

Should I Stay or Should I Go? Human studies of foraging for reward

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Summary

Foraging behaviour is thought to be ubiquitous across the animal kingdom. Animals must typically integrate complex information to decide how long to exploit a 'patch' of resources before leaving to forage for other, more worthwhile, patches. Optimal Foraging Theory predicts how an animal should behave as a function of the travel time between patches, and the resources available within each patch. In humans, foraging theory has been applied in multiple domains – from information foraging accounts of selective attention, to value-based choices in executive function. In this research, I asked whether human foraging for reward adheres to the predictions of Optimal Foraging Theory developed in non-human animals. Participants in this task determined how long to remain in a patch of exponentially decreasing rewards (dwell time), based on a predetermined delay (travel time) prior to each patch. Across four experiments, I showed that: (1) individuals exploit resource-rich patches for longer periods of time when they follow greater versus shorter delays; (2) dwell times are based on the mean travel time of the environment, rather than patch-specific delays; and (3) dwell times are unaffected by the variance or (4) volatility of delays within each environment. Overall, these findings are consistent with the predictions of Optimal Foraging Theory, and indicate the generalisability of this theory to human decisions. This study paves the way for further research into the components of choice behaviour that may be pathologically altered in patients with disorders of motivated decision-making, such as Parkinson's disease.

This work has not been submitted for a higher degree to any other university of institution. The thesis is my own composition and all sources have been acknowledged. Ethics Committee approval has been obtained (5201300103).

A handwritten signature in black ink, consisting of a stylized 'A' followed by a horizontal line and a dot.

Should I Stay or Should I Go? Human studies of foraging for reward

Chapter 1: Introduction

When should we move on to greener pastures? Not unlike animals foraging for food, humans constantly make decisions determining when they should stop and move on to what lies next: looking for cheap petrol as the tank nears empty; working extensively on a project when there is another deadline to meet; choosing which checkout line to join at the grocery store; or determining which jobs to apply for given their benefits and drawbacks. This type of decision-making underlies foraging. Foraging is typical in ecological studies of animal behaviour where animals forage for food in a patchy environment, and have evolved to optimise their reward intake when foraging. This phenomenon is consistent across the taxa. How do animals optimise their foraging behaviour? When do they determine when to stop exploiting the patch they are currently in and move on to explore the environment?

In this chapter, I will outline theories of foraging behaviour within the context of behavioural ecology, and theories of optimal foraging that have been developed. I will then consider the way in which optimal foraging theory has been applied to humans to model human decision-making in foraging-type tasks.

Optimal Foraging Theory

From the 1960s, behavioural ecology was centred on understanding the behaviour exhibited by animals to maximise their reward intake. This foraging phenomenon was observed across the taxa, and raised the question of how animals adapt their foraging behaviour to the demands of the environment. In particular, a key question was whether animal behaviour conformed to that of an optimal forager.

Although several accounts of optimal foraging behaviour had emerged, the observed behaviours perceived to be optimal were based on species-specific observations of foraging behaviour in certain environmental contexts. Therefore, there was disparity concerning the foraging behaviours deemed to be optimal which is attributable to the differences among species, in particular: the way in which an animal transports itself by flying, swimming, walking, or running; whether the diet requirements involved capturing prey or searching for seeds; the availability of food, and whether it was scarce or plentiful; and whether the environment had seasonal constraints, such as extreme cold or heat. Thus, optimal foraging behaviour was attributed to a wide array of factors. Consequently, the foraging behaviour that was deemed to be optimal for one species would not be optimal – or even possible – for another species. For example – and perhaps intuitively – predatory animals that hunt their prey in large groups behave markedly different to animals foraging for food while at risk of predation.

Although the elements thought to comprise optimal foraging behaviour were predominantly disparate, there was some consistency in the observational accounts of foraging behaviour; which allowed for a general model of optimal foraging to be developed.

The General Model of Optimal Foraging Theory

Optimal foraging models are established on the basis that an animal aims to maximise the net reward gained. The general model of optimal foