η² = 0.74, but no significant effect of anticipated reward, F(1, 24) = 5.25, p = .024, nor an interaction of target time and reward, F(3, 72) = 0.19, p = .903; see Table S2 in the online supplemental material for summary data.

For the analysis of the effect of previously consumed reward, we found a similar effect of target time, F(3, 72) = 403.23, p < .001, ε = 0.47, η² = 0.77, but no significant effect of reward, F(1, 24) < 0.01, p = .968, and no interaction effect, F(3, 72) = 2.11, p = .106 (see Table S3 in the online supplemental material for summary data).

**Trial-by-trial effects of reward on time estimates.** Finally, a mixed effects panel regression model identical to that in Experiment 1 was used to test whether there were complex interactions that may have masked any effects of reward. As the data displayed heteroskedasticity, Breush–Pagan test, BP(14) = 426.2, p < .001, heteroskedasticity-consistent estimates were calculated. The model revealed effects of covariates similar to that of the first experiment (significant effects for target time and previous time estimate), but no significant effects of anticipated reward magnitude or previous reward magnitude (for all details, see Table S4 in the online supplemental material). This model accounted for a substantial amount of variance in time estimates, R² = .7, F(14, 3764) = 628.1, p < .001.

**Discussion**

Although we observed a general effect of the presence of reward on time estimates, different monetary amounts did not affect time estimates on a trial-by-trial basis. It is possible that the mere presence of reward in the main task phase caused overproductions of time as a result of differences in attention, rather than the economic value of the reward itself (see General Discussion). However, the reason for why monetary rewards did not exert trial-by-trial effects similar to fruit juice was likely due to the fact that money does not require actual ‘consumption.’ Whereas the consumption of primary rewards has immediate physiological value, any potential benefit derived from money occurs at an indefinite delay.

**Experiment 3 (Water)**

Having determined that the effect of fruit juice on time perception did not extend to secondary reinforcers, we hypothesized that the observed effect may generalize to tangible, physical rewards with similar orosensory properties. Thus, in Experiment 3, we used water as a reward, which constitutes a primary reward without caloric value.

**Participants and Apparatus**

A further 25 right-handed participants were recruited for a third experiment (mean age, 21.7 years; range, 18–32; 14 female, 11 male). Participants were compensated with AUD 20 for their participation. Different volumes of water were used as rewards (0.0, 0.5, 1.2, and 2.3 mL; Figure 1a). Each combination of delay and reward was presented 10 times in pseudorandom order, resulting in a total of 160 trials. This led to a total consumption of 162 mL of liquid. All other task components were identical to Experiment 1.

**Results**

In Experiment 3, of all trials collected, an average of 5.2 (range = 0–24) were missed, and a further average of 6.4 (range = 1–13) were excluded due to the standard deviation criterion (2.7% of all trials). No participants were excluded entirely.

Mean time estimates, time estimate variability, and temporal carry-over effects were again similar to those observed in Experiment 1 (see supplementary information).

**The general influence of reward on mean time estimates.** We tested whether the presence of water reward had an effect on standardized time estimates by comparing time estimates in the main reward phase with time estimates made in the two nonrewarded baseline phases, as in Experiment 1. As there was no significant difference between the first and second baseline phases, t(24) = −1.62, p = .118, we averaged these values. A two-tailed paired samples t test revealed that time estimates were significantly overproduced in the reward phase compared with the baseline phases, t(24) = 2.53, p = .018, d = 0.51, again suggesting a possible gross effect of the mere presence of reward on time estimates (see Table S1 in the online supplemental material).

**Effects of anticipated and previously consumed reward.** We next investigated whether water rewards influenced time esti-
mates within the main task phase, using two two-way repeated measures ANOVAs identical to those used in Experiment 1.

For the analysis of anticipated rewards, the ANOVA revealed a significant effect of target time, \( F(3, 72) = 263.99, p < .001, \) \( \eta^2 = 0.53 \), but no significant effect of anticipated reward, \( F(1, 24) = 0.61, p = .441 \), nor an interaction of target time and anticipated reward, \( F(3, 72) = 1.35, p = .264 \); see Table S2 in the online supplemental material.

For the analysis of previously consumed reward, we found a similar effect of target time, \( F(3, 72) = 295.99, p < .001, \) \( \eta^2 = 0.53 \), but no significant effect of previously consumed reward, \( F(1, 24) = 0.49, p = .489 \), and no interaction effect, \( F(3, 72) = 0.52, p = .669 \) (see Table S3 in the online supplemental material).

**Trial-by-trial effects of reward on time estimates.** We next analyzed whether either the magnitude of anticipated reward or previously consumed reward had an effect on time estimates on a trial-by-trial basis. Again, a mixed effects panel regression model was estimated to test whether there were complex interactions that masked any effects of reward, with variables identical to those used for the first experiment. As the data displayed heteroskedasticity, Breush–Pagan test, \( BP(14) = 440.65, p < .001 \), heteroskedasticity-consistent coefficients were estimated. The model revealed effects similar to that of the first experiment (significant effects for target time, previous delay and previous time estimate), but no significant effects of anticipated reward magnitude or previous reward magnitude (for details see Table S5 in the online supplemental material). This model accounted for a substantial amount of variance in time estimates, \( R^2 = .64, F(14, 3654) = 469.92, p < .001 \).

**Discussion**

While this experiment again demonstrated a general effect of the presence of reward on time estimates, we found that water did not affect time estimates on a trial-by-trial basis. Thus, it appeared that the orosensory qualities of liquid primary rewards were not sufficient to elicit the changes in time perception that we observed with fruit juice reward. It is possible that more specific, physiological characteristics of fruit juice were necessary to affect time estimates. This possibility was tested in the next experiment.

**Experiment 4 (Aspartame)**

In Experiment 4 and 5, we aimed to disassociate two prominent characteristics of the fruit juice reward used in Experiment 1, to determine whether its perceptual (sweetness) and alimentary (caloric) qualities alone were sufficient to influence time estimates. Given that the effect observed in Experiment 1 operated on a very short, trial-to-trial time scale, we speculated that the effect may be due to a cephalic phase response (an anticipatory metabolic response) triggered by the sensation of the liquid (Power & Schulkin, 2008), as nutrients could not be properly digested within this time. If this is the case, it is possible that the orosensory properties (e.g., sweetness) of the juice alone may act as a cue for future nutritional value, and thereby induce an effect. Thus, we first hypothesized that the sweet flavor of liquid alone might be sufficient to influence time estimates.

**Participants and Apparatus**

A further 25 right-handed participants were recruited for a fourth experiment (mean age, 20.3 years, range, 18–33; 14 female). Participants were compensated with AUD 20 for their participation. In Experiment 4, the liquid rewards were different volumes of a noncaloric, 0.02% aspartame solution (0.0, 0.7, 1.4, and 2.8 mL). Each baseline phase consistent of 32 trials, while main treatment task phase was 128 trials, resulting in a total consumption of 158.4 mL of liquid. All other task components were identical to Experiment 1.

**Results**

Two participants in Experiment 4 missed more than 10% of responses and were excluded from analysis. Of the remaining participants, an average 2.74 responses were missed per person (range = 0–11). A further average of 4 responses were excluded per person (range = 1–7) due to the standard deviation criterion (1.9% of all trials).

Mean time estimates, time estimate variability, and temporal carry-over effects were similar to those observed in Experiment 1 (see supplementary information).

**The general influence of reward on mean time estimates.** We tested whether there was a general influence of reward on standardized time estimates by comparing time estimates in the main reward phase with time estimates made in the two nonrewarded baseline phases, as in Experiment 1. As we found a significant difference between the first and second baseline phases, \( t(22) = -3.01, p = .006, d = 0.63 \), we compared the estimates in the main phase to each baseline phase separately. Time estimates were significantly overproduced in the main reward phase compared with both the first, \( t(22) = 6.37, p < .001, d = 1.33 \), and second nonrewarded baseline phases, \( t(22) = 2.99, p = .007, d = 0.62 \). This again suggested that the mere presence of reward affected time estimates (see Table S1 in the online supplemental material).

**Effects of anticipated and previously consumed reward.** We next identified whether artificially sweetened rewards influenced time estimates within the main task phase, using an identical analysis to that of Experiment 1.

For the analysis of anticipated rewards, the ANOVA revealed a significant effect of target time, \( F(3, 66) = 420.1, p < .001, \) \( \eta^2 = 0.56 \), \( \eta^2 = 0.8 \), but no significant effect of anticipated reward, \( F(1, 22) = 0.1, p = .753 \), nor an interaction of target time and reward, \( F(3, 66) = 1.17, p = .329 \) (see Table S2 in the online supplemental material).

For the analysis of previously consumed reward, we found a similar effect of target time, \( F(3, 66) = 395.47, p < .001, \) \( \eta^2 = 0.51 \), \( \eta^2 = 0.8 \), but no significant effect of previously consumed reward, \( F(1, 22) = 0.03, p = .861 \), and no interaction effect, \( F(3, 66) = 0.22, p = .882 \) (see Table S3 in the online supplemental material).

**Trial-by-trial effects of reward on time estimates.** We again used the same mixed effects panel regression model as for the previous experiments. These data again displayed heteroskedasticity, Breush–Pagan test, \( BP(14) = 209.74, p < .001 \), therefore heteroskedasticity-consistent coefficients were estimated. The model revealed the expected significant effect of target time, previous delay (10 s), as well as a small but significant effect for
total volume of consumed reward. The effect of previous time estimate was also significant. It is important to note that however, no significant effects of anticipated, or previously consumed reward were found (for details see Table S6 in the online supplemental material). Overall, this model accounted for a substantial amount of variance in time estimates, $R^2 = 0.68$, $F(14, 2770) = 423.15, p < .001$.

Discussion

The experiment using aspartame suggested that different magnitudes of artificially sweetened rewards had no effect on time estimates. However, despite equivalent ratings of subjective sweetness, compared with artificial sweeteners, caloric carbohydrates have a unique effect on taste and reward pathways in the brain, and more strongly active dopaminergic midbrain areas (Frank et al., 2008). Given that dopamine has been strongly associated with temporal processing (Bermudez & Schultz, 2014; Meck, 2014), it is possible that the caloric content of fruit juice was the key component necessary to affect time perception. This hypothesis was tested in the last experiment.

Experiment 5 (Maltodextrin)

Results from Experiment 4 suggested that sweet flavour alone was not sufficient to influence time estimates. An alternative possibility was that the caloric content of the fruit juice influenced time estimates. To test this, we performed a final experiment, using maltodextrin, a tasteless compound with a caloric content similar to that of glucose.

Participants and Apparatus

A further 25 right-handed participants were recruited (mean age, 22.7 years, range, 18–29; 18 female). Participants were compensated with AUD 20 for their participation. In Experiment 5, the liquid rewards were different volumes of a tasteless, 6.4% maltodextrin (DE 18) solution (0.0, 0.7, 1.4, and 2.8 mL). Each baseline phase consisted of 32 trials, while main treatment task phase was 128 trials, resulting in a total consumption of 158.4 mL of liquid. All other task components were identical to Experiment 1.

Results

1 participant missed more than 10% of responses and was excluded from the analysis. Of the remaining participants, an average 3.17 responses were missed per person (range = 0–17). A further average of 3.33 responses were excluded per person (range = 1–8) due to the standard deviation criterion (2.1% of all trials).

Mean time estimates, time estimate variability, and temporal carry-over effects were similar to those observed in Experiment 1 (see supplementary information, and Table 2 for carry-over effects).

The general influence of reward on mean time estimates. We tested whether there was a general influence of reward on standardized time estimates by comparing time estimates in the main reward phase with time estimates made in the two nonrewarded baseline phases, as in Experiment 1. As we found significant overproductions of target times in the second, relative to the first baseline phase, $t(23) = 3.11, p = .005, d = 0.60, 4$, we compared the estimates in the main phase to each baseline separately. Time estimates in the main reward phase were significantly overproduced compared with those in the first nonrewarded baseline phase, $t(23) = 4.78, p < .001, d = 0.98$, but not compared with the second nonrewarded baseline phase, $t(23) = 1.41, p = .171$. This suggested a possible gross effect of reward on time estimates, which may have carried over into the second baseline task phase (see Table S1 in the online supplemental material).

Effects of anticipated and previously consumed reward. We next identified whether tasteless, caloric rewards influenced time estimates within the main task phase, using an identical analysis to that of Experiment 1.

For the analysis of anticipated reward, the ANOVA revealed a significant effect of target time, $F(3, 69) = 480.92, p < .001, \varepsilon = 0.54$, $\eta^2 = 0.77$, but no significant effect of anticipated reward, $F(1, 23) = 0.08, p = .787$, nor an interaction of target time and anticipated reward, $F(3, 69) = 0.27, p = .847$ (see Table S2 in the online supplemental material).

For the analysis of previously consumed reward, we found a similar effect of target time, $F(3, 69) = 492.45, p < .001, \varepsilon = 0.51$, $\eta^2 = 0.8$, and the effect of consumed reward closely missed the significance threshold, $F(1, 23) = 3.51, p = .074, \eta^2 = 0.04$. There was no interaction effect, $F(3, 69) = 1.32, p = .274$; see Table S3 in the online supplemental material.

Trial-by-trial effects of reward on time estimates. Again, we applied the mixed effects panel regression model used in the preceding experiments. These data again displayed heterokedasticity, Breush–Pagan test, $BP(14) = 242.3, p < .001$, therefore heterokedasticity-consistent coefficients were estimated. The model revealed the expected significant effect of target time, previous delay (8 and 10 s), as well as a significant effect of previous time estimate. No significant effects of anticipated reward

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<td>0.042</td>
</tr>
<tr>
<td>Previous delay (6 s)</td>
<td>−0.86*</td>
<td>0.046</td>
</tr>
<tr>
<td>Previous delay (8 s)</td>
<td>−1.120†</td>
<td>0.053</td>
</tr>
<tr>
<td>Previous delay (10 s)</td>
<td>−1.14*</td>
<td>0.067</td>
</tr>
<tr>
<td>Previous time estimate</td>
<td>0.072***</td>
<td>0.017</td>
</tr>
<tr>
<td>Anticipated reward (small)</td>
<td>0.006</td>
<td>0.042</td>
</tr>
<tr>
<td>Anticipated reward (medium)</td>
<td>0.026</td>
<td>0.042</td>
</tr>
<tr>
<td>Anticipated reward (large)</td>
<td>0.048</td>
<td>0.042</td>
</tr>
<tr>
<td>Previous reward (small)</td>
<td>0.091**</td>
<td>0.042</td>
</tr>
<tr>
<td>Previous reward (medium)</td>
<td>0.075†</td>
<td>0.042</td>
</tr>
<tr>
<td>Previous reward (large)</td>
<td>0.070</td>
<td>0.042</td>
</tr>
<tr>
<td>Total volume of consumed reward</td>
<td>−0.0001</td>
<td>0.0005</td>
</tr>
<tr>
<td>Observations</td>
<td>2,860</td>
<td></td>
</tr>
<tr>
<td>$R^2$</td>
<td></td>
<td>.671</td>
</tr>
<tr>
<td>Adjusted $R^2$</td>
<td></td>
<td>.662</td>
</tr>
</tbody>
</table>

† $p < .1$. * $p < .05$. ** $p < .01$. *** $p < .001$.
magnitude were found. The model also revealed a significant effect of the previously consumed ‘small’ reward. Moreover, both the ‘medium’ and ‘large’ previously consumed rewards narrowly missed the significance threshold (for details see Table 2). Overall, this model accounted for a substantial amount of variance in time estimates, $R^2 = 0.67, F(14, 2822) = 411.6, p < .001$.

In summary, the mixed effects panel regression model suggested a small effect of previously consumed, but not anticipated reward magnitude on time estimations. Consumption of reward in the previous trial was associated with later time estimates, but the marginal effects of consumed rewards relative to baseline were similar for each reward magnitude (0.09, 0.08, and 0.07 s, respectively).

**General Discussion**

In the present study, we tested whether the anticipation and consumption of different primary rewards and one secondary reward could alter time estimations. We found that for a range of suprasecond delays, time estimates were overproduced after the consumption of fruit juice on a trial-by-trial basis in a dose dependent manner. We also observed a marginally significant effect of a caloric maltodextrin solution on time estimates, but this did not appear to be dose dependent. These results were robust when taking into account other factors that are known to influence time estimations, such as the previously experienced delays and the previous responses (Wiener et al., 2014).

We also showed that the effect of reward consumption on time estimates did not extend to money (a secondary reward), water (a noncaloric, tasteless primary reward), or aspartame (a noncaloric sweet reward), although we did find a general effect of the presence of reward in all experiments. Anticipating rewards did not alter time estimates for any of the tested rewards.

These results contribute to previous demonstrations of the influence of contextual factors on time perception, and in particular those involving physiological factors (Campbell, Murphy, & Boothroyd, 2001; Gable & Poole, 2012; Wearden & Penton-Voak, 1995). Our results are consistent with those from nonhuman animal studies that have observed overproductions of time as a result of carbohydrate consumption (Meck & Church, 1987), as well as human neuroimaging studies that have linked homeostasis and interoception to time perception (Craig, 2009; Wittmann, van Wassenhove, Craig, & Paulus, 2010).

The effects in our experiments were found to be exclusive to reward consumption (experienced utility), and not reward anticipation (utility from anticipation; Loewenstein, 1987). This contrasts with previous findings such as the underestimation of time for images of prospective food rewards (Gable & Poole, 2012), which are somewhat equivalent to the reward cues in our task. However, individuals have a strong conditioned physiological response to the visual characteristics of food (Nederkoorn, Smulders, & Jansen, 2000), and thus, compared with the symbolic reward cues in our task, the images of food in the previous study may act in a way more similar to actual reward receipt. Nevertheless, it is somewhat surprising that the anticipation of rewards did not alter time estimates, as dopamine neurons are well-known to respond to expected reward, particularly when the relationship between a cue and reward receipt has been established (Schultz et al., 1997).

In addition to the effects of specific rewards on time perception, we also found that time estimates were affected by other variables in the previous trial. Previous durations (i.e., the target time of the previous trial) exerted a contrastive effect, such that responses were negatively correlated with the previous duration of the previous trial. Additionally, previous responses exerted an assimilative effect, such that responses were positively correlated between trials (taking into account the target time of each trial). These findings are in line with previous research that has reported dissociable effects of previous decisions and previously perceived durations on temporal discriminations for subsecond intervals (Wiener et al., 2014). However, in our experiment we used a temporal production task and suprasecond delays, and thus we extend these previous findings to a different time estimation paradigm and a larger scale of timing. Note, however, that the observed effect of previously consumed rewards remained robust despite the influence of preceding context.

In all five experiments, we found that the mere presence of reward caused overproductions of time, relative to nonrewarded baseline tasks that were in all other ways identical. One possible explanation is provided by pacemaker-accumulator models of time perception (Church, 1984). The addition of each of the rewards may have captured attentional processes, which would attenuate the accumulation of pacemaker signals (Zakay & Block, 1998), leading to an underestimation of the rate of time passing, and therefore overproductions of the target time. Thus, this general effect may not have been due to the rewarding qualities of each of the tested substances alone, but rather due to the inclusion of an additional, potentially distracting factor which competed with executive resources. Indeed, other time production experiments that have introduced concurrent tasks find similar effects (Brown et al., 2013). The visual stimuli in Experiment 2 (which indicated monetary amount but had no physically rewarding properties) still caused general underestimation effects between task blocks, which supports the idea that the mere inclusion of irrelevant information can alter time estimates (Schweitzer, Trapp, & Bar, 2017). A future experiment employing an explicitly nonrewarding stimulus could provide evidence for this interpretation.

The receipt of money, water, and aspartame, however, did not affect time estimates within the main task phase. As a secondary reward, money does not hold immediate physiological value, and while water and aspartame have similar immediate orosensory characteristics to fruit juice and maltodextrin, they lack the caloric, nutritional content that is present in both. Thus, the caloric content of the fruit juice is a strong candidate for the source of its effect on time perception. Previous research has identified that the caloric and taste components of food elicit neural activity in different brain regions, and that caloric compounds tend to more strongly activate classic dopaminergic midbrain areas, relative to artificial sweeteners (Chambers, Bridge, & Jones, 2009; Frank et al., 2008; Smeets, Weijzen, de Graaf, & Viergever, 2011; Tellez et al., 2016). Given the theoretical accounts of dopamine activity accelerating the rate of timing passing (Buhusi & Meck, 2002; Lake & Meck, 2013), we might have expected that caloric compounds would result in underproductions of the target time, which is not what we observed. However, more recent optogenetic studies have shown that the direct activation of dopamine neurons can actually lead to overproductions of time (Soares, Atallah, & Paton, 2016). This evidence provides an alternative explanation for our results,
consistent with increased dopaminergic activity after caloric consumption. From a psychological perspective, this explanation of our results relies on the assumption that the detection or processing of calories recruits attentional resources, which could impede the accumulation of pacemaker signals (Lake & Meck, 2013).

Notably, the effect of the maltodextrin solution was only marginally significant, and while the estimates of effect size were comparable to that of fruit juice, increasing the volumes of maltodextrin did not induce increasing overproductions of time. There are a number of possible explanations for this. First, while maltodextrin has a comparable glycemic index to glucose, it does not decrease hypothalamic activity to the same degree (Smeets, de Graaf, Stafleu, van Osch, & van der Grond, 2005). Similarly, it does not induce a rise in insulin as rapidly as glucose (Smeets et al., 2005). Moreover, fruit juice contains a complex combination of nutrients, the physiological interactions of which may have complicated effects. For instance, the combination of glucose and fructose in ecological ratios may be important. Alternatively, it is also possible that perceptual sweetness can enhance the detection of calories, and thus a combination of these two qualities may be necessary to elicit reliable, dose-dependent changes in time perception.

We note that the trial-by-trial effect of fruit juice on time estimates operates on a rather short time scale, and thus is unlikely to result from the absorption or metabolism of nutrients, as has been previously suggested (Meck & Church, 1987). However, the mere orosensation of caloric compounds (compared with artificially sweetened solutions) appears to affect behavior in other domains including exercise physiology (Chambers et al., 2009; de Ataide e Silva et al., 2014; de Salles Painelli, Nicastro, & Lancha, 2010; Jeukendrup & Chambers, 2010; Rollo & Williams, 2011) and self-control (Molden et al., 2012), which has led to the proposal that there exists an unidentified class of oral carbohydrate receptors which anticipate the actual digestion of calories. Granted that caloric content can affect time perception as our results suggest, one possibility, which we did not test directly in this study, is that this effect operates via a similar mechanism. A similar effect has precedence in the sports physiology literature (Chambers et al., 2009; Jeukendrup & Chambers, 2010), where differences in the concentration and duration of carbohydrate exposure may alter the effect on motor performance (Devenney, Collins, & Shortall, 2016). It would be valuable for future research to address whether such differences also alter the effect observed in our experiment.

Given the small timescale of the effect, we might have expected that the underestimations induced by caloric rewards would have lessened at longer target times. However, we did not observe any interaction effects of target time and previously consumed reward. This may point to a simple effect of reward that does not differ as a function of delay. Alternatively this may also be explained by either the limited range of short target times employed here, or by the limited range of reward magnitudes. However, the lack of an interaction effect suggests that the effect may last up to 12 s after consumption of calories (a 4-s intertrial interval plus 3 s for cue presentation followed by a 5-s target time). Future studies may be able to investigate this further, for example by having longer trials, or by testing whether substantially larger rewards might have stronger effects.

We observed a dose-dependent effect of fruit juice on time perception. One implication of this result is that consumption on a larger scale may impact decision making behavior beyond simple perceptual judgments. For example, glucose consumption has been shown to decrease the perceived angle of hill slants, suggesting that spatial perception is a function of the relative energy resources required for locomotive effort (Schnall, Zadra, & Proffitt, 2010). Given that there are metabolic costs associated with passive waiting, increased energy resources may decrease the perceived duration of time—as we observe in our experiment—and lead to altered decision making. Delay discounting (Loewenstein, Read, & Baumeister, 2003), and foraging (Stephens & Krebs, 1986), are both decision-making processes that specifically involve a representation of time. Recent research has demonstrated that glucose consumption can decrease discount rates (compared with artificial sweeteners; Wang & Dvorak, 2010). Similarly, it has been shown that the “hunger hormone” ghrelin decreases patience (Anderberg et al., 2015). These studies recapitulate the notion that patience should be enhanced as organisms become sated, as the requirement for nutrition is less urgent. Our results are consistent with this notion, and provide a plausible psychophysiological explanation for the above effect. Further research may be able to identify whether other nutritional compounds (e.g., proteins, fats) have similar effects on time perception.

In conclusion, our study suggests that time perception changes as a result of the consumption of fruit juice rewards, and that larger amounts of consumption lead to larger overproductions of time. In showing that maltodextrin has a similar, but less extensive effect, our study suggests that caloric content is the critical driver of the effect. This highlights the role that homeostatic factors have in altering our fundamental perception of the world, and suggests that the consumption of primary rewards may have an underestimated, but important influence on time-dependent behaviors.

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3.3 SUMMARY

Using a novel variant of a temporal production task, Study 1 investigated whether the anticipation or consumption of different rewards could affect perception. This study first showed that the consumption of fruit juice lead to subsequent overproductions of time, for target times across the range of 2-5 seconds. Notably, this effect scaled in proportion to the volumes of consumed fruit juice. In follow-up experiments, alternative rewards were tested. Money, water, and aspartame did not appear to significantly affect time perception. However, maltodextrin produced a similar effect to that of fruit juice on time productions, which suggested that the observed effect was likely to be due to the common caloric content of both fruit juice and maltodextrin.

As reported in Chapter 1, reward related factors such as arousal, motivation and dopamine, have all previously been found to affect time perception (Buhusi & Meck, 2002; Gable & Poole, 2012; Gil & Droit-Volet, 2012). However, the effects of arousal and dopamine have predominantly been reported to increase the speed of a hypothetical pacemaker, leading to overestimations (underproductions) of time. Similarly, the behavioural theory of timing (BeT) predicts that increased reinforcement rate should also increase the speed of the pacemaker (Killeen & Fetterman, 1988). The results demonstrated in Study 1 were not consistent with this model. Instead, they were more similar to those of Gable & Poole (2012), who showed that images of appetising food were underestimated at target times from 400-1600 ms. They are also similar to the findings of Soares, Atallah and Paton (2016), who found that directly activating dopaminergic neurons in the substantia nigra of mice lead to underestimations of durations from 600-2400 ms. Psychologically, these results, as well as those reported in Study 1, are consistent with the dynamics of an
attentional mechanism which diverts attentional resources toward calorie detection and away from timing information (Zakay & Block, 1995). The interplay of attention, dopamine, and time perception will be discussed further in Chapter 6.

Time perception was only affected by primary rewards containing calories. Given that the other rewards like money (which have also been shown to induce dopamine responses, Kim, Shimojo, & O'Doherty, 2011; Levy & Glimcher, 2012) did not affect time estimates, this might suggest that calories are critical to the observed effects, rather than a general dopaminergic effect of reward. Caloric compounds like glucose constitute a major biological energy source and have previously been reported to affect behaviour and cognition (e.g. Chambers, Bridge, & Jones, 2009; Gailliot & Baumeister, 2007; Orquin & Kurzban, 2016). Thus an effect of calories on time perception may act via a similar mechanism. The results observed in this study were also consistent with those previous reported in a non-human animal study, where rats fed with carbohydrates exhibited overproductions of time in a peak-interval procedure (Meck & Church, 1987). However, the timescale of the effects observed in Study 1 also suggest that this was unlikely to be due to direct metabolic consequences of calorie ingestion. The potential mechanism of this caloric effect will be explored in more detail in Chapter 6.

There were no observed effects of anticipated reward for any of the tested rewards in Study 1. One possibility is that because the rewards were not contingent on accurate responses (and were therefore not instrumentally informative), the reward cues were not sufficiently salient to cause a meaningful psychological or physiological response.

The second main theme of this thesis relates to the idea that individuals use subjective, non-veridical representations of time to inform their temporal decision making behaviour. Chapter 2 presented some background information on decision
making behaviours that involve time representations, including intertemporal choice and foraging. If non-veridical time perception leads to changes in these behaviours, then the findings of Study 1 imply that calorie consumption may also affect these decision making behaviours (e.g. Wang & Dvorak, 2010). Chapter 5 presents a study explicitly exploring this possibility, in specific relation to foraging.

More broadly, the findings reported in this chapter support the possibility that a hypothetical pacemaker is physiological in nature and can be affected by homeostatic factors (Craig, 2009a). If this is the case, then individual differences in physiological parameters ought to be related to individual differences in time perception. The next chapter, Chapter 4, presents a study investigating this possible relationship in specific relation to cardiac physiology, as well as the relationship between temporal decision making and cardiac physiology.
Chapter 4: Cardiac signals are independently associated with temporal discounting and time perception

4.1 AIMS OF STUDY 2

The second main theme of this thesis related to the proposition that temporal decision processes operate on subjective, non-veridical representations of time. Chapter 2 discussed extant models of temporal decision making and outlined how these require a representation of time. It also discussed a number of models that specifically incorporate non-veridical time representations into the decision making process (e.g. Blanchard, Pearson, & Hayden, 2013; Namboodiri, Mihalas, Marton, & Shuler, 2014). One theoretical consequence of this proposal would be that individual differences in time perception ought to predict individual differences in temporal decision making. Indeed, there is also existing evidence that has suggested that impulsive individuals under-reproduce intervals (Moreira, Pinto, Almeida, & Barbosa, 2016; van den Broek, Bradshaw, & Szabadi, 1992). This idea was the basis of the primary hypothesis tested in Study 2: individuals that under-reproduce target times will have higher discount rates.

In addition, Chapter 1 discussed how time perception may be associated with periodic biological processes such as heart rate. Given previous studies that have found associations between temporal bisection tasks and cardiac signals (e.g. Cellini et al., 2015), it is possible that duration reproduction would also be associated with cardiac signals. More specifically, heart rate variability (HRV) has been suggested as an index of parasympathetic nervous system (PNS) function (Berntson et al., 1997), which has, in turn, been suggested to facilitate self-regulation (Thayer & Lane, 2000; 2009). Thus, the second hypothesis of Study 2 was that individuals with higher HRV
would be able to inhibit early terminations of duration reproductions, leading to relative over-reproductions of time. This regulatory aspect of cardiac physiology also has implications for self-regulation in decision making and previous research has found that higher HRV was associated with self-control (Segerstrom & Nes, 2007). Thus, the third hypothesis of Study 2 was that individuals with higher HRV would have a better capacity for self-control and therefore lower discount rates.

The literature reviewed in both Chapter 1 and Chapter 2, as well as the findings reported in Study 1, suggest the possibility of relationships between time perception, temporal decision making, and physiological parameters. The three hypotheses of Study 2 propose that all three of these are correlated with each other. To test these hypotheses, in Study 2, participants performed a time perception task and a temporal decision making task while their electrocardiogram (ECG) was recorded. To measure time perception, participants completed a duration reproduction task with target times spanning ~1-15 s and their data were fitted to a psychophysical function. To measure temporal decision making, participants completed a standard temporal discounting task, with monetary amounts spanning $20-30 and time delays from 1-12 months, and their data were fitted to a hyperbolic function to recover their discount rates. The ECG signal was processed in order to recover measures of mean heart rate, heart rate variability, and the low- and high-frequency components of heart rate variability. To test the hypotheses, measures from both behavioural tasks, and the physiological measures, were compared with correlational analysis.

The full manuscript for this study was published in Frontiers in Behavioural Neuroscience (Fung, Crone, Bode, & Murawski, 2017) and is presented here in its native format.

4.2 MANUSCRIPT

[Manuscript begins on following page]
Cardiac Signals Are Independently Associated with Temporal Discounting and Time Perception

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Cardiac signals reflect the function of the autonomic nervous system (ANS) and have previously been associated with a range of self-regulatory behaviors such as emotion regulation and memory recall. It is unknown whether cardiac signals may also be associated with self-regulation in the temporal domain, in particular impulsivity. We assessed both decision impulsivity (temporal discounting, TD) and time perception impulsivity (duration reproduction, DR) in 120 participants while they underwent electrocardiography in order to test whether cardiac signals were related to these two aspects of impulsivity. We found that over the entire period of task performance, individuals with higher heart rates had a tendency toward lower discount rates, supporting previous research that has associated sympathetic responses with decreased impulsivity. We also found that low-frequency components of heart rate variability (HRV) were associated with a less accurate perception of time, suggesting that time perception may be modulated by ANS function. Overall, these findings constitute preliminary evidence that autonomic function plays an important role in both decision impulsivity and time perception.

Keywords: temporal discounting, time perception and timing, heart rate, interval timing, heart rate variability (HRV)

INTRODUCTION

Cardiac signals have previously been associated with a wide range of psychopathologies, including substance abuse (Levin et al., 1992; Ingialdsson et al., 2003), panic disorder and generalized anxiety disorders (Yeragani et al., 1993; Friedman and Thayer, 1998), obsessive compulsive disorder (Pittig et al., 2013), depression (Kemp et al., 2010), schizophrenia (Clamor et al., 2016) and post-traumatic stress disorder (Cohen et al., 1997). The link between cardiac signals and psychopathology is usually explained by the fact that these psychopathologies affect the function of the autonomic nervous system (ANS), which, in turn, directly impacts cardiac activity.

More recently, cardiac signals such as heart rate variability (HRV) have also been related to cognitive function in healthy individuals. For example, higher resting HRV has been associated with more adaptive attention to emotional stimuli (Park and Thayer, 2014), smaller startle responses (Ruiz Padial et al., 2003), better deliberate suppression of unwanted memories (Gillie et al., 2014) and thoughts (Gillie et al., 2015), more accurate and faster working memory retrieval (Hansen et al., 2003), and better self-control over dietary choices (Segerstrom and Nes, 2007). Furthermore, HRV has been shown to increase transiently during emotion
regulation (Butler et al., 2006), and during difficult memory retrieval (Gianaros et al., 2004). Further to this, a direct causal relationship between ANS function and cognition has also been demonstrated via vagus nerve stimulation (for working memory processes; Clark et al., 1999).

Cardiac measurements have also been associated with performance in higher-level decision-making tasks. For example, individuals with low resting heart rates have been found to be more likely to make risky decisions (Schmidt et al., 2013). Transient heart rate, however, has been shown to slow directly after a loss in a gambling task, and this decrease in heart rate begins earlier (often prior to the outcome) in individuals who have better general performance in the task (Crone et al., 2004). It has also been shown that individuals with a higher power in the low frequency component of resting HRV generally perform better on gambling tasks (Drucaroff et al., 2011), and there is some evidence that direct vagus stimulation (which increases HRV) can enhance performance in these tasks (Martin et al., 2004). Furthermore, HRV (and its high frequency component) decreases during “stressful” unfair economic offers (such as those in the ultimatum game; Armin et al., 2011; Dulleck et al., 2014). These pressure-induced decreases in HRV have been shown to be more pronounced in individuals who cope less efficiently under high pressure situations (Laborde et al., 2014). While the reasons for these associations are not yet fully understood, these relationships demonstrate that in addition to their association with clinical disorders, cardiac signals are also associated with aspects of decision behaviors in healthy individuals.

One popular account, referred to as the neurovisceral integration model, posits that cardiac signals, and in particular HRV, index the state of a self-regulation network that spans across both the ANS and the central nervous system (Thayer and Lane, 2000, 2009). According to this model, the self-regulation network facilitates physiological, cognitive, and behavioral adaptability to environmental change. It predicts that a lack of such adaptability is associated with low HRV, whereas high HRV reflects a healthy, adaptive system.

The neurovisceral integration model places specific emphasis on the inhibitory role of the parasympathetic nervous system (PNS), the dysfunction of which results in prolonged and inappropriate physiological, emotional and behavioral responses (Thayer and Lane, 2000). As it has a relatively rapid influence on cardiac activity, one common method of estimating PNS function is via the high-frequency spectral component of HRV (HF-HRV; Berntson et al., 1997). Other studies have interpreted the low-frequency component of HRV (LF-HRV) as a reflection of sympathetic cardiac influence (Drucaroff et al., 2011; Dulleck et al., 2014), although this interpretation has been criticized (Reyes del Paso et al., 2013; see Discussion). The neurovisceral integration model also delineates neuroanatomical evidence for the relationship between cardiac signals and cognitive function. Specifically, this relies on the central autonomic network, which is responsible for central cardiac control, and comprises of the ventromedial prefrontal cortex (vmPFC), the central nucleus of the amygdala, anterior cingulate cortex, the insula, as well as several hypothalamic nuclei (Benarroch, 1993). Many of these areas have significant structural overlap with those that support the types of cognitive functions typically associated with cardiac signals (Thayer and Lane, 2000). In particular, cerebral blood flow in vmPFC has been correlated with changes in HRV induced by both emotional images (Lane et al., 2009) and working memory tasks (Gianaros et al., 2004). It has been suggested that vmPFC is the main locus of interaction between cognitive function and cardiac control (Thayer and Lane, 2000).

One fundamental aspect of self-regulation that has not previously been investigated from the perspective of cardiac physiology is regulatory behavior in the temporal domain, principally, impulsivity. While impulsivity is a multifaceted construct, two key aspects are of interest here: decision impulsivity, related to trading off immediate and delayed rewards, and impulsivity as it relates to time perception, which is required for appropriately timing actions (Evenden, 1999).

The main behavioral model of decision impulsivity is temporal discounting (TD; Bickel, 2015). It is typically characterized using a TD task, which assesses individuals' choices between different magnitudes of reward available at different delays (Frederick et al., 2002). The rate of discounting (i.e., the rate of devaluation of reward per unit of time) has been shown to be relatively stable and heritable (Anokhin et al., 2015; Bickel, 2015), and has recently been proposed as an endophenotype (Bickel, 2015). Higher discount rates are apparent in multiple psychopathologies such as substance abuse, problem gambling, attention deficit hyperactive disorder, schizophrenia, depression and obesity (Bickel et al., 2012).

In the time perception domain, impulsivity is based on the notion that impulsive individuals overestimate, and hence under-reproduce time intervals (Wittmann and Paulus, 2008; Rubia et al., 2009; Moreira et al., 2016). For example, by using a duration reproduction (DR) task (in which participants reproduce a sample interval with a manual response), it has been shown that individuals with an impulsive personality traits tend to terminate their reproductions earlier than those without impulsive personality traits, as if they perceive the passage of time to be faster than it objectively is (van den Broek et al., 1992). Performance deficits in these types of time estimation tasks have been related to a range of psychiatric conditions: Parkinson’s disease, depression, bipolar disorder, schizophrenia, attention deficit hyperactivity disorder, autism, as well as anxiety disorders (Allman and Meck, 2012; Teixeira et al., 2013). Notably, there is considerable overlap in psychiatric disorders associated with abnormal cardiac signals, time perception and TD (Kemp et al., 2010; Allman and Meck, 2012; Bickel et al., 2012; Teixeira et al., 2013; Clamor et al., 2016).

Unlike TD, time perception has previously been investigated with respect to cardiac signals. For instance, one such study found that individuals with higher resting HRV were more accurate in a DR task (Pollatos et al., 2014). Another study found that individuals were more accurate in this task when they had a
higher rate of heart rate slowing during the encoding of intervals (Meissner and Wittmann, 2011). Thus, there is some existing evidence that time perception accuracy and autonomic function are associated.

As the vmPFC is one of the primary regions involved in both central cardiac control and impulsivity (Kim and Lee, 2011), our first hypothesis was that specific aspects of cardiac signals are associated with behavioral performance during impulsivity-related tasks. Specifically, we hypothesized that HF-HRV (as an index of PNS function) would be associated with lower discount rates, and longer reproductions of time. Given that a common mechanism may underlie both decision impulsivity and time perception (Wittmann and Paulus, 2008; Moreira et al., 2016), and that damage to the vmPFC often results in both abnormal time perception and steeper TD (Berlin et al., 2004; Moreira et al., 2016), another hypothesis was that these two behavioral measures are related. To test these hypotheses, we measured cardiac activity while participants were completing a TD task and a DR task.

**MATERIALS AND METHODS**

**Participants**

One hundred twenty healthy, right-handed participants (mean age 25, range 21–38, 63 female) from the general population were recruited via advertisement at The University of Melbourne. These individuals were primarily undergraduate students. Participants received AUD 15 for their participation. This study was approved by the University of Melbourne’s Human Research Ethics Committee (no. 1238359) and carried out in accordance with the Declaration of Helsinki. All participants gave informed written consent.

**Decision Impulsivity Task**

Discount rates were measured using a TD task in which participants made binary choices between smaller amounts of money available at earlier times, and larger amounts of money available at later times. There is substantial evidence that the devaluation of reward over time follows a hyperbolic function of the form

\[ V = R \cdot \frac{1}{1 + kD} \]  

(1)

where \( V \) is the subjective value of the reward, \( R \) is the objective reward amount received at delay \( D \), and \( k \) is the discount rate (Mazur, 1987). Participants made a series of choices between immediately available amounts ranging from $20 to $30, and delayed (1, 2, 4, 6, 9 and 12 months) amounts that were chosen based on an algorithm constrained to estimate a threshold function that followed Equation 1 (Vul et al., 2010), as well as a softmax psychometric link function to map subjective values into choice probabilities (Miedl et al., 2012).

**Time Perception Task**

Time perception was measured using a DR task in which, after being presented with a black square for a given duration, participants were asked to press and hold a response key to reproduce the duration (Zakay and Block, 1997). There were six durations ranging from 2 s to 15 s, spaced evenly on a logarithmic scale. We calculated the mean accuracy (reproduction minus sample interval), and mean coefficient of variation (CV; standard deviation divided by the sample interval; Gibbon, 1977) for each participant and each sample interval. Additionally, using least squares regression, we fitted a power function to each participant’s reproduced durations (Stevens and Galanter, 1957), of the form

\[ \mu(t) = \alpha(t)^\beta \]  

(2)

where \( \mu(t) \) is perceived duration and \( t \) is the sample duration. These parameters indicate differences in time perception between the encoding and the reproduction of an interval. The scale parameter \( \alpha \) shifts the slope of the psychophysical function. Relative to unity, a smaller \( \alpha \) parameter implies either a constantly accelerated perception of time during reproduction or a constantly decelerated perception of time during encoding. The exponent \( \beta \) models the shape of the psychophysical function: relative to unity, a smaller exponent implies concavity in the function (a decreasing slope), whereas a larger exponent implies convexity (an increasing slope). A smaller exponent could be interpreted as either an acceleration of perceived time during the reproduction of longer intervals, or a compression of time during the encoding of longer intervals. Ultimately, deviations from unity for both of these parameters indicates deviation from veridical time and thus inaccuracy in time perception. Both of these parameters were used for statistical analyses. Compared to a logarithmic Weber-Fechner law (\( \alpha \log(t + c); \) Grondin, 2001), the fit of the data to Equation 2 had a larger \( R^2 \) (mean 0.83) for 75 participants (80% of cases).

**Equipment and Physiological Recording**

The Psychophysics Toolbox (Brainard, 1997) running on MATLAB 8.4 was used for stimulus presentation, and a RB-540 Cedrus button box was used to capture responses.

Electrocardiogram (ECG) was measured using two amplified adhesive Ag/AgCl EEG electrodes in a modified Lead II Einthoven configuration: one positioned under the right clavicle and one above the left side of the third rib, as well as two implicit reference electrodes positioned underneath the left clavicle. These electrodes interfaced with a BioSemi ActiveTwo system running ActiView acquisition software, and recorded at a sampling rate of 512 Hz. Data were recorded for the entirety of the experimental session (approximately 1 h).

**Experimental Procedure**

After preparing the ECG, participants were asked to complete a block of the TD task (Figure 1A). In each trial, a fixation cross appeared for a duration drawn from a uniform distribution on the interval from 1 s to 3 s. Subsequently, two choice options were presented on the screen, one above the other, for 4 s (e.g., “$19.02 in 2 months” and “$10 today”). On the following screen, the two options were then presented.
FIGURE 1 | (A) Temporal discounting (TD) paradigm schematic. In each trial, a fixation cross first appeared for 1 s–3 s. Subsequently, two choice options were displayed, one above the other, for 4 s. During the response window, the choice options were displayed side by side, for 2 s. A fixation cross then appeared for an inter-trial interval of 1 s. (B) Duration reproduction (DR) paradigm schematic. In each trial, a fixation cross first appeared for 1 s–3 s. Subsequently, a black square was displayed for a pseudo-randomly chosen duration (the sample interval). A white fixation cross then signaled the response window. Once participants initiated a response, another black square was presented until participants terminated their response (the reproduced interval).

side by side for 2 s. Screen positions of the choice options (top/bottom, left/right) were counterbalanced throughout the experimental session. Participants chose one of the two options by pressing one of two buttons on a response pad. After an option was selected, a fixation cross was displayed for a 1 s inter-trial interval. The task terminated when the threshold estimation algorithm converged, or the task reached 80 trials. Participants were explicitly instructed to treat each trial as independent. To establish incentive compatibility, participants were told that a dice would be rolled at the end of the experiment for a chance to win the choice made in one of the trials.

Participants then completed the DR task (Figure 1B). In each trial, participants were first presented with a black fixation cross for between 1 s and 3 s, randomly drawn from a uniform distribution. This was followed by a black square, which was presented for one of six pseudo-randomly chosen intervals (see Time Perception Task). A white fixation cross then appeared until participants initiated a response to reproduce the interval. Once a response was initiated, an identical black square was presented until termination of the response. The next trial began immediately after response termination. There were five repetitions of each interval for a total of 30 trials. Participants were instructed to avoid chronometric counting, to mitigate the effect of sub-vocal rhythm strategies, which can improve accuracy artificially (Rattat and Droit-Volet, 2011).

Participants then completed a second block of the TD task, identical to the first. The purpose of splitting the TD task over two blocks was to test the effect of a feedback manipulation (reporting overestimation vs. underestimation) after the DR task on the second TD task. These results are not reported in this article as we found no effects on performance between conditions (see below for control analyses).

Finally, participants completed a series of questionnaires, administered via web-browser, that were used to assess adherence to task instructions (not reported here in detail). After completion of all experimental tasks, participants were debriefed. A dice was rolled to determine whether they won extra money from the TD task. If a participant won, one trial from the TD was selected, and the participant was paid the chosen amount of money at the chosen delay.

ECG Protocol
In order to estimate general cardiac parameters for a sufficiently long period of time, ECG was recorded over the entirety of the experimental session. Data were detrended and underwent automatic artifact correction using Kubios HRV software (Tarvainen et al., 2014). Any remaining artifacts were manually removed after visual inspection. The software automatically detected R-wave peaks, and any incorrectly identified peaks were manually removed. Heart rate was calculated as the total number of R-wave peaks divided by the total recording time in minutes. We used rMSSD (square root of the mean squared differences of successive R-R intervals) as a measure of HRV. An exemplar ECG indicating automatically identified R-wave peaks is shown in Figure 2.

We further decomposed HRV into component frequency domains using a Fast-Fourier transform. Power in the high frequency (HF-HRV; 0.15–0.4 Hz) band is widely believed to reflect HRV responses to parasympathetic inputs (Berntson et al., 1997), but is also affected by respiratory patterns (Grossman and Kollai, 1993). Power in the low frequency (LF-HRV; 0.04–0.15 Hz) band has been assumed to reflect changes of sympathetic origin (Berntson et al., 1997), although this assumption has been contested (Reyes del Paso et al., 2013; see Discussion). Note that our approach did not allow us to
measure fluctuations in cardiac activity between task phases, but we aimed to obtain a reliable estimate of general and sustained activity across time while participants were engaged in the tasks. Therefore, these measures constituted a combination of general cardiac activity during task performance and the short rest periods for each individual, while neglecting task-phase specific fluctuations.

**Data Analysis**

We excluded participants who chose an option with a negative monetary amount in the TD task more than once (3 participants excluded), missed more than 10 responses in the TD task (10 participants excluded) or whose mean responses in the DR task were more than 3 s away from the sample average (3 participants excluded). Note that the above constituted attentional criteria only, and we did not exclude participants based on impulsivity measures. This makes it unlikely that the retained participants differed in impulsivity from the excluded ones, who showed strong a lack of attention to the task. One additional participant failed to complete the experiment. In addition, we excluded another 17 participants due to inability to calculate cardiac measures due to poor ECG quality. All analyses were performed on data from the remaining participants for which we had complete data sets (94 participants).

Discount rate, time perception parameters and cardiac variables were non-normally distributed. Specifically, discount rates were right-skewed, the scale parameters from the DR psychophysical function were right-skewed, while the exponents were left skewed, and HRV and both frequency components of HRV were heavily right-skewed. We therefore used non-parametric analyses where appropriate. We used a paired Wilcoxon signed-rank test to identify whether there were any differences in discount rate between each block of the TD task. Kruskal-Wallis tests were used to assess the main effects of sample interval on DR task measures. Spearman correlations were used to explore relationships between: (a) DR measures; (b) discount parameters; and (c) ECG measures.

For all statistical tests, the significance level was set to \( p < 0.05 \). Multiple comparisons corrections were carried out for each set of correlational analyses (a, b and c, above) using the Holm-Bonferroni method (Holm, 1979). All statistical analyses were performed using R, version 3.2.1.

**RESULTS**

**Temporal Discounting**

First, we established whether data from both TD blocks could be pooled for the following analyses. The median discount rate \( k \) for the first and second blocks of the TD task were 0.07 (range = 0.01–0.12) and 0.07 (range = 0.01–0.22), respectively. A Wilcoxon signed-rank test did not reveal significant differences between \( k \), measured in the two blocks (\( T = 0.50, p = 0.619 \)). Thus, for subsequent analyses we used the participant mean of \( k \) in the two blocks.

**Duration Reproduction**

Reproduced durations exhibited several characteristics commonly seen in temporal reproduction data. Reproduced durations increased monotonically with the sample interval (\( H_{(5)} = 746.74, p < 0.001 \)), implying that participants followed instructions. Moreover, longer sample intervals were systematically under-reproduced (sample interval on accuracy; \( H_{(5)} = 380.21, p < 0.001 \)). We quantified this effect with quantile regression (median): for every second increase in the sample interval, there was a 0.25 (SD = 0.01) second decrease in the reproduced duration, relative to a perfect reproduction (\( p < 0.001 \)).

We also found an increase in response variability with longer sample intervals (\( H_{(5)} = 407.62, p < 0.001 \)). According to scalar property, timing variability scales proportionally with the interval to be timed (Gibbon, 1977). To test whether the scalar property held for our data, we computed the CV (the standard deviation of the estimation divided by the mean estimation). The CV was significantly affected by the sample interval (\( H_{(5)} = 53.05, p < 0.001 \)), in line with other recent research that has reported violations of the scalar property (Wearden and Lejeune, 2008; Lewis and Miall, 2009). This change in CV was well described by a simple logarithmic regression with a slope of \(-0.042 (p = 0.024, R^2 = 0.76, SEM = 0.01)\), coinciding with data from previous studies (Lewis and Miall, 2009).

We then fitted a psychophysical function (Equation 2) to the reproduction data. The mean estimated value of the scale parameter \( \alpha \) was 1.035 (SD = 0.42). It was not significantly different from unity (\( t_{(93)} = 0.80, p = 0.426 \)), suggesting that, on average, there was no constant deviation from vertical time. The mean exponent \( \beta \) was estimated at 0.899 (SD = 0.17). It was significantly different from unity (\( t_{(93)} = -5.37, p < 0.001 \)), suggesting that participants psychophysical functions were concave, corroborating the increasing underestimation with larger sample intervals noted in previous literature (Lewis and Miall, 2009). Within participants, the scale and exponent parameters were strongly negatively correlated (\( r = -0.87, p < 0.001 \)), while the exponent and CV were strongly positively correlated (\( r = 0.93, p < 0.001 \); Table 1).

**Cardiac Function**

First, we confirmed that there were no significant differences in physiological measurements between feedback conditions using one-way Kruskal-Wallis rank sum tests (see above). There were
Reproduction measures (mean accuracy, CV, and psychophysical function. We calculated Spearman rank correlations between DR and cardiac function. We then tested the relationship between DR and cardiac function, allowing us to use the cardiac measures here as stable estimates for sustained cardiac activity across the experiment.

The mean heart rate across participants was 84.91 bpm (SD = 15.55). The mean rMSSD across participants was 36.06 ms (SD = 16.57). The mean HF-HRV across participants was 221.71 ms² (SD = 623.38). The mean LF-HRV across participants was 1145.39 ms² (SD = 846.96). All measures of HRV were negatively correlated with mean heart rate (all \( p < 0.001 \), except for HR and HF-HRV, \( p = 0.02 \), see Table 1 for correlation coefficients), and positively correlated with each other (all \( p < 0.001 \), see Table 1 for correlation coefficients).

The Relationship between Temporal Discounting and Cardiac Function
We first tested the relationship between TD and cardiac function. To do so, we calculated Spearman rank correlations between the discount rate \( k \) and mean heart rate, rMSSD, as well as LF-HRV and HF-HRV components. All test statistics are reported in Table 1. We found a significant negative correlation between discount rate and mean heart rate (\( r = -0.23, p = 0.032 \)). However, this relationship did not survive correction for multiple comparisons (\( p = 0.108 \)). To illustrate the relationship between mean heart rate and discount rate, we divided our sample around the median heart rate value, and plotted hyperbolic discount functions for each group over a 12-month period (Figure 3). Note that individuals with higher heart rates had a shallower discount function.

The Relationship between Duration Reproduction and Cardiac Function
We then tested the relationship between DR and cardiac function. We calculated Spearman rank correlations between reproduction measures (mean accuracy, CV, and psychophysical scale (\( \alpha \)) and exponent (\( \beta \)) parameters), and between mean heart rate, rMSSD, as well as LF-HRV and HF-HRV components. All uncorrected test statistics are reported in Table 1. We found significant negative correlations between HF-HRV and the exponent \( \beta \) of the reproduction function (\( r = -0.22, p = 0.039 \)), as well as LF-HRV and the exponent (\( r = -0.31, p = 0.004 \)), suggesting that individuals with higher power in both HRV frequency components had a relatively more concave psychophysical function. Because HF-HRV more closely indexes cardiac parasympathetic tone when heart period is taken into account (Grossman and Kollai, 1993), we used a Spearman semi-partial correlation to reanalyze the relationship between HF-HRV and the exponent, while controlling for heart period. The relationship between these two variables remained significant (\( r = -0.26, p = 0.014 \)). After correction for multiple comparisons, the relationship between LF-HRV and the exponent remained significant (\( p = 0.02 \)), but the relationship between HF-HRV and the exponent closely missed the critical threshold (\( p = 0.056 \)).

### Table 1 | Correlations between behavioral and cardiac measures (N = 94).

<table>
<thead>
<tr>
<th></th>
<th>( k )</th>
<th>Accuracy</th>
<th>CV</th>
<th>Scale</th>
<th>Exponent</th>
<th>HR</th>
<th>RMSSD</th>
<th>HF-HRV</th>
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<tbody>
<tr>
<td>Accuracy</td>
<td>0.17</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CV</td>
<td>-0.12</td>
<td>0.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scale (( \alpha ))</td>
<td>0.10</td>
<td>0.23**</td>
<td>-0.87***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exponent (( \beta ))</td>
<td>-0.03</td>
<td>0.21*</td>
<td>0.93***</td>
<td>-0.87***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HR</td>
<td>-0.23*</td>
<td></td>
<td>-0.05</td>
<td>-0.13</td>
<td>0.05</td>
<td>-0.10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RMSSD</td>
<td>0.11</td>
<td>0.05</td>
<td>-0.06</td>
<td>0.16</td>
<td>-0.15</td>
<td>-0.37***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HF-HRV</td>
<td>-0.06</td>
<td>0.01</td>
<td>-0.09</td>
<td>0.20</td>
<td>-0.22*</td>
<td>-0.25**</td>
<td>0.89***</td>
<td></td>
</tr>
<tr>
<td>LF-HRV</td>
<td>0.15</td>
<td>-0.08</td>
<td>-0.20</td>
<td>0.28**</td>
<td>-0.31**</td>
<td>-0.36***</td>
<td>0.71***</td>
<td>0.64***</td>
</tr>
</tbody>
</table>

Note: reported \( p \)-values are uncorrected. *\( p < 0.05 \); **\( p < 0.01 \); ***\( p < 0.001 \). \( k \), discount rate; CV, coefficient of variation; HR, heart rate; RMSSD, Square root of the mean squared differences between successive RR intervals; HF-HRV, high frequency HRV power; LF-HRV, low frequency HRV power.
We also found a significant positive correlation between LF-HRV and the scale parameter $\alpha$ ($r = 0.28$, $p = 0.009$), suggesting that individuals with higher LF-HRV power either perceived time as either relatively fast during the encoding of the interval, or relatively slow during reproduction. This relationship remained significant after correction for multiple comparisons ($p = 0.043$). To illustrate the relationship between LF-HRV and DR, we divided our sample around the median LF-HRV value, and plotted mean reproduced duration as a function of sample interval (Figure 4). Note that in those with high LF-HRV, short intervals were slightly overproduced, and longer intervals are substantially underproduced, while in those with low LF-HRV, reproduced durations were more accurate. Overall, these findings supported our hypothesis of a relationship between time perception and cardiac function.

The Relationship between Temporal Discounting and Duration Reproduction

Finally, we tested the relationship between TD and DR. We calculated Spearman rank correlations between DR measures (mean accuracy, standard deviation, CV and psychophysical scale and exponent parameters), and the discount rate $k$. No significant correlations were found. All test statistics are reported in Table 1.

DISCUSSION

In order to investigate the relationship between time perception, decision impulsivity and cardiac signals, we assessed cardiac activity of individuals while they performed DR and TD tasks. We found a negative correlation between the mean heart rate and discount rate, suggesting that individuals with higher heart rates were more patient. We also found positive correlations between LF-HRV and the parameters of the psychophysical function for DR, suggesting that those with higher LF-HRV power perceived time differently during the encoding and reproduction of the interval, and had poorer sensitivity to longer intervals. Additionally, we found a positive correlation between HF-HRV and the exponent parameter of the psychophysical function, suggesting that those with high HF-HRV power increasingly underestimated longer intervals.

TD has previously been related to other physiological measures, such as pupil dilation (Lempert et al., 2016), but to our knowledge, our study is the first to relate it to cardiac signals. The neurovisceral integration model (Thayer and Lane, 2000, 2009) is built on the notion that greater regulatory control is associated with greater inhibitory parasympathetic functionality. Thus, it would predict that discount rate was negatively associated with HRV. Here, we observed that healthy individuals with higher heart rates had lower discount rates, indicating lower impulsivity, which does not support this prediction.

However, recent work has shown that during TD tasks, choices toward delayed rewards are more likely when sympathetic responses (measured via pupil dilation) to these options are greater (Lempert et al., 2016). As heart rate is primarily mediated by sympathetic activity, it is possible that the observed association between heart rate and discount rate constitutes a similar phenomenon: individuals with lower discount rates were also the ones with higher sympathetic responses, which reflected their tendency to choose delayed rewards. In support of this interpretation, previous studies have shown that higher levels of impulsivity (measured using personality questionnaires) were associated with lower resting heart rates (Mathias and Stanford, 2003) and with lower heart rates during the preparation of an independent task (Allen et al., 2009). Thus our findings provide further evidence that sympathetic nervous system responses may be associated with decision impulsivity.

We also observed a correlation between the parameters of the psychophysical function for DR and both LF- and HF-HRV. It is generally accepted that HF-HRV reflects PNS cardiac influence (Berntson et al., 1997), although it has also been reported that this can be confounded by respiratory patterns (Grossman and Kollai, 1993). While we did not directly measure respiratory activity in this study, an analysis controlling for this possible influence (Grossman and Kollai, 1993) did not alter our results. It has also been noted that interindividual associations between HF-HRV and parasympathetic cardiac influence are modest (Grossman and Taylor, 2007). Thus, while these findings appear to indicate that individuals with higher parasympathetic cardiac influence had poorer sensitivity to longer intervals, some caution should be taken in interpreting our results solely along these lines.

The interpretation of LF-HRV is more contentious than that of HF-HRV. In the psychological literature, increased LF-HRV has previously been related to fatigue and attentional deficits.
signals may constitute a time-keeping mechanism (between HRV frequency components and time perception results are consistent with the psychological attention-based noradrenaline (measures of SNS activity, such as skin conductance level, studies could clarify this by employing more interpretable on the physiological source of the observed result. Future observe any relationships between time perception and HRV (in turn, associated with increased time perception accuracy, rather than the decrease in accuracy we observed in those with high LF-HRV (Cellini et al., 2015). One possible resolution of this discrepancy is that this previous study used different time scales (around 1 s) and different timing mechanisms may be recruited for different durations (Ivry and Spencer, 2004). This interpretation is also inconsistent with the relationships between HRV, working memory and time perception, as higher vagal control has been associated with better working memory (Hansen et al., 2003), which is, in turn, associated with increased time perception accuracy (Broadway and Engle, 2011). Further to this, we did not observe any relationships between time perception and HRV in the time domain (rMSSD). Thus, it is difficult to comment on the physiological source of the observed result. Future studies could clarify this by employing more interpretable measures of SNS activity, such as skin conductance level (Mella et al., 2011), or levels of neurotransmitters such as noradrenaline (Zygmont and Stanczyk, 2010). However, our results are consistent with the psychological attention-based interpretation of LF-HRV, and more broadly the associations between HRV frequency components and time perception measures support previous suggestions that periodic internal signals may constitute a time-keeping mechanism (Craig, 2009; Wittmann, 2015). It is important to note that some of the observed correlations (e.g., between discount rates and mean heart rate) were only significant before correction for multiple comparisons. The uncorrected results are nevertheless interesting, given the absence of existing literature on this topic, and the exploratory nature of our study. We emphasize that these findings require further investigation.

Some limitations of the current study could be addressed in future work. For example, in addition to using directly interpretable measures of SNS activity, future studies could also employ other non-invasive physiological measures, such as eyeblink rate or pupillometry. On the other hand, an assessment of action, as opposed to choice impulsivity (such as a Go-Nogo task), or personality traits, may also be desirable (Glicksohn et al., 2006). It would also be of interest to investigate whether the observed correlations between cardiac measures and time perception would extend to other time estimation paradigms, such as a temporal bisection task, or shorter or longer intervals. Finally, this line of inquiry may be of potential utility in the diagnosis and treatment of psychopathologies that involve impulsivity, such as substance abuse, problem gambling, attention deficit hyperactive disorder, schizophrenia, depression and obesity (Bickel et al., 2012).

We note that as our physiological measures were not isolated to the presentation of stimuli, we were not able to determine whether the observed correlations were driven by task-related responses or trait-like autonomic function. Further studies with baseline measures, longer recordings, and more isolated task phases may be able to address this question, as well as whether the observed relationships were mediated by other personality traits.

While we found that cardiac signals were independently correlated with both TD and DR, we did not find any direct relationship between these two components of impulsivity (Wittmann and Paulus, 2008; Moreira et al., 2016). One possible reason for this is the difference in temporal scale (months in TD vs. seconds in DR), which may recruit different cognitive mechanisms. Future research could address this by using a discounting task with time delays more similar to those used in time perception tasks.

In conclusion, our study shows that differences in ANS function may help to explain inter-individual heterogeneity in both TD and time perception. The association between TD and heart rate supports the notion that low arousal might be related to higher impulsivity, similar to previous perspectives on trait impulsivity (Eysenck, 1993) and previous research using alternate measures (Mathias and Stanford, 2003; Allen et al., 2009; Lempert et al., 2016). Given the conflicting interpretations of cardiac indices, our results concerning DR are difficult to interpret from a physiological perspective. Psychologically, however, our results appear to reflect an association mediated by differences in attention. We found no evidence for a relationship between TD and time perception, which reinforces the idea that these measure different aspects of impulsivity, which appears to be a rather complex construct (Evensen, 1999). Our findings further show that ANS function could provide distinct indices for such aspects of impulsivity, opening up
new avenues for future research to decompose impulsivity beyond TD and time perception (e.g., response inhibition; Krypotos et al., 2011).

**AUTHOR CONTRIBUTIONS**

BJF and DLC contributed to the design of the study, collection and analysis of the data, and drafting of the manuscript. SB and CM contributed to the design of the study, statistical analysis, and drafting of the manuscript. All authors gave final approval for publication.

**REFERENCES**


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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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4.3 SUMMARY

Study 2 assessed the relationships between time perception, temporal decision making, and cardiac signals. In this study, measurements of duration reproduction, temporal discounting, and ECG were made, and correlational analyses were applied to test the relationships between them. We found no evidence for a relationship between duration reproduction and temporal discounting. This failed to support the idea that individual differences in time perception and temporal decision making are related, at least for the range of time intervals and decision process tested here. However, we observed correlations between duration reproduction measures and different frequency components of HRV, consistent with the idea that time perception is related to cardiac physiology. We separately observed correlations between discount rates and mean heart rate, consistent with the low-arousal theory of impulsivity.

If temporal decision making operates on subjective, non-veridical time perception, then individual differences in time perception should be related to individual differences in temporal decision making. Indeed, previous studies have identified commonalities in the factors that affect both time perception and temporal decision making (e.g. arousal, Gil & Droit-Volet, 2012; Sohn et al., 2015; and dopamine, Buhusi & Meck, 2002; Pine, Shiner, Seymour, & Dolan, 2010), and models have been developed that incorporate subjective time into temporal decision making processes (e.g. Blanchard et al., 2013; Namboodiri et al., 2014). Study 2 failed to provide support for this idea. Of course, absence of evidence for such a relationship is not the same as evidence of the absence of the relationship. There are some critical limitations that may explain why we did not observe this relationship. For example, the duration reproduction task does not allow appropriate inference of the rate of a hypothetical pacemaker (Glicksohn & Leshem, 2011), which may be the key link between time perception and temporal decision making. Similarly, the
timescales of each behavioural task were very different, as the duration reproduction task measured time perception in the range of seconds whereas the temporal discounting task involved durations in the range of months. These two different scales may recruit different timing mechanisms (Ivry & Spencer, 2004). A more detailed discussion of these limitations is presented in Chapter 6.

The hypothesis that higher HRV would be related to relative over-reproductions of time was not supported by the findings of Study 2. However, in general, the finding that the low- and high-frequency HRV components were related to time perception supports the notion of a physiological pacemaker (Craig, 2009a), which was also supported by the findings reported in Study 1. Nonetheless, given issues of the interpretation of these cardiac indices, it is difficult to make specific inferences about why these signals should be related to duration reproduction.

The hypothesis that higher HRV would be related to lower discount rates was also not supported by the findings of Study 2. More generally however, the finding that mean heart rate was related to discount rates is consistent with the low-arousal theory of impulsivity (Eysenck, 1967; 1993) and other empirical work that has demonstrated negative correlations between measures of impulsivity and physiological arousal (Mathias & Stanford, 2003; Takahashi, Ikeda, Fukushima, & Hasegawa, 2007; Takahashi et al., 2010). Given that impulsivity has also been shown to be related to physiological factors in other studies, these factors may be good candidates for an experimental rather than correlational study. Chapter 5 presents evidence that physiological factors can indeed causally affect temporal decision making.

While Study 2 failed to provide evidence for a direct relationship between time perception and temporal decision making, that these two processes were independently associated with cardiac signals provides some general support for a
commonality between time perception and temporal decision making. This contributes to the literature presented in both Chapter 1 and Chapter 2, which provided evidence that psychological arousal affects both time perception (Gil & Droit-Volet, 2012) and temporal decision making (Sohn et al., 2015). However, an experimental study would constitute more compelling evidence. In the next empirical chapter, a final study is presented which experimentally manipulated physiological factors to test whether this would affect temporal decision making.
Chapter 5: Consumption of caloric reward decreases temporal persistence

5.1 AIMS OF STUDY 3

Study 3 continued to address the second main theme of this thesis: the proposition that temporal decision processes operate on subjective representations of time. Study 2 failed to provide evidence for a direct relationship between time perception and temporal decision making. However, another consequence of the general proposition is that factors that influence time perception ought to, in turn, affect temporal decision making. This research question evokes a difference in temporal decision making as a causal consequence of a change in time perception, and as such, requires an experimental design. In general, this would constitutes stronger and more interesting evidence that a correlational finding.

One of the potential limitations of Study 2 was that the timescales involved in the time perception task and temporal decision making task were different orders of magnitude (this is discussed in more detail in Chapter 6). In addition to intertemporal choice, Chapter 2 discussed models of foraging and patch-leaving paradigms. These paradigms generally rely on decision making behaviours that incorporate more similar timescales to those commonly used in interval timing tasks: a range of seconds to minutes. Thus, Study 3 focused on foraging as a model of temporal decision making.

Specifically, Study 3 employed a task similar to a continuous time patch-leaving paradigm albeit with discrete monetary rewards (McGuire & Kable, 2012; 2015). In each block of this task, participants were given a fixed amount of time (5 minutes) to earn as much reward as possible. In any “trial” of the task, participants could accept a small reward ($0.01) at any time, and then move to the next trial (i.e. travel to a new patch). However, if they waited, the reward would mature to a larger
amount ($0.15) at a random delay. Thus, in order to maximise reward rate, participants had to estimate an optimal time to stop waiting for the larger reward, as in a continuous patch-leaving task.

To address the primary research question of whether factors known to influence time perception can also influence temporal decision making, an experimental manipulation of a relevant factor was required. The obvious choice was to employ the same factor found to affect time perception reported in Study 1: caloric reward. Not only had this already been found to affect time perception, but the broader literature reported in Chapter 1 and Chapter 2 also places importance on physiological factors as key determinants of both time perception and temporal decision making. Further to this, Chapter 2 also provided some background literature relating to how animals should calibrate their tolerance to delay based on physiological factors. This included a discussion of the energy-budget rule in risk sensitive foraging theory, where animals with positive energy-budgets are relatively risk averse. Thus, Study 3 employed a caloric drink (similar to that used in Study 1) to manipulate subjects relative energy-budgets. Given that delays carry implicit risk, animals with positive energy-budgets may also be more averse to waiting for rewards. This was the basis for the primary hypothesis: consumption of calories results in shorter waiting times.

It is important to note that the predictions made by this extension of the energy-budget rule do not conflict with the results observed in Study 1. These results suggested that calorie consumption will decrease the rate of a hypothetical pacemaker. However, as discussed in Section 2.2.1 it is not entirely clear how a decrease in pacemaker rate should affect foraging behaviour as this may affect the representation of travel time, of foraging time, or both (Hills & Adler, 2002). This will be discussed in greater detail in Chapter 6.
A secondary question that Study 3 aimed to address was whether behaviour would conform to the marginal value theorem, which states that an organism should leave a resource patch when the marginal reward rate falls below that of the environment at large (Charnov, 1976). A previous study employing an almost identical paradigm found that changing the distributions of when the large rewards would mature affected the time participants were willing to wait (McGuire & Kable, 2012). This was consistent with the marginal value theorem in that participants stopped waiting earlier (left the patch) when the potential maximum reward rate over the block was higher (although the findings in this paper were not interpreted as such, McGuire & Kable, 2012). In order to replicate this finding and more explicitly relate this to the marginal value theorem, Study 3 manipulated the average reward rate by sampling from different delay distributions in alternating blocks of the task. The secondary hypothesis of Study 3 was that higher average reward rates would lead participants to stop waiting earlier.

The full manuscript for this study was published in *Proceedings of the Royal Society B: Biological Sciences* (Fung, Bode, & Murawski, 2017) and is presented here in its native format.

5.2 MANUSCRIPT

[Manuscript begins on following page]
High monetary reward rates and caloric rewards decrease temporal persistence

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Temporal persistence refers to an individual’s capacity to wait for future rewards, while forgoing possible alternatives. This requires a trade-off between the potential value of delayed rewards and opportunity costs, and is relevant to many real-world decisions, such as dieting. Theoretical models have previously suggested that high monetary reward rates, or positive energy balance, may result in decreased temporal persistence. In our study, 50 fasted participants engaged in a temporal persistence task, incentivised with monetary rewards. In alternating blocks of this task, rewards were delivered at delays drawn randomly from distributions with either a lower or higher maximum reward rate. During some blocks participants received either a caloric drink or water. We used survival analysis to estimate participants’ probability of quitting conditional on the delay distribution and the consumed liquid. Participants had a higher probability of quitting in blocks with the higher reward rate. Furthermore, participants who consumed the caloric drink had a higher probability of quitting than those who consumed water. Our results support the predictions from the theoretical models, and importantly, suggest that both higher monetary reward rates and physiologically relevant rewards can decrease temporal persistence, which is a crucial determinant for survival in many species.

1. Introduction

Patience is often treated as a virtue, as acting patiently can lead to long-term gains. Conversely, acting impatiently can also be advantageous in some circumstances, particularly when the potential time spent waiting for rewards is uncertain, or when the value of alternative behaviours is high. Temporal persistence refers to the duration of time individuals will wait in the face of increasing opportunity costs, and is a crucial aspect of many real-world decisions. For example, an individual may decide to wait for a bus, but after waiting for 15 min, may abandon waiting and take a taxi instead, despite the fact that this option was available from the beginning. One explanation for this apparent inconsistency is that real-world delays carry implicit uncertainty [1,2], and that individuals’ beliefs about potential waiting times are continuously updated by experience of the environment [3–5]. From the perspective of optimal foraging—where animals try to maximize their rate of reward intake while minimizing the opportunity cost of time [6]—any decision to abandon waiting should occur once the opportunity cost of time outweighs the potential future reward [7–9]. In our example, this might mean giving up waiting for the bus after the opportunity cost of waiting exceeds the cost of a taxi.

Not much is known about how humans calculate temporal opportunity costs. In one neurocomputational model, opportunity cost is directly proportional to the recently experienced average reward rate [10]. This is because higher experienced reward rates signal high reward availability, thus periods of inactivity are more costly, relative to when reward availability is lower. Under this framework, actions should be performed more quickly (i.e. with...
more vigour) in order to offset the relatively high temporal opportunity cost [11]. The model proposes that this increase in speed is facilitated by an increase in tonic dopamine in the striatum [12,13], and therefore tonic dopamine levels are proportional to both experienced reward rate and subjective temporal opportunity costs. Previous imaging studies have provided support for this idea by showing covariation between average reward rate and the tonic activity of dopaminergic midbrain areas [12,14]. This encoding of opportunity cost by tonic dopamine is consistent with the reported effects of dopaminergic manipulations on perceived durations: dopamine agonists cause overestimations of time, which ought to increase subjective opportunity costs, while dopamine antagonists cause underestimations of time, which ought to have the opposite effect [15,16]. The effect of dopaminergic agents on perceived durations and subjective opportunity costs may also help to explain findings in delay discounting, where enhancing dopamine levels can lead to more impulsive choices [17]. Thus, the putative dopaminergic encoding of opportunity cost could be viewed as equivalent to an urgency signal [18], one which affects measurements across multiple timing domains, including reaction times [19], duration perception [15,16,19], delay discounting [17] and possibly temporal persistence.

Another framework, risk-sensitive foraging theory [20], also outlines how temporal persistence might change in response to internal signals, such as an increase or decrease in energy balance [21]. According to this framework (widely referred to as the energy budget rule), organisms with a negative energy balance should take more foraging risks (be risk-prone) in order to minimize the probability of starvation, while organisms with a positive energy balance should be risk-averse [22]. In humans, this has been supported by evidence showing that a positive energy balance increases risk-aversion for the acquisition of both monetary [23] and physiological rewards [24]. Any potential delay to reward carries implicit risk, and it has been proposed that risk and delay might be psychologically analogous, if not equivalent [1,2]. Thus, under the energy budget rule, it follows that organisms with more energy should exhibit aversion to delay, and decreased temporal persistence, relative to organisms with less energy. However, to our knowledge, whether energy balance affects temporal persistence in humans has not been tested.

The two frameworks discussed above make testable predictions. Firstly, temporal persistence should decrease during periods in which experienced average reward rates are high, due to increased subjective opportunity costs. Secondly, temporal persistence should also decrease when energy balance is high, due to an increase in aversion to delay. In this study, we tested these theoretical predictions independently, using a modified version of a temporal persistence task [3]. Prior work based on this task has shown that individuals adapt their temporal persistence to their experience with delays drawn from different distributions [3]. In our experiment, we used different distributions of delays to manipulate the reward rate between blocks. Additionally, in between blocks our fasted participants received either a sweet, caloric solution or water as a control, in order to manipulate relative energy balance. These two manipulations allowed us to determine whether high average reward rates or the consumption of a caloric solution would decrease temporal persistence.

2. Material and methods

(a) Participants

Fifty participants from the general population (mean age 23, range 18–40, 30 female, five left-handed) were recruited via advertisement at The University of Melbourne. All participants reported no dietary restrictions (fructose intolerance, diabetes, fluid imbalance or phenylketonuria) and provided written informed consent. Participants were instructed to refrain from eating or drinking for 4 h prior to the experiment in order to decrease satiety. Participants were compensated with at least AUD 10 for their participation, as well as an additional amount contingent on their task performance (maximum total AUD 20). The study protocol was approved by The University of Melbourne Human Research Ethics Committee (no. 1441974).

(b) Stimuli, apparatus and procedure

We measured temporal persistence using a task in which participants could wait for a randomly timed, delayed, monetary reward ($0.15) or could at any time decide to ‘quit’ waiting and accept a small, immediate, monetary reward ($0.01; figure 1; [3,7]). In each block of this task, participants were given a fixed amount of time (5 min) to earn these rewards. A bar was displayed at the bottom of the screen indicating the cumulative duration of the block. At 5 min, the bar filled and the block was terminated. During these 5 min, tokens would appear on the screen serially, one at a time. Initially, they would be valued at $0.01, but after an uncertain delay (see below for procedure) would mature to a value of $0.15. At any point, participants could press a button to take the token, and earn the corresponding value. After a 2 s inter-trial interval, a new token would appear. Participants were instructed to maximize their earnings during each 5-min block using whatever strategy they preferred. For example, a participant may have adopted a policy to continuously accept the small tokens, which would allow them to earn $0.01 every 2 s. Alternatively, by always waiting until the tokens matured before taking them, more would be earned with each token, but this process would have a high opportunity cost (the potential reward forgone by waiting). Participants were told that they would be paid exactly half of their total winnings in the task, but guaranteed a minimum payment of AUD 10.

In each block, we determined the timing of the delayed reward by sampling from one of two different delay distributions, which alternated between blocks. These two different distributions constituted two different timing environments in which the optimal quitting time and potential reward rate differed (optimal quitting times and average earnings under this policy were derived by performing a normative analysis as detailed in [3]). The possible delays for the first timing environment were described by a uniform distribution on the interval 0 to 12 s. The optimal policy in this environment was to always wait for the full 12 s, which would have earned approximately $5.58 in each block. The delay distribution of the second, ‘heavy-tailed’ timing environment was described by a generalized Pareto distribution of the form:

$$F(t) = 1 - \left(\frac{1 + kt}{\sigma}\right)^{-1/k},$$

with parameters $k = 8$, $\sigma = 3.4$ and the upper bound set at 90 s. The optimal quitting policy in this environment was to quit at 2.13 s, which would have earned approximately $5.70 in each block. Thus, the potential reward rate of the heavy-tailed timing environment was higher than in the uniform environment. To ensure full exposure to the range of each distribution, delays were not sampled entirely randomly, but were instead sampled randomly from each quartile of the distribution in a
Participants first completed two practice blocks of the task (one block of each timing environment), prior to completing a further eight blocks (10 blocks in total). In between blocks 5 through 8, participants consumed either 75 ml of water (control condition) or 75 ml of a sweet, caloric solution (caloric reward condition). This solution consisted of 6.4 g of a maltodextrin (a tasteless carbohydrate) and 20 mg of aspartame per 100 ml water. This solution was intended to mimic ecologically feasible rewards in terms of both energy content and sweetness, while allowing for future studies which could disassociate these two aspects. It was made clear to the participants that they could refrain from the experiment if they found the drink unpalatable. No participants were excluded on this basis, and 18 of the 25 participants in the caloric condition reported that they found the caloric drink ‘rewarding’, as opposed to ‘not rewarding’, upon debriefing. Importantly, in order to minimize any possible confounds between drink consumption and time-on-task, blocks in which participants did not consume liquid were balanced before and after blocks in which participants did consume liquid. After completion of the experimental task, participants were debriefed, and their total winnings computed and paid.

The Psychophysics Toolbox [25] running on MATLAB v. 8.4 was used for stimulus presentation.

(c) Data analysis
As quitting decisions were the data of interest, we excluded data from two participants (both in the caloric reward condition) who failed to make any quitting decisions in either distribution, during the drinking blocks. The final sample included data from 48 participants.

While instances where participants abandoned waiting provided a direct measure of their persistence (or lack thereof), the exclusive use of these events neglects the information in instances where the token matured prior to a quitting decision. These events indicate that participants were willing to wait at least as long as it took for the large monetary reward to become available, and are equivalent to censored data in survival analysis. Thus, we adopted a technique from survival analysis, known as frailty modelling [26], which allowed us to model the probability of quitting as a function of time, while accounting for censored data, as well as accounting for dependence of events within subjects (the frailty is comparable with a random effect). Specifically, we used a semiparametric penalized likelihood estimation with a lognormal frailty as we assumed that our random effects were normally distributed. The hazard function for this shared frailty model was

\[
\lambda_i(t|x) = \eta \lambda_0(t) \exp^\top X_i = \eta \lambda_1(t),
\]

where \(\lambda_0(t)\) is the baseline hazard function, \(X_i\) the covariate vector associated with the vector of regression parameters \(\beta\) and \(\eta\) is the random effect associated with the \(i\)-th individual.

We first assessed the effect of timing environment (monetary reward rate) on temporal persistence, using only data from blocks in which participants did not drink, by including timing environment as a regressor in the frailty model. To assess whether caloric reward altered temporal persistence, we created an additional model using only the data from the blocks in which participants consumed liquid, and two further models to calculate hazard ratios for each timing environment separately. In an additional analysis, we also created separate models for each timing environment and each liquid type, in order to assess whether consumption of liquid (relative to not consuming liquid) had an effect on temporal persistence within each treatment group. Hazard ratios were calculated from the coefficients in all of the above models, and reported along with 95% CIs. We also
performed a control analysis to determine whether the differences in the distribution of rewards in each timing environment affected the actual rate of reward experienced by participants, and whether either treatment affected reward rates within each timing environment. To calculate average experienced reward rate, we divided the cumulative reward by the cumulative duration at each decision point, and averaged these values over each block.

All statistical analyses were performed using R (v. 3.2.1). All frailty models were created using the statistical package frailtypack [27], with number of knots set to the default of 7, and the smoothing parameter estimated by cross-validation. For all statistical tests, the significance level was set to \( p < 0.05 \), and multiple comparisons were corrected using the Holm–Bonferroni method [28].

3. Results

(a) Differences between timing environments

Firstly, we determined whether there were differences in behaviour between the two timing environments. To this end, we estimated a shared lognormal frailty model with timing environment as a regressor, using data pooled from both treatment conditions, and only from the blocks in which participants did not consume liquid.

The model revealed a significant effect of the heavy-tailed timing environment (\( \beta = 1.11, \text{s.e.} = 0.03, z = 39.95, p < 0.001 \)). The hazard ratio was 3.05 (CI = 2.89–3.22), indicating that the probability of quitting was around three times as high in the heavy-tailed timing environment compared to the uniform timing environment. This suggests that individuals decreased their temporal persistence when reward rates were higher. Survivor functions estimated using pooled data for each timing environment are shown in figure 2.

We then performed a control analysis to confirm that the differences between the timing environments affected the actual rate of reward experienced by participants. As we were interested in the effect of recently experienced reward rates on decision making, we calculated reward rate by dividing the cumulative reward by the cumulative duration at each decision point. We compared the mean reward rates between timing environments using data pooled from both treatment conditions, and only from the blocks in which participants did not consume liquid.

The mean experienced reward rate in the uniform timing environment was 1.52 cents s\(^{-1}\) (s.d. = 0.02 cents s\(^{-1}\)), and for the heavy-tailed timing environment it was 1.62 cents s\(^{-1}\) (s.d. = 0.02 cents s\(^{-1}\)). This difference was statistically significant (\( t_{47} = -2.46, p = 0.018 \)), demonstrating that, on average, participants achieved a higher average reward rate in the heavy-tailed timing environment.

(b) Differences between drink condition

Having identified that participants altered their temporal persistence for each timing environment, we next assessed whether caloric reward had an effect on temporal persistence. To do this, we used a full factorial shared lognormal frailty model, with both treatment condition and timing environment, and their interaction, as regressors. We used data only from the blocks in which participants consumed liquid.

We re-established the significant effect of the heavy-tailed timing environment (\( \beta = 1.45, \text{s.e.} = 0.05, z = 27.68, p < 0.001 \)), which had a hazard ratio of 4.25 (CI = 3.84–4.71). We also observed a significant main effect of the caloric reward (\( \beta = 0.3, \text{s.e.} = 0.06, z = 4.97, p < 0.001 \)), with a hazard ratio of 1.35 (CI = 1.2–1.52). Further to this, we also found a significant interaction effect between the heavy-tailed timing environment and the caloric reward (\( \beta = -0.5, \text{s.e.} = 0.07, z = -7.58, p < 0.001 \)), with a hazard ratio of 0.60 (CI = 0.53–0.69).

To compute hazard ratios for the effect of treatment condition within each timing environment, we created two ‘simple effects’ models treating the uniform and heavy-tailed timing environments separately. Within the uniform timing environment, the model re-established a significant effect of the caloric reward (\( \beta = 0.23, \text{s.e.} = 0.08, z = 3.04, p = 0.002 \)). The hazard ratio of the caloric reward group was 1.26 (CI = 1.08–1.46), indicating that, relative to water, the probability of quitting was more likely after consuming caloric reward. Survivor functions estimated using pooled data for each treatment condition in the uniform timing environment are shown in figure 3a.

We also found a significant effect of the caloric reward within the heavy-tailed timing environment (\( \beta = 0.11, \text{s.e.} = 0.05, z = 2.15, p = 0.032 \)), with a hazard ratio of 1.12 (CI = 1.01–1.23), indicating that relative to water, the probability of quitting was more likely after consuming caloric reward. Survivor functions estimated using pooled data for each treatment condition in the heavy-tailed timing environment are shown in figure 3b.

The effects in all three of these models remained significant after correction for multiple comparisons. The observed pattern of results suggested that overall, caloric reward increased quitting probabilities, but to a smaller degree within the heavy-tailed timing environment.

We then ran an analysis to identify whether the caloric treatment condition affected experienced reward rate as a result of the increase in quitting probability, compared to the control condition. To do this, we used only data from blocks in which participants consumed liquid, and treated each timing environment separately.
Within the uniform timing environment, consumption of water did not significantly affect the probability of quitting ($\beta = 0.003$, s.e. = 0.05, $z = 0.05$, $p = 0.959$). However, consumption of caloric reward did significantly affect the probability of quitting ($\beta = 0.28$, s.e. = 0.05, $z = 6.21$, $p < 0.001$). This was equivalent to a hazard ratio of 1.32 (CI = 1.21–1.44), and suggests that the consumption of caloric reward decreased temporal persistence, relative to blocks in which the same participants did not consume liquid.

Within the heavy-tailed timing environment, the consumption of water had a significant effect on the probability of quitting ($\beta = -0.14$, s.e. = 0.03, $z = -3.96$, $p < 0.001$), equivalent to a hazard ratio of 0.87 (CI = 0.81–0.93). This suggested that water consumption increased temporal persistence, relative to blocks in which the same participants did not consume liquid. The consumption of caloric reward also had a significant effect on quitting probability ($\beta = 0.13$, s.e. = 0.03, $z = 3.89$, $p < 0.001$), equivalent to a hazard ratio of 1.14 (CI = 1.07–1.22).

With the exception of water consumption in the uniform timing environment, the effects of drink consumption in both timing environments were significant after correction for multiple comparisons. Overall, these results suggest that, relative to blocks in which there was no liquid consumption, there was a systematic effect of the consumption of caloric reward across both timing environments, such that temporal persistence was decreased. They also suggest that water consumption significantly increased temporal persistence, but only within the heavy-tailed timing environment.

4. Discussion

In this study, we assessed whether individuals changed their persistence in waiting for monetary reward as a result of differences in timing environment (average experienced reward rate) and differences in energy balance. In line with our predictions, we found that temporal persistence was lower in the presence of a higher average reward rate and when participants consumed a caloric drink. Decision-makers should make quitting decisions when the opportunity cost of waiting exceeds a certain threshold [7], or when they are averse to the risk inherent in delay [12]. Thus, we interpret these relatively expedited quitting times as a consequence of increased subjective opportunity costs [10], and increased risk-aversion (in line with the energy budget rule; [22]), respectively.

The neurocomputational model of Niv et al. [10] predicts that the latency of actions should decrease when average reward rate is high, in order to offset the relatively high opportunity cost of time [10]. Our results support this prediction by indicating lower temporal persistence when in an environment with a higher average reward rate. This is consistent with the results of a previous study using the same paradigm and similar timing environments [3], as well as previous studies employing different paradigms that have manipulated reward rates to show effects on vigour, measured by reaction times ([11,13], and see [29]), and the force of responding [12]. Thus, our findings further support the notion that reward rate and opportunity cost (possibly encoded by tonic dopamine) can affect timing over a broad range of tasks and timescales. This appears to apply to motor control (i.e. reaction times, [19]), perception (i.e. time perception, [15,16,19]), as well as decision making (delay discounting, [17]; and now temporal persistence). In sum, these

(c) Effect of drink consumption versus no consumption

We further subdivided the data to assess how liquid consumption and liquid type affected the probability of quitting in each timing environment. For each timing environment, and for each liquid type, we estimated a shared lognormal frailty model to identify whether liquid consumption altered temporal persistence relative to non-consumption, within each group.
findings point to a general, reward-sensitive mechanism that calibrates many time-related functions.

One alternative interpretation of this result is that participants tailored their persistence by estimating the exact temporal distribution of rewards, rather than the average reward rate. However, previous work has suggested that humans are more likely to use heuristic approaches—such as average experienced reward rate—to determine the latency of actions [10,30]. This question could be further investigated by comparing temporal persistence under timing conditions that have identical reward rates, but distinct statistical distributions. We also note that while the apparent difference in average experienced reward rate between the timing environments was small, it has been argued that the matching of behaviour to reward rates is innate [31], and thus participants may not have needed to be explicitly aware of differences between the reward rates in each timing environment to alter their behaviour.

We also found that relative to those who consumed water, participants who consumed a sweet, caloric drink had decreased temporal persistence. Given that delays carry implicit uncertainty [1,2], the energy budget rule predicts that temporal persistence should be lower when energy balance is positive [22]. Our results constitute the first empirical demonstration of this in humans. A possible alternative explanation for this result is that caloric rewards increased task performance, as they have been shown to do in other cognitive domains [32]. However, optimal task performance in the uniform timing environment required prolonged persistence, which directly conflicts with the observed effect of caloric rewards in this condition.

In our experiment, participants who consumed water did not systematically alter their temporal persistence, which suggests that this effect was due specifically to the flavour or energy content in the caloric reward, rather than primary rewards in general. As we combined both maltodextrin and aspartame in the caloric treatment condition, we are unable to disassociate the alimentary and hedonic aspects of the liquid, i.e. whether the caloric content of the liquid is sufficient to decrease temporal persistence, or whether a sweet flavour must also be present. However, previous studies have shown that calorie-rich nutrients affect reward pathways independently of palatability [33–35], and tasteless carbohydrates can affect aspects of behaviour, such as exercise performance [36,37] and self-control [32], whereas artificially sweetened solutions do not. Thus, while we are unable to attribute the effect to caloric reward with certainty, we find it more likely that caloric content—rather than sweetness—affects behaviour. The possibility that either caloric content or flavour is responsible for the effect on temporal persistence could be explored in a future study.

We also note that for the heavy-tailed timing environment, participants who consumed water (who had relatively negative energy balance) abandoned waiting later than was optimal. Thus, for our experimental design, the energy budget rule for temporal persistence appeared to be maladaptive. One possible explanation for this is that our timing environments are not perfectly representative of ecological reward timing distributions. Future studies could address this by assessing task performance in a wider range of timing distributions.

Caloric rewards have previously been proposed to enhance behaviour in the cognitive domain of self-control [38], which would suggest that caloric reward might have increased, rather than decreased temporal persistence. Indeed, a number of studies have reported that calories and other satiety factors have such an effect. For instance, glucose consumption has been shown to enhance patience in inter-temporal choice (compared with artificial sweeteners [39]; or fructose [40]). Similarly, it has been shown that the ‘hunger hormone’ ghrelin decreases patience [41], suggesting that a low energy budget increases subjective temporal opportunity costs. In addition, there is evidence that the consumption of fruit juice rewards can cause underestimations of time [42], which implies a ‘slower’ subjective pacemaker, and therefore a lower subjective temporal opportunity cost. These studies recapitulate the idea that opportunity costs ought to decrease as organisms become satiated, as there is a less urgent requirement for nutrition. Thus, an alternative prediction for our experiment would have been that physiological rewards (such as the sweet, caloric solution used in our experiment) would decrease temporal opportunity costs and increase temporal persistence. However, our results do not support this. Instead, we speculate that the consumption of calories led to elevated tonic dopamine levels in reward-related midbrain areas, rather than an inhibition of dopaminergic activity, as has previously been suggested [43], although we note that we do not have direct evidence for this. However, an increase in tonic levels of dopamine in response to caloric consumption is consistent with human imaging studies [35,44,45]. It would also be consistent with the time perception literature, where increasing dopamine levels leads to earlier time estimations [15,16]. Furthermore, similar effects have been reported in other reward-based decision making tasks, where increases in dopamine levels have been shown to increase impulsive choices [17] and actions [46].

Our results show that heightened reward rate and increased energy balance appear to affect temporal persistence in a similar way. One apparent question is whether these effects are facilitated by a common mechanism. Previous research has suggested that the value of money is a modern derivative of the desire for primary rewards [47], and that the predictions of the energy budget rule are met when average monetary reward rate is used as a proxy for metabolic energy balance [48]. Likewise, money and juice reinforcers cause overlapping neural responses [49]. It is therefore possible that both high monetary reward rates and the consumption of calories affect behaviour via a common psychophysiological mechanism, i.e. they both signal the general availability of reward. This should result in an increase in the perceived opportunity cost of time and increased motivational drive, whether the source is external [10] or internal [50]. However, if such a common mechanism was limited in scalability, increasing opportunity cost would not have an unlimited effect on behaviour. This may account for the smaller effect of positive energy balance in the heavy-tailed environment, where these two factors were combined. Given the hypothesis of a common mechanism, and the fact that energy balance non-specifically affects temporal persistence towards monetary goals, it would be of interest for future work to determine whether monetary reward can also affect temporal persistence toward food-related goals.

Impulsivity is a broad, but heavily studied construct in psychology, economics and psychiatry [51], and relates to a wide range of psychiatric disorders [52]. An individual’s temporal persistence—as measured by this paradigm—may
constitute a useful measure of impulsivity, as a lack of temporal persistence would imply an inability to delay gratification, and a higher likelihood reneging on a long-term goal (i.e., preference reversals [3]). The dominant behavioural model of impulsivity is intertemporal choice, which has been shown to be a relatively stable and heritable trait [52]. However, when used in laboratory experiments, intertemporal choice rarely engenders actual temporal opportunity costs, as individuals are not required to forgo alternatives while waiting for delayed rewards. Similarly, the delays to reward receipt are usually well specified, and the one-shot nature of the task does not allow for preference reversals. This highlights a distinction between impulsive choice and impulsive action, which capture different aspects of impulsive behaviour [53]. The temporal persistence task used in this experiment may involve a combination of these constructs: the trade-off between short- and long-term rewards commonly associated with impulsive choice, as well as the capacity to inhibit prepotent responses that is relevant to impulsive action. Given that our primary measures are responses to concurrent opportunity costs and time pressure, we consider our task to be perhaps more relevant to action impulsivity. Importantly, while the task only requires passive waiting to acquire larger rewards (rather than, for instance, physical effort), the uncertainty of the delays and possibility for preference reversals may be more representative of real decision scenarios. This may explain the discrepancy between the results of our experiment, and those that have used intertemporal choice to show that positive energy balance can increase patience [39]. A further question raised by our results is, therefore, whether the effect of increased energy balance on temporal persistence applies to impulsive behaviour more generally. This possibility may provide a promising avenue for further research.

In conclusion, in addition to demonstrating that individuals calibrate their temporal persistence depending on average experienced reward rates, we also demonstrated a clear effect of caloric reward on temporal persistence. Previous work has shown an effect of average experienced reward rates on reaction times and the force of responses [11–13], and we extend this effect to temporal persistence. Previous studies have also identified that humans become more risk-averse when satiated [23,24], but our study is the first to demonstrate that energy balance affects temporal persistence. This contributes to growing evidence that physiological rewards play a crucial role in modulating cognition and decision-making [21,39–41].

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**Ethics.** All participants provided written informed consent. The study protocol was approved in accordance with the guidelines instituted by The University of Melbourne’s Human Research Ethics Committee (no. 1441974), and research was conducted according to the principles expressed in the Declaration of Helsinki.

**Data accessibility.** All data are available at the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.1k79k [54].

**Authors’ contributions.** B.J.F. contributed to the design of the study, collected and analysed the data and drafted the manuscript; S.B. contributed to the writing of the manuscript; and C.M. contributed to the statistical analyses, and the writing of the manuscript. All authors gave final approval for publication.

**Competing interests.** All authors declare no competing interests.

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10.1901/jeab.2007.92-05)
5.3 SUMMARY

Study 3 investigated whether factors that influence time perception also affect temporal decision making. To do this, it adopted a decision making task similar to a patch-leaving paradigm, where participants had to trade off delayed monetary rewards against the opportunity cost of time. Study 3 used a similar caloric manipulation to that of Study 1 to assess the effect of energy-budget on temporal decision making. It also manipulated the average reinforcement rate between blocks of this task. The results showed that participants who consumed a caloric drink were more likely to give up waiting earlier. This finding was consistent with an extended energy-budget rule for delay tolerance. The results also showed that participants were more likely to give up waiting earlier in blocks with higher average reinforcement rates. This finding was consistent with an increased aversion to delay due to increased opportunity costs, and the marginal value theorem.

Study 3 found that consumption of calories caused fasted participants to stop waiting for larger rewards earlier than those who consumed water\textsuperscript{17}. The main interpretation for this was provided by the extended version of the energy-budget rule, where animals with positive-energy budgets should be risk-averse and therefore averse to the risk implicit in waiting for delayed rewards. This interpretation contrasts with empirical findings for impulsivity and temporal decision making more generally, where it has been reported that calorie consumption leads to increased patience in temporal discounting (Wang & Dvorak, 2010). A secondary interpretation for this finding is that the consumption of calories caused in an increase in the perceived average reward rate of the environment, which, in line with the marginal value theorem, lead to expedited quitting times. Notably this interpretation is not mutually exclusive with risk-aversion interpretation.
Three alternative explanations relate to the potential effects of calorie consumption on time perception. The first of these is that the consumption of calories lead to an overestimation of the time spent waiting and therefore earlier quitting times. However, this explanation is inconsistent with the results observed in Study 1, where calorie consumption lead to underestimations of time. Alternatively, the consumption of calories in Study 3 may have lead to an underestimation of the inter-trial interval (the “travel” time between patches), which would have lead to the observed results. Finally, one interpretation of the effect of calorie detection in Study 1 was that it increased motivation/attention, and detracted from temporal processing. It is possible that the early quitting times observed in the present study were a direct consequence of increased motivation, which was not observed in Study 1 as performance was not incentivised. Thus, the effect of calorie consumption of quitting times may have constituted an affect of motivation rather than an effect of time perception, *per se*. These possibilities are discussed in greater detail in Chapter 6.

The second principle finding of Study 3 was that in blocks with higher average monetary reward rates, participants also stopped waiting for larger rewards earlier. As with the above finding, this is also consistent with the marginal value theorem, where the overall average reward rate determines the opportunity cost of time, and how early animals should leave patches. The idea that average reward rates calibrate temporal persistence supports and extends previous findings showing that response times are decreased in environments with higher average reward rates (Guitart-Masip, Beierholm, Dolan, Duzel, & Dayan, 2011; Niv, Daw, Joel, & Dayan, 2007). One alternative explanation is that another characteristic of the reward delay distribution motivated earlier quitting decisions. However, in Study 3, reward rate and reward timing were confounded. An experiment that could manipulate overall reward
rate within a single, stable reward delay distribution may be able to disassociate these two aspects. There are also alternative explanations for these results which are discussed more fully in Chapter 6.

While it is important to emphasise that Study 3 did not explicitly measure time perception (although it arguably reflects the use of time perception in an ecological context), both of its findings could be interpreted to be consistent with an increase in the rate of the hypothetical pacemaker due to increased reward rate. This is the key principle of the behavioural theory of timing (BeT; Killeen & Fettermen, 1988) and thus this study lends some empirical support for this account. Importantly, participants stopped waiting earlier regardless of whether the rewards were monetary or physiological, and regardless of whether the rewards were contingent or extraneous to the task, suggesting a general, Pavlovian mechanism that is insensitive to the nature of rewards.
Chapter 6: General discussion

The aim of this thesis was to investigate the effect of reward on time perception and the relationship between time perception and temporal decision making. In regard to the former, it addressed the question of whether reward consumption could affect time perception in humans. Chapter 3 presented a series of experiments, providing evidence that the consumption of caloric rewards can lead to underestimations of supra-second delays. In regard to the latter, Chapter 4 investigated whether individual differences in time perception were related to individual differences in temporal decision making, and Chapter 5 addressed the question of whether factors that affect time perception could also affect temporal decision making.

The studies reported in this document thus provided support for the idea that rewards can affect time perception and that this may in turn impact temporal decision making. This final chapter will summarise the key findings of each of the previously presented studies. It will discuss how these results specifically contribute to the existing literature on time perception and temporal decision making, and suggest some broader implications for this research area. It will also clarify some limitations of the studies and the open questions that may be addressed by future studies.
6.1 OVERVIEW

Study 1 was presented in Chapter 3 and investigated whether the anticipation or consumption of reward could affect time perception. This study was primarily motivated by three aspects of the existing literature. Firstly, some models of time perception have proposed that the rate of the internal pacemaker is proportional to reward rate (Killeen & Fetterman, 1988; Section 1.2.2). However, while there have been investigations of the effect of reward on time perception in non-human animals (Bonem & Crossman, 1988), this has not been investigated in humans. Secondly, some non-human animal studies have shown that the effect of rewards can differ depending on the specific nutrient content of the rewards (Meck & Church, 1987), although this is not well understood. Thirdly, there is a gross overlap in the neurobiology of reward processing and time perception (Buhusi & Meck, 2002; Meck, 1988; Section 1.3 and Section 1.4), which further suggests that reward might affect time perception. Because dopamine neurons have been shown to respond to cues indicating expected reward as well as reward consumption itself (Mirenowicz & Schultz, 1994; Schultz, 1998), it is an open question whether the anticipation of reward can also affect time perception.

Study 1 recruited 25 participants and assessed their performance on a novel variant of a duration production paradigm in order to test whether the anticipation or consumption of reward could affect time perception. Time estimates were analysed as a function of reward magnitude, controlling for other potentially confounding factors. The results of this experiment showed that the consumption of fruit juice led to underestimations of delays across the range of 2-5 seconds, but that anticipating future rewards did not affect time perception at any of these target times. A further 100 participants were subsequently recruited in order to test a range of different reward types — money (secondary reward), water, aspartame (sweet and noncaloric),
and maltodextrin (tasteless and caloric) — in a further four experiments. The results of these experiments showed that only maltodextrin produced a similar effect on time productions, which suggested that the observed effect was likely to be due to the common caloric content of both fruit juice and maltodextrin. Both of these results were robust to the influence of other factors that affected time estimates, including carry-over effects. Importantly, these effects also operated on a short, trial-to-trial timescale, and were therefore unlikely to be a direct result of nutrient value. Additionally, we did not observe any effects of reward anticipation for any of the tested reward types.

The second main theme of this thesis proposed that agents making temporal decisions would do so on the basis of their subjective, internal representation of time. Study 2 was presented in Chapter 4 and addressed the specific hypothesis that individual differences in time perception are related to individual differences in temporal decision making (e.g. Zauberman, Kim, Malkoc, & Bettman, 2009). Another key motivation for this study was existing literature that linked both time perception and temporal decision making to physiological arousal (Section 1.3.1 and Section 2.3.3). In particular, heart rate variability (HRV) has been suggested to index the function of a self-regulation network underlying cognitive and behavioural inhibition (Thayer & Lane, 2000; 2009), which may also be involved in impulsivity and time perception. Thus, Study 2 investigated the relationship between time perception, temporal discounting, and autonomic cardiac signals.

In Study 2, 120 participants completed a duration reproduction task and a temporal discounting task, while their heart rate was recorded using electrocardiography. The resulting duration reproduction data were fit to a
psychophysical function and discount rates were derived from the temporal discounting data. The relationships between these measures were assessed using correlational analyses. The results of these analyses failed to provide evidence that parameters from the duration reproduction task were related to discount rates in the temporal discounting task. However, the results also indicated that both behavioural measures were independently correlated to indices of cardiac activity. Specifically, there was a negative relationship between temporal discounting and mean heart rate, as well as relationships between the low-frequency (LF) and high-frequency (HF) bands of heart rate variability (HRV) and the exponent and scale parameters of the psychophysical functions for duration reproduction.

Study 3 was presented in Chapter 5 and addressed the specific hypothesis that factors known to alter time perception could, in turn, affect temporal decision making. This experiment focused on two candidate factors. The first factor was a similar caloric primary reward to that shown to physiologically affect time perception in Study 1. The second factor was average reinforcement rate, which has been proposed to proportionally affect time perception (Killeen & Fettermann, 1988; Section 1.2.2). As foraging tasks use timescales similar to those used in interval timing, Study 3 employed a foraging task similar to a patch-leaving task. In this task, subjects could choose to wait for randomly delivered monetary rewards, or stop waiting and expedite the next trial (equivalent to travelling to a new resource patch). To maximise rewards in this task, subjects should adopt a strategy that is a trade-off between the potential gains earned from waiting versus the potential losses forfeited by waiting (i.e. opportunity costs). In principle, this meant estimating an optimal target time at which to stop waiting.
50 participants were recruited and asked to fast for four hours prior to completing this task. Half of these participants consumed an extraneous (i.e. unrelated to the task) sweet, caloric solution in between blocks, while the other half consumed water as a control. By changing the distribution of reward frequency in alternate blocks, both groups of participants experienced different average rates of monetary reinforcement. The times at which participants stopped waiting were analysed as a function of each of these factors. The results showed that both of the experimental factors significantly affected when participants stopped waiting. Participants who consumed the caloric solution stopped waiting significantly earlier than those that consumed water. When participants experienced higher average rates of monetary reinforcement they also stopped waiting significantly earlier, regardless of whether they consumed calories or water.
6.2 IMPLICATIONS

This section discusses some general implications of the findings from all of the reported studies. This is divided into three subsections. The first subsection relates to the first main theme of this thesis: the relationship between reward and time perception. This subsection will examine the factors that were found to be related to the hypothetical pacemaker. This principally relates to Study 1, where the effect of primary rewards on time perception was directly investigated. It also relates to Study 2, which — while it did not directly investigate reward — examined whether time perception was associated with physiological arousal. The second subsection specifically discusses the empirical findings of Study 1 and Study 3 in terms of the dopamine clock hypothesis and will show that this framework does not appear to fully account for the results in both studies. The third and final subsection will focus on the role of time perception in temporal decision making, and in doing so will provide an interpretation that consolidates the empirical findings of this thesis.

6.2.1 Reward, arousal, and time perception. The idea that reward is linked to time perception has been reflected to different degrees in many different parts of the literature. For instance, one of the earliest and most popular models of time perception, the behavioural theory of timing (BeT), proposed that the rate of the hypothetical pacemaker is proportional to the rate of reinforcement (Killeen & Fetterman, 1988). More contemporary neurobiology has also highlighted the relationship between reward and dopamine (Schultz, 1998), and dopamine and time perception (Buhusi & Meck, 2002). Arousal is also intimately associated with reward and time perception. It has previously been proposed that arousal can be increased by the cumulative delivery of rewards (Killeen, Hanson, & Osborne, 1978), and it is also commonly affiliated with dopaminergic neurobiological mechanisms (McClelland,
Arousal has also long been related to time perception (Treisman, 1963), both psychologically (e.g. the effect of arousing images, Gil & Droit-Volet, 2012) and physiologically (e.g. an association with galvanic skin response, Mella, Conty, & Pouthas, 2011). Thus reward, arousal, and time perception have been shown to be closely associated.

The empirical findings of this thesis provided some support for the general notion that time perception is linked to reward and arousal. Study 1 showed that the consumption of primary rewards containing calories could lead to changes in temporal productions. Study 2 showed that cardiac indices of autonomic arousal were related to duration reproduction. If Study 3 is treated as an ecological time estimation task, then the consumption of caloric rewards and changes in average monetary reinforcement rate also affected time perception. This section aims to elaborate on the findings from Study 1 and Study 2, in relation to reward and arousal, respectively.

In the case of Study 1, underestimations of time were specific to the consumption of primary rewards containing calories. The results of this study showed no effects of the consumption of other types of primary and secondary rewards, nor any effect of the anticipation of any kind of reward. Given that both secondary rewards and cues that are predictive of upcoming rewards have been shown to affect dopamine responses (Mirenowicz & Schultz, 1994; Valentin & O'Doherty, 2009), it might have been expected that these would also elicit changes in time perception. Similarly, despite the robust finding that dopamine neurons respond to caloric rewards (Small, Jones-Gotman, & Dagher, 2003; Wang et al., 2014; Wise, 2006), the effect observed in Study 1 was not generally consistent with the dopamine clock hypothesis, where increases in dopamine should increase the rate of the pacemaker (Balci, 2014). This was also inconsistent with the general effects of arousal on time perception, which are also usually interpreted as a increase in pacemaker rate (Treisman, 1963).
Instead, the findings of Study 1 showed that the consumption of caloric primary rewards led to time estimates that were consistent with decrease in the rate of the pacemaker.

These inconsistencies raise questions about whether the consumption of caloric rewards is at all similar to a manipulation of reward or arousal, and suggest that calories themselves have a more specific effect that is qualitatively different from those previously explored in the literature. Given that the effects of caloric compounds — particularly glucose — have been noted elsewhere in reasonably separate areas of the literature (de Ataide e Silva et al., 2014; Gailliot & Baumeister, 2007; Orquin & Kurzban, 2016), the psychophysiological mechanisms of caloric effects merit some specific elaboration in order to provide an explanation of why calories could affect time perception in this manner.

Firstly, the results in Study 1 corresponded approximately with an experiment performed in rats, where carbohydrates were found to lead to underestimations of time in a peak-interval procedure (Meck & Church, 1987). Given that serotonin has been associated with later responses in production tasks (Sysoeva, Tonevitsky, & Wackermann, 2010; Wackermann, Wittmann, Hasler, & Vollenweider, 2008; Wittmann et al., 2007; see Section 1.3.4 for details), the authors of this study attributed their finding to the increased serotonin synthesis that occurs after the digestion of carbohydrates (Wurtman, 1982). While this would also seem to be a reasonable physiological explanation for the results of Study 1, the effect observed in the present experiments occurred in a timespan incompatible with the metabolism and synthesis of neurotransmitters as it takes 10-15 minutes for glucose to enter the brain after oral ingestion (Zourek, Jankovec, & Hykova, 2011). Thus, the results of Study 1 speak against this interpretation and instead suggest an alternative mechanism.
One possibility is that there are immediate behavioural effects of oral calorie detection even without digestion. Evidence to support this interpretation comes firstly from the exercise and physiology literature, where it has been shown that merely mouth-rinsing with carbohydrates increases exercise performance (for reviews, see de Ataide e Silva et al., 2014; Jeukendrup & Chambers, 2010; Painelli, Nicastro, & Lancha, 2010; Rollo & Williams, 2011). Given that the solutions are not ingested, they cannot have direct effects on performance in terms of energy supplementation. In these studies, the carbohydrate used to enhance performance is often maltodextrin, which is tasteless, thereby removing the possible confound of a taste-cue for energy intake (Carter, Jeukendrup, & Jones, 2004; Fares, Kayser, Fares, & Kayser, 2011; Lane, Bird, Burke, & Hawley, 2013). Moreover, mouth-rinsing with artificial sweeteners has been shown to have no effect on performance (Chambers, Bridge, & Jones, 2009), providing further evidence that actual caloric content is necessary to enhance performance. An fMRI study of the effect found that carbohydrate consumption was associated with increased neural activity in sensorimotor regions, as well as increased performance on a hand-grip task (Turner, Byblow, Stinear, & Gant, 2014). By measuring motor effort continuously and concurrently with a carbohydrate mouth rinse, it has been shown that increases in motor effort occur immediately upon orosensation (Gant, Stinear, & Byblow, 2010). Because of this, the effect is usually interpreted as a result of detection of calories in the mouth acting centrally to modulate brain areas associated with motivation (de Ataide e Silva et al., 2014; Jeukendrup & Chambers, 2010; Painelli et al., 2010; Rollo & Williams, 2011).

Section 1.4.2 discussed a number of studies that showed an association between motivational factors and time perception. Importantly, these studies demonstrated that higher levels of motivation affected time perception in a manner consistent with a decrease in pacemaker rate (Conti, 2001; Meade, 1959; 1963;
Rosenzweig & Koht, 1933). For example, using a temporal bisection procedure, Gable and Poole (2012) found that the durations of high-approach-motivation images (appetising food) were underestimated compared to images of other stimuli. These motivational effects have been explained by assuming a common and finite attentional resource for temporal and non-temporal information, and that motivation causes a reallocation of attention towards one’s current goals (Alonso, Brocas, & Carrillo, 2014; Buhusi & Meck, 2009; Zakay & Block, 1995). Thus, different fields of literature have independently shown that calorie detection can engage motivational mechanisms, and that motivation is associated with a decrease in pacemaker rate. These two points therefore provide a clear interpretation for the effect of oral calorie detection on time perception observed in Study 1.

The second area of literature to examine the effects of caloric compounds on behaviour relates to the ego depletion phenomenon and is largely separate from the sports and exercise literature. The ego depletion model proposed that capacity for cognitive control is a limited resource, and that as a result, self-control should be depleted after cognitively demanding tasks (Baumeister, Vohs, & Tice, 2016; Muraven & Baumeister, 2000). Given that it is a primary source of energy for the brain, it was also argued that this limited resource had a literal correspondence to blood-glucose levels (Gailliot & Baumeister, 2007; Gailliot et al., 2007). Studies initially supported the ego depletion claim (Muraven, Tice, & Baumeister, 1998) and also showed that this depletion of cognitive control could be rescued by glucose consumption (Gailliot et al., 2007; Scholey, Harper, & Kennedy, 2001). Similarly, researchers claimed that decreases and increases in blood-glucose levels could explain performance decrements and enhancements in these tasks, respectively (Dvorak & Simons, 2009; Gailliot et al., 2007; Scholey et al., 2001). However, these findings have attracted considerable skepticism and debate. The phenomenon of ego depletion
has been called into question by critique of the statistical inference used in these studies (Schimmack, 2012), by empirical work (Lange & Eggert, 2014; Lange, Seer, Rapior, & Rose, 2014), by meta-analyses (Carter & McCullough, 2014), and by multi-lab replication endeavours (Hagger et al., 2016). Moreover, there is some evidence of considerable individual differences in the enhancing effect of glucose on cognitive control (Kurzban, 2010), including that the effect is seen only in those individuals who have implicit beliefs in limited willpower (Job, Walton, Bernecker, & Dweck, 2013). There is also a lack of neurophysiological evidence for a relationship between glucose and cognitive control: glucose levels in the brain are, in general, not substantially affected by different behaviours (Kurzban, 2010) and there are many homeostatic factors that would confound a possible relationship between behaviour and glucose levels (Gibson, 2007; Kurzban, 2010). However, while it seems that peripheral or central blood-glucose levels may not be affected by the amount of cognitive control exerted by individuals, there is nonetheless evidence that glucose can indeed alter behaviours like self-control (even when not digested, Carter & McCullough, 2013; Molden et al., 2012; Sanders, Shirk, Burgin, & Martin, 2012), memory (Messier, 2004; Smith, Riby, Eekelen, & Foster, 2011), as well as a range of other behaviours (for review, see Orquin & Kurzban, 2016). One interpretation that has recently come to replace that of ego depletion is that calorie consumption causes a change in cognitive control via motivational factors (Botvinick & Braver, 2015; Hagger, Wood, Stiff, & Chatzisarantis, 2010; Inzlicht, Schmeichel, & Macrae, 2014; Molden et al., 2012), which parallels the interpretation given in the exercise and physiology literature. Given that these cognitive changes due to calorie detection are due to a motivational mechanism, the same interpretation may also apply to the effect of calorie consumption on time perception observed in Study 1.
In summary, these two independent streams of literature — exercise physiology and cognitive control — demonstrate that the orosensation of calories can affect both motor function and cognition via motivational mechanisms. Thus, they provide a reasonable basis for the interpretation that calorie consumption affects time perception via a similar motivational mechanism; potentially because of a decrease in pacemaker rate due to limited attentional resources (Alonso et al., 2014; Buhusi & Meck, 2009; Zakay & Block, 1995). If motivational effects can bias time perception in this way, it is perhaps surprising that Study 1 found no effects of reward anticipation (an effect of the predictive reward cue) on time estimates. One possible explanation relates to the fact that in the experiment participants received reward regardless of whether they were accurate in their estimates or not. While it was an important feature of the task in order to avoid possible confounds of strategic responding, the lack of contingency between performance and subsequent reward delivery meant that the cues were entirely non-instrumental, which may have meant that they were not sufficiently motivationally salient (Manohar, Finzi, Drew, & Husain, 2017). Overall, the results of Study 1 make two important contributions to the reviewed literature. Firstly, they extend the effect of calorie orosensation to the novel domain of time perception, which is involved in both motor function and cognition. Secondly, given the timescale of the effect and the lack of an effect for artificially sweetened solutions, the results of Study 1 speak against the possibility of direct neurotransmitter anabolism and instead provide additional evidence for the existence of an oral calorie detector that is independent of those that detect sweetness (e.g. Chambers et al., 2009; Molden et al., 2012). Finally, within the field of time perception, the results from Study 1 suggest that non-human animal research into time perception may benefit from avoiding caloric rewards in training, as this may implicitly bias behaviour (McMurray, Conway, & Roitman, 2017).
Apart from providing support for the idea of oral calorie detectors, the results of Study 1 do not speak any more directly to possible neural or physiological mechanisms that may facilitate the effect of calories on behaviour or cognition. However, one likely candidate relates to the autonomic nervous system and physiological arousal. It has been suggested that the taste of glucose innervates the vagus nerve (the main nerve of the parasympathetic nervous system; PNS; Anseloni, Ren, Dubner, & Ennis, 2005; Messier & White, 1987), causing an increase in HRV (Stockhorst, Huenig, Ziegler, & Scherbaum, 2011). Individuals with higher HRV have been shown to have better performance in behaviours that are affected by calorie consumption, for example self-control (Maier & Hare, 2017; Segerstrom & Nes, 2007) and memory (Clark, Naritoku, Smith, Browning, & Jensen, 1999). This suggests that the autonomic nervous system may play a facilitating role in the effect of calories on behaviour and cognition. More specifically, in terms of time perception, direct vagus nerve stimulation reduces the activity of the sympathetic nervous system (SNS; Clancy et al., 2014) which, in turn, underlies most measures of physiological arousal. As mentioned above and in the preceding chapters, physiological arousal has been shown to be associated with changes in time perception consistent with an increase in the rate of the pacemaker (e.g. Mella et al., 2011). Therefore the taste of glucose may also reduce SNS activity, which would be consistent with a reduction in pacemaker rate due to decreased physiological arousal.

More generally, higher baseline measures of HRV have also been correlated with better performance in both duration reproduction (Pollatos, Yeldesbay, Pikovsky, & Rosenblum, 2014) and temporal bisection tasks (Cellini et al., 2015), which supports the idea that higher PNS activity and lower SNS activity should lead to better
time perception. However, the results of Study 2 appear to conflict with this account. To recapitulate, Study 2 found negative correlations between the exponent parameter of the psychophysical function for duration reproduction and both LF-HRV and HF-HRV. HF-HRV is commonly used as an index of parasympathetic nervous system (PNS) activity (Berntson et al., 1997), thus the results of Study 2 suggested that individuals with higher PNS activity had more concave functions and relatively less accurate time reproductions. This result was surprising given that, on the basis of the existing literature, the opposite should have been expected.

One explanation of this finding would have been that these individuals with high HF-HRV also had relatively increased SNS activity, which would indicate increased physiological arousal and a faster pacemaker. Indeed, LF-HRV has previously been used as an index of SNS function (Berntson et al., 1997; Drucaroff et al., 2011; Dulleck, Schaffner, & Torgler, 2014) which would be consistent with this account. However, this interpretation of LF-HRV is highly controversial (Houle & Billman, 1999; Reyes Del Paso, Langewitz, Mulder, van Roon, & Duschek, 2013) as the origins of LF-HRV have been variously related back to either SNS activity (Malliani, Pagani, Lombardi, & Cerutti, 1991), a combination of SNS and PNS activity (Reyes Del Paso et al., 2013), baroreflex function (Goldstein, Bentho, Park, & Sharabi, 2011), and a central low-frequency oscillatory process (Cooley et al., 1998). Thus, the idea that higher LF-HRV is indicative of a faster pacemaker is problematic. In addition to this issue of physiological interpretation, data from the duration reproduction paradigm cannot clearly be interpreted from the perspective of a pacemaker-accumulator model (for a detailed critique as well as other issues with duration reproduction, see Glicksohn & Leshem, 2011). Specifically, it is not clear whether individuals rely on the same timing mechanisms for encoding and reproduction (Wiener, Matell, & Coslett, 2011), hence it is not possible to make
unambiguous inferences about the rate of an internal pacemaker when using a duration reproduction task. For example, an individual with a relatively slow pacemaker rate would exhibit this relative difference both in the encoding of the sample interval and during the reproduction of the interval, therefore this difference is likely to “cancel out”. Thus, differences between the sample interval and the reproduced interval could imply either a slower pacemaker rate during encoding or a faster rate during reproduction. Due to the issues with interpretation of both the physiological and behavioural measures in Study 2, it is difficult to explain why the results appear to contradict previous studies.

To overcome both of these issues, future experiments could employ different measures of time perception and sympathetic arousal. For example, temporal production and temporal comparison procedures can be interpreted from the pacemaker-accumulator perspective. Galvanic skin response (Boucsein, 2012), salivary alpha-amylase (Nater & Rohleder, 2009), cardiac pre-ejection period (Brenner, Beauchaine, & Sylvers, 2005), and pupil dilation (Bradley, Miccoli, Escrig, & Lang, 2008; de Gee et al., 2017), are popular and non-invasive measures of physiological arousal. An experimental design involving any of these measures may be able to more clearly assess the association between time perception and physiological arousal.

The other key finding of Study 2 was that the rate of temporal discounting was negatively correlated with mean heart rate: individuals with higher heart rates were more patient. In Chapter 4, it was predicted that temporal discounting would be associated with HRV. This was due to the neuro-visceral integration model, which proposes that differences in HRV are related to the state of a self-regulation network.
that spans across both the ANS and the central nervous system (Thayer & Lane, 2000; 2009). This model would imply that higher discount rates are associated with lower capacity for self-regulation and therefore lower HRV. Previous studies have shown, for example, that individuals with higher baseline HRV persist longer at a difficult anagram task (Segerstrom & Nes, 2007) and have better self-control in terms of dietary choices (Maier & Hare, 2017). The results of Study 2 did not support this model as no differences in HRV were observed as a function of discount rate. In fact, higher heart rates occur due to a lack of PNS cardiac inhibition, and thus the results of Study 2 directly conflict with the neuro-visceral integration model.

The finding that mean heart rate was negatively correlated with discount rates can be better understood in light of the low-arousal theory of impulsivity (Eysenck, 1967; 1993). This model posits that individuals with chronically low baseline arousal act impulsively in order to compensate for this hypoarousal. Previous studies have supported this by showing that individuals with lower resting heart rates have higher questionnaire-based impulsivity traits (Mathias & Stanford, 2003) and that individuals with lower levels of salivary alpha-amylase have higher discount rates (Takahashi, Ikeda, Fukushima, & Hasegawa, 2007; Takahashi et al., 2010). Our results also support this model as individuals with lower heart rates (low arousal) had higher discount rates.

One notable limitation of this aspect of Study 2 was that the ECG parameters were confounded with task performance — that is, the measures reflected a combination of cardiac signals during the performance of both tasks, rather than baseline cardiac activity or task specific activity. This is important both in terms of the neuro-visceral integration model and the low-arousal theory of impulsivity. For example, it has been shown that there are transient increases in HRV when expending self-regulatory effort, such as choosing to consume a healthy rather than unhealthy
In terms of the low-arousal theory, impulsive individuals have been shown to exhibit relatively higher heart rates when presented with a demanding attentional task (Mathias & Stanford, 2003). Similarly, after a stress manipulation, the negative association between salivary alpha-amylase and discount rates has been shown to reverse (Takahashi, Ikeda, & Hasegawa, 2008). The ECG measured across the entire experiment in Study 2 could not adequately assess whether there were any potential task-related changes in cardiac activity due to either the duration reproduction task or the temporal discounting task.

Future studies could address this limitation in two ways. Firstly, baseline and task-related measures of cardiac signals (or other measures of sympathetic arousal) could be disassociated in order to assess whether baseline heart rate or task-related heart rate are associated with discount rates. Secondly, an experimental manipulation of arousal could be introduced to assess its effects on physiological responses as well as temporal discounting (e.g. arousing images, Sohn et al., 2015).

To summarise this section, Study 1 provided evidence that rewards can affect time perception. However, this was specific to primary rewards containing calories and was not consistent with the suggested effects of dopamine or arousal on an internal pacemaker. Instead, this effect appeared to be closely related to the caloric effects noted elsewhere in the literature, that impact behaviour and cognition more broadly. These have been interpreted as due to a motivational mechanism that responds to calorie detection, which is consistent with previously reported effects of motivational states on time perception.
Study 2 provided some support for the idea that time perception is related to autonomic nervous system function. However, the results of this study conflict with results previously reported in the literature. Future studies will be required to investigate this discrepancy. Study 2 also failed to support predictions of the neurovisceral integration model, in that temporal discounting was not associated with HRV. However, a negative association between discount rates and mean heart rate was found, which provides support for the low-arousal theory of impulsivity. Both of the key findings of Study 2 provide a solid foundation for future studies that aim to investigate the physiological underpinnings of time perception and temporal decision making.

6.2.2 The dopamine clock hypothesis. One of the primary motivations for the investigations reported in this thesis was the dopaminergic link between reward and time perception. Thus, the reported results merit some discussion in terms of how they relate to the dopamine clock hypothesis. It is of course important to note that dopamine was not directly measured in any of the presented studies. However, as discussed in Chapter 1 and Chapter 2, there is good evidence that dopamine is involved in many of the processes examined in the empirical chapters.

To briefly recapitulate, Study 1 tested whether the anticipation or consumption of rewards affected time perception. Both reward predictive cues and reward consumption are known to elicit striatal dopamine responses (Mirenowicz & Schultz, 1994; Romo & Schultz, 1990; Schultz, 1998). This applies specifically to caloric primary rewards (Small et al., 2003; Wang et al., 2014; Wise, 2006) but also to secondary rewards like money (Valentin & O'Doherty, 2009). Study 2 examined the relationship between time perception and cardiac signals of sympathetic arousal. Dopamine is one of the primary neurotransmitters that has been associated with
arousal (McClelland et al., 1987; Robbins, 1997), although its specific relationship to the cardiovascular system is complex (Baum & Shropshire, 1973; Goldberg, 1972). (Given this complexity and because the data from Study 2 were not interpretable in relation to pacemaker rate, Study 2 will not be discussed in this section in much detail.) In addition to testing the effect of calorie consumption on temporal decision making, Study 3 manipulated average monetary reinforcement rate. Average reinforcement rate has been proposed to be encoded in the dynamics of tonic striatal dopamine (Niv, Daw, & Dayan, 2005; Niv, Daw, Joel, & Dayan, 2007). Thus, all of the experiments reported in this thesis have high relevance to dopaminergic mechanisms and can therefore contribute to the notion of a dopamine-dependent pacemaker.

In general, most pharmacological evidence has supported the idea that dopamine levels are proportional to the rate of the internal pacemaker (Abner, Edwards, & Douglas, 2001; Buhusi & Meck, 2002; Cevik, 2003; Cheng, Macdonald, & Meck, 2006; Cheng & Liao, 2007; Cheng, Hakak, & Meck, 2007; Cheung et al., 2006; Chiang et al., 2000; Drew, Fairhurst, Malapani, Horvitz, & Balsam, 2003; Lustig & Meck, 2005; MacDonald & Meck, 2005; 2006; Maricq & Church, 1983; Maricq, Roberts, & Church, 1981; Matell, Bateson, & Meck, 2006; Matell, King, & Meck, 2004; Meck et al., 2012; the exceptions to these findings will be discussed below). This is broadly consistent with the psychological factors that are associated with dopamine and the role of these factors in early models of time perception. For example, in Scalar Expectancy Theory (SET), pacemaker rate can be increased by arousal (Treisman, 1963) and in the behavioural theory of timing (BeT), pacemaker rate is proportional to reward rate (Killeen & Fetterman, 1988).
The results of Study 3 provide some support for this version of the dopamine clock hypothesis, given some assumptions about how subjects performed the task. The paradigm used in Study 3 was analogous to a continuous time patch-leaving task, in which there was an optimal time to quit waiting. For the purposes of this section of the discussion, quitting at this time can be viewed as a temporal production subcomponent with an optimal quitting “target time”. In the experiment, when the average monetary reward rate was increased, subjects responded earlier relative to the condition with lower average reward rates (i.e. they “overestimated” the target time). This can be explained as an increase in pacemaker rate due to the increased level of tonic dopamine encoding average reward rate (Niv et al., 2005; 2007; see below). Furthermore, it is also consistent with an increase in pacemaker rate due to increased reinforcement rate as described in BeT.

In Study 3, the consumption of calories, relative to water, also led to subjects quitting earlier and thus “overestimating” the target time. From the perspective of the dopamine clock hypothesis, this can be explained by an increase in pacemaker rate due to the dopamine release elicited by calorie consumption (Small et al., 2003; Wang et al., 2014; Wise, 2006). Importantly, this consumption of calories was unrelated to the performance of task. One assumption of BeT is that extraneous reinforcers — rewards not contingent on performance — should also increase the pacemaker rate (Killeen & Fetterman, 1988). Previous empirical studies have supported this, showing that when pigeons received extraneous rewards during the inter-trial intervals of a temporal discrimination task, their responses in the task were consistent with a faster pacemaker (i.e. more ‘long’ responses, Morgan, Killeen, & Fetterman, 1993). In essence, this meant that pacemaker rate appeared to be sensitive to the “global reinforcement context”, a proposition that was also supported by the results of Study 3.
Thus, both increased monetary reinforcement rate and the extraneous consumption of calories led to earlier responses in the experiment in Study 3. If this task is viewed as similar to a temporal production task, these results support the idea that increases in dopamine increase the rate of the internal pacemaker. However, one notable alternative explanation relates to the idea that changes in pacemaker rate could affect subjects’ perception of different delays inconsistently (Hills & Adler, 2002). If changes in pacemaker rate only affected subjects’ perception of the inter-trial interval (i.e. the “travel time”), then the results observed in Study 3 would be consistent with a decrease in pacemaker rate due to increased average reward rate and calorie consumption. However, animals have been shown to have difficulty incorporating post-reward delays like inter-trial intervals into their decisions (Blanchard, Pearson, & Hayden, 2013; Kacelnik, 2003; Kacelnik & Bateson, 1996; Pearson, Hayden, & Platt, 2010), thus it seems unlikely that a change in the representation of the inter-trial interval alone should affect behaviour in the manner observed in Study 3.

While the results of Study 3 appear to support the dopamine clock hypothesis, the results of Study 1 present some issues for the interpretation of the effect of calorie consumption on pacemaker rate. Study 1 found that time was underestimated after the consumption of calories, which is consistent with decrease in the rate of an internal pacemaker rather than an increase. This contrasts with the explanation that calorie consumption should increase dopamine (Small et al., 2003; Wang et al., 2014; Wise, 2006) which should in turn lead to an increase in pacemaker rate (Buhusi & Meck, 2002).

However, there are some exceptions to the canonical interpretation of the dopamine clock hypothesis that may provide a resolution to this discrepancy. Firstly, higher baseline attentional capacity has been shown to moderate the effect of
dopaminergic agonists on time perception in humans. Specifically, individuals with fewer attentional lapses have been shown to underestimate durations after consuming amphetamine, while individuals who have more attentional lapses overestimate intervals after drug consumption (Lake & Meck, 2013). The experimental paradigms in Study 1 and Study 3 differed substantially in their attentional demands. In Study 1, the temporal production procedure was reasonably undemanding, with only four possible target times. On the other hand, to maximise reward in Study 3 required constant attention to the variable timing of token maturation. Thus, one possible explanation for the different effects of calorie consumption in each experiment were differences in the attentional demands required in each paradigm. In light of this possibility, it would be of interest for future studies to assess individual differences in baseline attentional capacity in order to see if this is an important factor in how time perception is affected as a result of calorie consumption.

The same human study mentioned above also found that individuals who rated amphetamine as more enjoyable underestimated durations, whereas individuals who liked the drug less overestimated durations (Lake & Meck, 2013). This finding again rather neatly reflects the adage “time flies when you’re having fun”, but further suggests that the inverse phenomenon is true: “time drags if you don’t like amphetamine”. This was interpreted by the authors as a result of attentional resources being diverted away from temporal information and toward the hedonic aspects of the drug (Zakay & Block, 1995). In Study 1, the effect of caloric primary rewards was similar to the effect of amphetamine in individuals who reported enjoying the drug. One further explanation for the discrepancy between Study 1 and Study 3 is that in Study 1, the hedonic aspects of the caloric drink captured attentional resources, leading to underestimations of time, while in Study 3, the hedonic aspects of the drink
were ignored due to the demands of the foraging task. It would therefore also be of interest for future studies to assess whether the effect of calories on time perception differs between individuals depending on their enjoyment.

A final explanation relates to the perception of the context of caloric reward in the experiments. As mentioned above, it has been shown that pacemaker rate is sensitive to extraneous reinforcers delivered outside the context of the time perception task (Bizo & White, 1994; Killeen & Fetterman, 1988), which is consistent with the interpretation that irrelevant calorie consumption increased pacemaker rate in Study 3. Yet this is evidently inconsistent with the results of Study 1 if the primary rewards are also considered to be extraneous. However, while they were indeed not contingent on performance, reward delivery was much more tightly coupled to the experimental procedure. This was the case in an experiment performed by Bizo & White (1995), who also aimed to test how extraneous reinforcement affected pacemaker rate in pigeons. However, in their temporal discrimination task, instead of delivering these reinforcers passively during the inter-trial intervals, they incorporated a third response target (in addition to the ‘long’ and ‘short’ response targets) that would deliver reinforcers. There were a number of experimental conditions with different schedules of reinforcement on this third response. However, across almost all of these conditions, the results were opposite to the predictions of BeT: with higher rates of reinforcement from this third response target, pacemaker rates decreased. The authors interpreted this as evidence that “pacemaker rate is sensitive to the context for reinforcement”. The fact that these “extraneous” reinforcers were tightly coupled to the experimental procedure here may have altered how they were perceived in relation to the task at hand. Thus, the fact that caloric rewards were also tightly coupled to the experimental procedure in Study 1 (relative to Study 3) may have also resulted in a similar effect to that observed in this experiment.
There are a number of other factors that differed in these two experiments. For example, there were differences in the delivery of the liquids in each study. In Study 1, small volumes (0.5 - 2.3 mL) were delivered over a longer time scale, while in Study 3, larger volumes (75 mL) were delivered four times, in between blocks. These different schedules entailed differences in the timing of calorie consumption relative to the behaviour of interest, as well as the possibility for relatively longer-term metabolic effects of the calories in Study 3. Similarly, the precise nutritional makeup of the liquids were not identical (Study 1 did not employ a combination of aspartame and maltodextrin, although the concentration of maltodextrin in each study was equivalent). Furthermore, the total volume of liquid ingested in each study was not the same: participants in Study 1 consumed a total of ~160 mL of liquid, while in Study 3 participants ingested 300 mL of liquid. It is plausible that these differences could be responsible for the apparent differences in the results of the two studies, particularly if there exists a non-monotonic relationship between calorie consumption and time perception. However, it seems highly unlikely that such an apparent reversal of effects would be observed with such small differences in total volumes, relative to the ecological range of volumes of nutrient consumption. Other differences between the two studies include differences in the “target times” (Study 1 used target times from 2 - 5 seconds, while the optimal quitting times in Study 3 were 2.13 and 12 seconds), and differences in incentivisation (there was a monetary incentive in Study 3, while there was none in Study 1). In addition to the explanations provided above in the above paragraphs, any of these factors (as well as other unobserved factors) may explain why calories seemingly had opposite effects on the rate of the internal pacemaker. However, one further possible explanation relates more closely to how
time perception is computationally incorporated into temporal decision making. Considering that this was a key theme of this thesis, this explanation merits a more detailed discussion and will be presented in the latter half of the next section.

6.2.3 Temporal decision making and opportunity cost. The second main theme of this thesis related to the idea that temporal decision making operates on non-veridical time perception. Chapter 2 outlined two prominent models of temporal decision making — intertemporal choice and foraging — and showed how both of these rely on a representation of time. Study 2 and Study 3 independently used these respective models to test for evidence that non-veridical time perception informs temporal decision making. This section will first discuss the broad implications of the results of these studies in terms of this proposition. It will then more precisely discuss the role of time perception in temporal decision making and use the framework of opportunity cost to provide an explanation for the differing effects of calorie consumption observed in Study 1 and Study 3. Finally, these interpretations will be related to some broader literature regarding dopamine and the timing of behaviour.

Study 2 tested whether time perception was related to temporal decision making by assessing whether individual differences in duration reproduction were correlated with individual differences in temporal discounting. This study was motivated by previous theoretical work suggesting that non-linearities in time perception may be responsible for the hyperbolic shape of the discount function (Takahashi & Han, 2012) and previous empirical work that showed that individual differences in future time horizons were correlated with discount rates (Zauberman et al., 2009). However, Study 2 failed to provide evidence that psychophysical measures of duration reproduction and discount rates were related. Of course, absence of evidence does not constitute evidence of an absence. Indeed, the choice of paradigms
used in this experiment may explain why such a relationship was not observed. Specifically, the duration reproduction task (or indeed most other time perception procedures) captures an aspect of time perception that is distinctly different to the representation of time in temporal discounting. In temporal discounting, the representation of time is a prospective projection of delay, more similar to the prospective future time horizons measured in the previously mentioned study (Zauberman et al., 2009). Compared to a basic time perception task like concurrent rhythmic counting, the delay in temporal discounting is abstract and non-sequential. Similarly, the temporal discounting task used in Study 2 captured intertemporal preferences between timescales on the range of months, whereas the duration reproduction paradigm focused on sub-minute ranges. Thus, the time perception task and the temporal decision making task may have reflected aspects of time perception which have distinct and perhaps unrelated mechanisms. Paradigms that entail a more similar concept of time may be able to more straightforwardly relate individual differences in time perception to individual differences in temporal decision making. For example, foraging tasks similar to that presented in Chapter 5 operate using concurrent timing, on timescales commonly used in interval timing tasks. Likewise, experiential discounting tasks (Section 2.1.1) have reward delays in the range of seconds to minutes (e.g. Gregorios-Pippas, Tobler, & Schultz, 2009; Jimura, Myerson, Hilgard, Braver, & Green, 2009; Schweighofer et al., 2006). Future research seeking to investigate individual differences in time perception and temporal decision making could use these paradigms to maximise the chances of measuring a common time construct.

Study 3 tested whether factors that are known to affect time perception could also affect temporal decision making. In this experiment, two different factors were manipulated. Firstly, Study 1 identified that the consumption of calories could alter
time perception, thus Study 3 sought to test whether calorie consumption could also alter foraging behaviour. Secondly, Study 3 also tested whether different average reinforcement rates would affect temporal decision making, as pacemaker rate has also been shown to vary as function of this (Bizo & White, 1994; 1995; Fetterman & Killeen, 1991). A quote from Killeen and Fetterman (1988) was presented at the beginning of this thesis in Section 1.2.2, from their original article describing the behavioural theory of timing. This quote is reproduced here:

“A faster pacemaker due to higher overall rate of reinforcement means less residence time in any particular state and thus steeper delay of reinforcement gradients. It means that the amount of time an animal perseveres in any food patch or foraging activity will be related to the overall density of food in its environment.”

Firstly, this quote identifies the key assumption of BeT, that pacemaker rate is proportional to the rate of reinforcement (Killeen & Fetterman, 1988). Notably, this quote almost directly reflects the finding in Study 3, by contextualising the consequences of a higher pacemaker rate in a patch-leaving task. If the subjects in Study 3 were relying on an internal pacemaker to time their responses to stop waiting, then the finding that they responded earlier when monetary reinforcement rate was higher supports this assumption. The latter part of the quote also relates this increase in pacemaker rate rather ecologically to the “overall density of food”, which could be equated with the caloric drink offered to the subjects in between blocks of Study 3. As such, this quote captures the possibility that increases in both monetary reward rate and caloric “reward rate” contribute to an increase in pacemaker rate. Thus the results of Study 3 appear to generally support the idea that factors that are known to affect time perception can also affect temporal decision making. However, this interpretation is rather broad and does not adequately specify the exact role of time perception in
temporal decision making, nor does it relate to extant foraging models that might predict how changes in pacemaker rate should affect temporal decision making behaviour. Notably, this broad interpretation also appears to be inconsistent with the results of Study 1, where calorie consumption was consistent with a decrease in pacemaker rate. To more precisely understand the relationship between pacemaker rate and temporal decision making, as well as to explain the apparent discrepancy between the results of Study 1 and Study 3, the findings of these studies will be interpreted from the perspective of some of the models introduced in Chapter 2.

The marginal value theorem is considered to be the dominant foraging algorithm for deciding when to leave a patch (analogous to quitting in Study 3) and the key principle of this is that agents should leave a resource patch once their reward rate falls below that of the broader environment (Charnov, 1976). Chapter 2 noted that this requires two qualitatively different representations of time (Gibbon & Church, 1990), the time spent in a patch and the travel time (which approximately contribute primarily to the calculation of local reward rate and global reward rate, respectively). Hills & Alder (2002) showed how a change in pacemaker rate and the representation of time for either of these aspects should affect behaviour. The intuition behind their predictions is that if the representation of patch time is overestimated related to travel time, animals will underestimate their local reward rate. (To retain the notation used in Chapter 2, the local reward rate \( \frac{R}{P_p} \), will be underestimated if the representation of foraging time \( P_p \) is overestimated.) As a result, their estimate of local reward rate will fall below the global reward rate sooner and the animal will leave the patch earlier. The results of Study 3 — for both calorie consumption and higher reinforcement rate — are therefore consistent with either the duration of patch time being overestimated or the duration of travel time being underestimated. Arguably, the former interpretation makes more sense, as it is evident that changes in pacemaker rate
should affect the perception of elapsed time, but it is less clear that changes in pacemaker rate should affect the perception of prospective travel time, or the representation of previously learned travel times. This interpretation is also consistent with those provided in the section above and concords with the effect of reinforcement rate on pacemaker rate that BeT proposes. However, it remains inconsistent with the interpretation of the change in pacemaker rate due to caloric rewards reported in Study 1.

One alternative explanation assumes that agents track only a single global average reward rate, rather than both global and local reward rates (Niv et al., 2007). Because this long-term average reward rate quantifies the potential reward forfeited if an agent continues to forage in the same patch, it is equivalent to the opportunity cost of time. Notably, a decision algorithm that only estimates a single average reward rate is still consistent with the results of Study 3, and indeed this was the primary interpretation given in Chapter 5: both higher average reward rates and the caloric drink (as an ecological reward) would increase the opportunity cost of time and lead to earlier quitting times. However, if time perception is necessary for the estimation of this single reward rate, then the effect of non-veridical time perception on behaviour is different to that proposed above. In order for perceived opportunity costs and reward rates to be increased by monetary reinforcement and calorie consumption, then the rate of the pacemaker must be decreased. In other words, if the consumption of calories decreases pacemaker rate, the perceived rate of reward per unit time would increase, thereby increasing opportunity cost and leading to earlier quitting times. This possibility is therefore consistent with the result of caloric rewards observed in Study 1, where opportunity cost was not a determinant of time estimates, as well as in Study 3, in which opportunity cost was a key driver of decision behaviour. This
Another final interpretation can be made from the perspective of the training-integrated maximized estimation of reinforcement rate (TIMERR) model that was outlined in Section 2.2.3 (Namboodiri, Mihalas, Marton, & Shuler, 2014). To briefly review, this model similarly relies on the principle that reward rates determine the opportunity cost of time, and that this guides decision making. In TIMERR, however, the perception of reward rate relies not on the rate of elapsed time, but the time window over which past rewards are integrated. If this window is longer, estimated reward rates (opportunity costs) are lower and future delays will be better tolerated, while the converse is true if this window is shorter. Importantly, other models of time perception in temporal decision making implicitly take a perspective that time perception is independent and more fundamental than temporal decision making (Balcı et al., 2011; Bateson, 2003; Blanchard et al., 2013; Cui, 2011; Hills & Adler, 2002; Ray & Bossaerts, 2011; Zauberman et al., 2009). Therefore, temporal decision making is at the behest of non-veridical time perception. In contrast, TIMERR proposes that non-veridical time perception is generated as an epiphenomenon of decision processes, specifically the optimal representation of reward rate (Namboodiri et al., 2014). In TIMERR, if the window of past reward integration is longer, durations will be underestimated, while if the window is shorter, durations will be overestimated. Considering this, TIMERR makes predictions of how subjective time is represented on the basis of temporal decision making behaviour. TIMERR predicts that when average reward rates are high and stable, the window of past reward integration does not need to be long to accurately estimate reward rates (in the appendix of Namboodiri et al., 2014), thus tolerance to delay will be lower and
subjects should abandon waiting sooner. This is consistent with the behaviour observed in Study 3 when reward rates were relatively higher, and according to the model this would be commensurate with an overestimation of time (which was not measured). However, in Study 1, subjects were not engaged in a reward-based decision process. The dominant determiner of the window of past reward integration in this case might be the energy state of the agent. Because organisms with higher energy requirements cannot wait indefinitely for reward, TIMERR predicts that the window of past reward integration should be shorter in order to increase the organisms relative sensitivity to delay (also in the appendix of Namboodiri et al., 2014). As energy requirements were decreased by calorie consumption in Study 1, the window should be relatively longer, which should be commensurate with an underestimation of time. This is consistent with the observations of Study 1. However, the model does not quantify how the interaction of these factors should influence time perception and temporal decision making, thus it is not possible for TIMERR to predict the net effect on temporal decision making when energy requirements are manipulated concurrently during a reward maximisation task, as in Study 3. Thus, while TIMERR can account for the effect of calories on time perception observed in Study 1 and the effect of average reward rates on temporal decision making in Study 3, it does not make clear predictions about the effect of calorie consumption in Study 3.

The preceding paragraphs highlighted the importance of opportunity cost in determining temporal decision making behaviour, such as foraging. (Intertemporal choice has also been treated as an opportunity cost decision problem, e.g. Cools, Nakamura, & Daw, 2011; Daw & Touretzky, 2002.) From a normative perspective,
opportunity costs should affect not only temporal decision making behaviour, but should also generalise to the cost of time of all actions. This idea has been formally described in a neurocomputational model put forward by Niv et al. (2007), that proposes that average reward rates calibrate general behavioural vigour. In this model, average reward rate is encoded by tonic levels of dopamine in the striatum. An increase in tonic dopamine invigorates motor output, so that the force with which actions are performed is quicker, thereby offsetting temporal opportunity costs. This model has received considerable empirical support, both in terms of behavioural and neuroimaging experiments. For example, it has been shown that actions are performed with more vigour when average reward rates are higher (Guitart-Masip, Beierholm, Dolan, Duzel, & Dayan, 2011) and that this relationship can be strengthened by enhancing dopamine pharmacologically with L-DOPA (Beierholm et al., 2013). The encoding of average reward rate in levels of tonic dopamine has been also been supported by imaging experiments in humans (Rigoli, Chew, Dayan, & Dolan, 2016) and electrophysiological experiments in rats (Hamid et al., 2015).

The proposition that dopamine encodes average reward rate and invigorates behaviour is important for two reasons. Firstly, Section 1.4 detailed how dopamine related to the psychological constructs of reward and motivation, and the debate about which one of these constructs dopamine principally subserves (Bromberg-Martin, Matsumoto, & Hikosaka, 2010a). The opportunity cost model unifies dopamine’s role in both of these constructs: reward receipt and prediction elicit phasic dopamine responses (Montague, Dayan, & Sejnowski, 1996; Schultz, 1998; Schultz, Dayan, & Montague, 1997; Wise, 1980) which contribute to a tonic, average signal that controls the invigorating aspects of motivation (Berridge, 2007; Ikemoto & Panksepp, 1999; Robbins & Everitt, 2007; Salamone, Correa, Farrar, & Mingote, 2007)\textsuperscript{19}. Secondly,
by identifying reward rate with striatal dopamine, this model is also germane to the neuroanatomy and neuropharmacology of time perception as well as the dopamine clock hypothesis (Section 1.3).

Because opportunity cost is highly relevant to temporal decision making, it is of crucial interest to this thesis to understand how the tonic dopamine model of opportunity cost model relates to the dopamine clock hypothesis. In the preceding sections, there were a number of interpretations that already suggested a role of the pacemaker in opportunity cost. Fundamentally, these can be reduced to two mutually exclusive alternatives. The first treats opportunity cost as proportional (if not equivalent) to the rate of the pacemaker. This is consistent with the interpretation of pacemaker rate in BeT and studies that have shown that pharmacologically induced increases or decreases in dopamine speed or slow the rate of the pacemaker, respectively (Buhusi & Meck, 2002). The second perspective treats opportunity cost as being computed on the basis of subjective time, which results in an inverse relationship between reward rate and pacemaker rate (i.e. subjective time acts as the denominator in the estimation of reward rate). Given that the level of tonic dopamine encodes opportunity cost (and motivation), this perspective is supported by studies that have shown that motivational states are associated with underestimations of time (Conti, 2001; Gable & Poole, 2012) and optogenetic studies that have shown that activating or deactivating dopamine neurons decreases or increases the rate of the pacemaker, respectively (Soares, Atallah, & Paton, 2016).

Taken in combination, the empirical results reported in this thesis better fit the latter interpretation: an inverse relationship between reward rate (and dopamine) and pacemaker rate. Study 1 supported this by showing that — in a procedure that did not entail opportunity costs or motivational aspects — the consumption of calories (which has been shown to elicit dopamine responses, Small et al., 2003; Wang et al., 2014;
Wise, 2006) had an effect consistent with a decrease in pacemaker rate. Study 3 also supported this, as a decrease in pacemaker rate due to high reward rates or calorie consumption would increase perceived opportunity costs and therefore earlier quitting times. However, this perspective conflicts with BeT and with studies using pharmacological manipulations of dopamine to affect time perception, thus more research will be required to fully explain the relationship between time perception, temporal decision making, and dopamine.

Notably, Study 2 did not provide strong evidence for either of these perspectives. However, it is worthwhile mentioning that the above interpretation — that lower pacemaker rates lead to increased opportunity costs — is consistent with the low-arousal theory of impulsivity (Eysenck, 1967; 1993; given that arousal increases the rate of the pacemaker, Gil & Droit-Volet, 2012; Treisman, 1963). While standard temporal discounting tasks do not entail the same opportunity costs as in most foraging tasks, pharmacological dopamine manipulations have been shown to effect intertemporal choice in a manner consistent with an increase in perceived temporal opportunity cost (Pine, Shiner, Seymour, & Dolan, 2010). Thus, assuming that dopamine controls both opportunity cost and pacemaker rate, a testable prediction that would support the above interpretation is that individuals who underestimate time (i.e. who have slower pacemakers) have higher discount rates.

It is worthwhile noting that a range of behaviours have been shown to be affected by pharmacological manipulations of dopamine in a manner consistent with increased opportunity cost. For example, increasing dopamine has been shown to lead to greater temporal discounting (Pine et al., 2010), impulsive behaviour in other temporal decision making tasks (Moustafa, Cohen, Sherman, & Frank, 2008), increased motor vigour in terms of response times (Beierholm et al., 2013; Guitart-Masip et al., 2011), response force (Rigoli et al., 2016), and visual saccades (Haith,
Reppert, & Shadmehr, 2012). Additionally, there is some evidence that increasing dopamine can generally expedite cognitive processing: by measuring magnetoencephalography, the normal neural activity seen in response to novelty was accelerated after L-DOPA administration (Eckart & Bunzeck, 2013). Moreover, variation in some of these behaviours has been correlated within individuals. For example, individuals who have inherently higher saccade vigour have also been shown to exhibit steeper temporal discounting of reward (Choi, Vaswani, & Shadmehr, 2014). Similarly, after the administration of a dopamine antagonist, individuals who showed decreases in temporal discrimination accuracy also showed slower reaction times (Rammsayer, 1989). In sum, this collection of findings suggests that dopamine may play a key role in determining the timing of behaviour across a large range of different procedures and timescales.

Finally, the notion that pacemaker rate and opportunity cost are inversely related is consistent with the aphorism “time flies when you’re having fun”. This is also consistent with the interpretation of the result of Study 1 given in Section 6.2.1, where calorie consumption acts on a motivational mechanism and draws attention away from the processing of temporal information. Conversely, if pacemaker rate and reward rate are inversely proportional, this would also explain the finding that boredom is associated with overestimations of time (Danckert & Allman, 2005; Eastwood, Frischen, Fenske, & Smilek, 2012). Boredom susceptibility has also been associated with dopaminergic receptor sensitivity (Wiesbeck et al., 1996), which may provide a neurobiological explanation for this phenomenon, consistent with a dopaminergic encoding of reward rate and the inverse dopamine clock hypothesis. Some researchers have proposed that boredom fulfils a functional role, acting as an aversive signal that the current state is no longer rewarding, which in turn motivates the exploration of alternative behaviours (Bench & Lench, 2013; Geana, Wilson,
Daw, & Cohen, 2016). Importantly, boredom is known to predict a range of maladaptive impulsive behaviours including gambling, binge eating, and psychotic tendencies (Boden, 2009; Branković, 2015; Bruursema, Kessler, & Spector, 2011; Hopley & Nicki, 2010; Moynihan et al., 2015; Stickney, Miltenberger, & Wolff, 1999; Todman, 2003; Watt & Vodanovich, 1992). Given that time cues have been shown to affect ratings of hedonic experiences, even when these cues are manipulated (London & Monello, 1974; Sackett, Meyvis, Nelson, Converse, & Sackett, 2010), interventions that manipulate how time is perceived may provide a novel method of alleviating boredom.
6.3 LIMITATIONS AND OPEN QUESTIONS

This section will describe some general methodological limitations of the experiments presented in this thesis, and some of the open questions that future studies could address to further this line of research. Firstly, there is at least one general limitation that applies across all three studies reported in this thesis. Specifically, all the experiments in this thesis suffer from sampling bias, given that each sample population primarily constituted students from the University of Melbourne (Henrich, Heine, & Norenzayan, 2010). While there is no specific reason to suspect that any of the observed results would not hold over a more general population, some care should be taken in any generalisations. This is perhaps especially the case in regard to Study 2, as temporal discounting is known to vary with age (e.g. Green, Fry, & Myerson, 1994; Green, Myerson, & Ostaszewski, 1999) and the restricted age range of this study may have not captured the natural range of discounting present in the population.

There are also some general limitations regarding the choice of paradigm in each study. Ideally, the results observed in each study could generalise to different time perception and temporal decision making paradigms. However, as described in Section 1.1 and Section 2.1, variations in both time perception and temporal decision making paradigms often lead to differences in behaviour, and subtle differences in these paradigms may alter the interpretation of any observed results. For example, the temporal production task used Study 1 required that subjects held a previously learnt internal reference of the tested target times. It is a possibility that the consumption of calories may have not affected the produced time, but rather the internal reference itself, which would drastically alter the interpretation of the results observed in Study 1. This possibility is unlikely for the specific instantiation of temporal production used in Study 1, as subjects had to wait for the full interval after their production and
the internal reference would have been updated on every trial. However, in general, it would be valuable to assess how calorie consumption affects time perception in other measurement procedures, such as temporal comparison, which is related to the judgement of elapsed time, rather than elapsing time.

More practical limitations also constrained some of the design choices in the studies. For example, the volumes of liquid rewards used in Study 1 and in Study 3 was kept reasonably small to avoid issues with satiety (e.g. Minamimoto, La Camera, & Richmond, 2009; Valentin, Dickinson, & O'Doherty, 2007). However, it would be of interest to assess whether the devaluation of caloric rewards would abolish the reported effects. This could simply be tested by using larger reward volumes, or perhaps higher calorie concentrations (see below). Likewise, the range of delays employed in Study 3 were chosen to maintain similarities to the timescales used in typical interval timing experiments and to ensure a sufficient number of trials. However, ecological foraging times are substantially longer and it may be possible to test whether energy-budget or reward rate manipulations would affect foraging behaviour over these longer timespans.

Given the emerging consensus that calorie detection can affect cognition and behaviour quite widely, future studies should aim to better characterise the specific qualities and features required for the observed effects. For example, Study 1 manipulated caloric reward magnitude with adjustments of liquid volume. This suggests an extension which manipulates caloric concentration rather than overall volume. Given that Study 1 only found dose-dependent effects on time estimates for fruit juice and not maltodextrin, it would be of particular interest to test whether greater concentrations of maltodextrin might elicit a dose-dependent effect. There have been some preliminary investigations in this line of research in the exercise and physiology literature, but there is conflicting evidence regarding whether the
concentration, or even duration of oral exposure to calories can alter the observed effects on motor effort (Devenney, Collins, & Shortall, 2016). Presuming that the mechanisms of the effect of calories on time perception and motor effort are similar (which they may not be), it may be more efficient to use the short, perceptual effect on time as a model, rather than the longer-term, motor effect (which is presumably subject to confounds like fatigue).

Relatedly, it is possible that other biologically valuable compounds may also alter time perception. Similar results to those of Study 1 were found in a study with rats (Meck & Church, 1987). In this study, nutrients other than carbohydrates were tested (e.g. lecithin and casein). The authors in this study proposed that these different nutrients affected the anabolism of different neurotransmitters and subsequently increased their concentration in brain areas important for timing (e.g. in the case of carbohydrates, an increase in serotonin synthesis). While the short timescale of the calorie effect observed in Study 1 argues against such a direct anabolic mechanism, it is plausible that conditioned metabolic responses to taste (i.e. cephalic phase responses, Power & Schulkin, 2008) may anticipate the increase in neurotransmitters and utilise these in greater concentrations ahead of time. Thus, it would be of interest to perform a more exhaustive test of different nutritional substances (as in this non-human animal study), to investigate this potential mechanism of action.

It has previously been reported that glucose ingestion can reduce temporal discounting (Wang & Dvorak, 2010; Wang & Huangfu, 2017), however isocaloric sugars (Wang & Huangfu, 2017) and fructose (Luo, Monterosso, Sarpelleh, & Page, 2015) do not appear to have this effect. To investigate whether the effect of calories in the reported experiments are specific to glucose (potentially due to processing in the insulin pathway), a test of these substances would be useful and straightforward. Similarly, the manipulation of energy-budget in Study 3 used both caloric content and
sweetness. Given that a previous study found that an artificially sweetened placebo could reduce discount rates (Kuhn, Kuhn, & Villeval, 2017), it would also be valuable to disassociate the sweet and caloric aspects of the energy-budget manipulation in Study 3.

An important limitation of Study 2 was the fact that none of the observed results were predicted by the review of the literature. While there are existing frameworks that are consistent with these results (at least for the association between temporal discounting and heart rate), these results should be treated as exploratory and would benefit from independent replication. As such, it is important that additional confirmatory research can investigate these findings more thoroughly in the future. As mentioned above, it would be ideal to extend this experiment in a number of key ways. Firstly, the time perception task and temporal decision making task could be designed to entail more similar time scales. The easiest way to do this would be to employ a temporal production or temporal bisection task (which could be interpreted from the perspective of a pacemaker-accumulator model), and either a patch-leaving task or an experiential discounting task (e.g. Schweighofer et al., 2006). Secondly, future studies could employ additional measures of sympathetic arousal, such as galvanic skin response (Boucsein, 2012), salivary alpha-amylase (Nater & Rohleder, 2009), cardiac pre-ejection period (Brenner, Beauchaine, & Sylvers, 2005), or pupil dilation (Bradley, Miccoli, Escrig, & Lang, 2008; de Gee et al., 2017). Thirdly, these could be measured during a baseline rest period, as well as during task performance. Finally, in addition to correlational analyses, future studies could benefit from experimental manipulation of arousal, for example by using images of attractive faces, in order to test the effects of arousal reactivity on time perception and temporal decision making (e.g. Sohn et al., 2015).
Another paradigmatic limitation relates to the specific instantiation of the patch-leaving task in Study 3. In Study 3, the reward delay distributions were chosen on the basis of an existing study (McGuire & Kable, 2012). One important aspect of the findings in Study 3 was that calorie consumption decreased quitting times regardless of whether this was optimal in terms of reward maximisation. It has previously been argued that the effect of opportunity cost on behaviour is likely to be a Pavlovian effect that “is not formally advantageous” (Rigoli, Chew, Dayan, & Dolan, 2016) and that it is an inflexible response which may not optimise behaviour in some contexts (Swart et al., 2017). In particular, it is possible that our reward delay distributions (timing environments) were not perfectly representative of ecological reward timing distributions. If humans and other animals are adapted more closely to different, ecological distributions of reward delays, this might explain why apparently maladaptive behaviour was observed. Thus, another noteworthy idea that relates to Study 3 is to more widely investigate different reward timing distributions. In particular, it would be interesting to emulate the delay distributions of rewards in ecological settings. Conversely, it may also be interesting to investigate how agents adapt to new foraging environments, by assessing how individuals learn entirely novel, non-ecological reward delay distributions.

A more extensive characterisation of how subjects behave in different timing environments might also shed light on an interesting finding in the foraging literature. In the marginal value theorem, agents should only be sensitive to the mean travel time between patches (the inter-trial interval in Study 3). However, empirical studies have shown that pigeons leave patches early when only the variance of travel times is increased (Kacelnik & Todd, 1992). These same studies have shown that animals are more sensitive to more recently experienced travel times (Kacelnik & Todd, 1992; Todd & Kacelnik, 1993). By systematically varying the statistics of the reward delay
distributions and the inter-trial interval in a patch-leaving task like that in Study 3, it
should be possible to fully characterise which aspects of these temporal statistics best
impacts behaviour. Indeed, this avenue of research would be similar to the
characterisations of variable-interval schedules of reinforcement used in traditional
operant conditioning research (Bradshaw, Szabadi, & Bevan, 1976; Herrnstein, 1964),
but framed in a dynamic foraging context.

The interpretation provided in the above section pointed to two possible
models for how pacemaker rate should relate to opportunity cost and therefore for
how time perception should relate to temporal decision making. Notably, only Study 2
measured both time perception and temporal decision making, and methodological
limitations (as well as null findings) meant that the results of this study did not inform
this interpretation. A clear extension to Study 3 that could more definitely address this
research question would be to characterise individual differences in foraging
behaviour in order to compare these to independently acquired time perception
measures. The results of such an experiment would more clearly indicate whether
slower pacemakers are associated with a higher perception of opportunity cost and
impulsive behaviour. Indeed, individual differences in temporal persistence in the
foraging task would be of interest on their own merit. For example, it has previously
been shown that gambling-related beliefs and the frequency of gambling are
associated with individuals’ behaviour in a patch-leaving task (Addicott, Pearson,
Kaiser, Platt, & McClenon, 2015). However, given that homeostatic factors appear to
influence how long participants will wait, such investigations would have to provide
tight control over participant satiety in order to elicit stable temporal preferences. One
possible starting point for this would be to employ a relatively stable reward delay
distribution, for example, an exponential distribution, which would have a uniform hazard rate. Given that stable preferences can be elicited, these could be explored as a potential clinical marker or behavioural phenotype for impulsivity.

An alternative extension of Study 3 that would also clarify whether pacemaker rate is inversely proportional to opportunity cost, would be to nest a time measurement procedure within the patch-leaving task. For example, it would be possible to elicit a temporal estimation for the duration of a “trial” in the patch-leaving task. Doing this for a subset of trials would provide a closer assessment of the relationship between opportunity cost and time perception, without relying on the stability of behaviour.

Beyond extensions to the experiments reported here, the framework suggested by these results may also apply more widely. One interesting line of inquiry would be to assess time perception in real-world conditions that vary in the richness of available reward. For example, locations like casinos or supermarkets are designed with a high density of reward cues, which may increase individuals perception of opportunity cost in these environments. The findings of this thesis suggest that time should be underestimated in these environments, relative to more neutral settings (see Noseworthy & Finlay, 2009). If this hypothesis is vindicated, this would provide a useful framework to understand how impulsive behaviour might be facilitated by the design of real-world environments.

A more conclusive test of the relationship between pacemaker rate, opportunity cost and dopamine would naturally entail direct neurotransmitter measurements. However, the direct measurement of striatal dopamine in healthy humans is not feasible given the invasiveness of electrophysiological recordings. This could however, be done non-invasively, for example, via the proxy of spontaneous
eye-blink rate (Karson, 1983; Taylor, 1999). Dopamine could also be measured indirectly, by observing BOLD activity in the striatum. Either of these measures would complement any of the potential future studies outlined above.

In summary, the findings reported in this thesis support a research program that attempts to unify the understanding of time perception and the understanding of decision making processes. In terms of the wider literature presented in this document, this seeks to demonstrate how the fundamental dimension of time is exploited by reward-seeking organisms, as well as how this dimension is measured by organisms in the first place.

Overall, the novel findings reported in this thesis add to this in a number of ways. Firstly, they show a robust association between time perception and physiological factors, supporting previous suggestions that the mechanisms underlying our perception of time are sensitive to homeostatic processes (Craig, 2009a; Wittmann, van Wassenhove, Craig, & Paulus, 2010). Why would it be the case that time perception is sensitive to these factors? One of the crucial functions of perceived time is to control the organisation of energy intake and expenditure (Park, Pagnini, Reece, Phillips, & Langer, 2016). Thus, it may be the case that energy levels and metabolic state inform our sense of time and thus our fundamental perception of the world.

Secondly, the findings reported here contribute to the understanding of how time perception is involved in temporal decision making, and suggest that organisms may modulate their sense of time in response to reward in order to maximise reward gain. This line of reasoning can be traced back to models like the behavioural theory
of timing (Killeen & Fetterman, 1988) and foraging theory. One implication is that
differences in our perception of time may be an epiphenomenon of reward-seeking
and reward-processing. In demonstrating the importance of energy levels and
experienced reward rates on temporal decision making, these findings create a bridge
between the traditionally separate literatures of behavioural ecology and
reinforcement learning.

Finally, the results of this thesis were interpreted both in terms of models of
temporal decision making and models of time perception. In consolidating these
models, the results reported here provide a novel interpretation of how time
perception is computationally incorporated into temporal decision making processes,
and shed light on the nature of a hypothetical pacemaker of time perception.
Conference presentations


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Notes

1. Treating the PSE of psychometric curves as an estimate of the arithmetic mean of the references is not an ideal model, as there is more timing uncertainty for longer intervals, and confounding influence from decision processes (García-Pérez, 2014).

2. While memory seems critical to temporal processing, models without explicit memory representations have been proposed (e.g. Eisler, 1975). However, there is some evidence that suggests that working memory capacity is related to time perception accuracy, which implies that memory is indeed relevant to the timing mechanism (Broadway & Engle, 2011).

3. Another biologically plausible feature of the opponent Poisson model is that multiple integrator populations could sequentially feed into one another, which could reproduce target times at arbitrarily long time scales (Simen et al., 2011b).

4. Although it should be noted that there are other, recent drift-diffusion models of interval timing (Luzardo, Ludvig, & Rivest, 2013; Rivest & Bengio, 2011).

5. This is also the “evening wake maintenance zone”, a point in time at which dopaminergic arousal must account for the effect of darkness on circadian rhythm (Barbato et al., 2000).

6. Differences in heart rate variability have been related to the state of a self-regulation network that spans across both the ANS and the central nervous system (Benaroch, 1993). According to the neuro-visceral integration model (Thayer & Lane, 2000; 2009), this network facilitates physiological, cognitive, and behavioral adaptability to environmental change, and predicts that HRV is positively associated with these regulatory functions.
7. This normalisation is accompanied by an increase in gamma frequency power in anterior cingulate, supplementary motor area and left prefrontal cortex (Wilson, Heinrichs-Graham, White, Knott, & Wetzel, 2013), all areas previously implicated in time perception.

8. A similar effect is also seen in bats (Kössl & Vater, 1989).

9. Psychologically, dopamine activity in the striatum appears to mediate the affective craving experienced in drug dependence and addiction (Volkow et al., 2006; Wong et al., 2006), although some researchers argue that dopaminergic processes do not necessarily engender affective responses corresponding to “wanting” or “liking” (Nicola, 2016).

10. There are some accounts which attempt to reconcile these ramping signals with the standard temporal difference learning model (e.g. Gershman, 2014).

11. Foraging theory also deals more generally with other issues that a foraging agent must face, such as optimal diet choice, optimal patch choice, and optimal movement (Pyke & Pulliam, 1977). Given the nature of this thesis, I focus solely on optimal departure time from resource patches.

12. If given simultaneous binary choices between different sequences (multiple trials) of delayed or immediate consumption, subjects often prefer increasing values over time, in some cases even when the total value of a decreasingly valued sequence of rewards is larger (Hsee, Salovey, & Abelson, 1994; Loewenstein & Prelec, 1992). This has been difficult to reconcile with the interpretation of temporal discounting in single choice tasks.

13. There are a number of other “anomalies” in temporal discounting, such as the ‘sign’ effect (Hardisty, 2011), and the magnitude effect (Andersen, Harrison, Lau, & Rutström, 2013). A review of these can be found in Loewenstein and Prelec (1992).
14. This group have also provided a richly detailed review of time perception and intertemporal decision making (Namboodiri, Mihalas, & Shuler, 2014).

15. This idea has at least a superficial similarity to eligibility trace models of reinforcement learning (e.g. Bogacz, McClure, Li, Cohen, & Montague, 2007).

16. While there is no universal model for risk-sensitive foraging, a variety of models have been developed that include parameters such as the normal energy intake and expenditure of an animal, the size of its energy stores, its natural life horizon, as well as environmental factors that may constrain energy intake, such as seasonality and the day/night cycle (McNamara & Houston, 1992).

17. There were two participants who were excluded from the analysis in Study 3, on the basis that they made no quitting decisions in either distribution, and this was taken as a sign that they did not follow instructions, or were not able to perform the task correctly. Both of these participants were in the water (control) condition. For transparency, the frailty analysis of calorie consumption versus water consumption on quitting times is reported here with these two subjects retained. The effect of the heavy-tailed timing environment remained significant ($\beta = 1.45$, $s.e. = 0.05$, $z = 27.8$, $p < 0.001$), with a hazard ratio of 4.27 ($CI = 3.86 - 4.73$). The effect of the caloric reward also remained significant ($\beta = 2.31$, $s.e. = 0.06$, $z = 38.34$, $p < 0.001$), with a hazard ratio of 10.12 ($CI = 8.99 - 11.39$). The interaction effect between the heavy-tailed timing environment and the caloric reward also remained significant ($\beta = -0.51$, $s.e. = 0.07$, $z = -7.71$, $p < 0.001$), with a hazard ratio of 0.6 ($CI = 0.53 - 0.68$). Thus, the results are robust even when these subjects are included in the frailty analysis.

18. While the above result constitutes a partial replication of previous studies that employed similar paradigms (McGuire & Kable, 2012; 2015), one possible inconsistency should be noted. As in the above study, McGuire & Kable (2012)
determined reward delay times from two different distributions, a uniform distribution and a heavy-tailed pareto distribution. In their paradigm, the maximum possible reward under the optimal policy was higher when delays were drawn from the heavy-tailed distribution, as was the case in Study 3. In line with the results reported in Study 3, McGuire and Kable (2012) found that participants waited less long when delays were drawn from the heavy-tailed distribution. However, unlike in the present study, participants earned more overall reward in the uniform, rather than the heavy-tailed condition. Similarly, in McGuire and Kable (2015), the distributions were engineered to encourage either low persistence or high persistence. However, here both the best possible reward rate and the experienced reward was higher in the high persistence condition. Thus, the interpretation that quitting times were calibrated by overall experienced reward rate (or even overall potential reward rate) might appear inconsistent with these previous studies. While it is possible that methodological differences may be the source of this discrepancy (e.g. length of blocks, experience with the task, experiencing one or both distributions), it is more likely that there were differences in how reward rate was calculated in each case. McGuire and Kable (2012) do not explicitly report reward rates, but rather total earnings for each distribution. Thus to infer reward rate, this must be divided by the total block length. As noted in the manuscript, the variable of interest in Study 3 was perceived reward rate and its effect on each quitting decision. Global reward rate was not of interest, as a subject could not have knowledge of rewards or delays that they were going to experience in the future. Thus, as stated in the manuscript, the metric used was the cumulative reward divided by the cumulative time spent on task (including the intertrial intervals), at each decision point. Consequently, this measure will differ from the global reward rate, and will be weighted toward periods of higher discrete reward intake. While this measure is therefore an imperfect reflection of global reward rate, it
better captures subjectively perceived reward rate, especially given the finding that animals tend to underweight the periods of time in between rewards (Kacelnik & Bateson, 1996; and see Section 2.2.3). It is worthwhile noting that, in Study 3, total earnings were not significantly different between timing distributions, thus an analysis using total earnings would not have demonstrated differences in overall reward rate.

19. There has also been some work extending the above model to aversive outcomes (Dayan, 2012; Nord et al., 2017), and it has been proposed that serotonin may play a role opposite that of dopamine, instead responding to aversive events and inhibiting impulsive behaviours (see Cools et al., 2011; and Doya, 2002). This accords with the pharmacological effects of serotonin on time perception (e.g. Wittmann et al., 2007), and temporal decision making (e.g. Katsuhiko Miyazaki, Miyazaki, & Doya, 2017; Schweighofer et al., 2008).


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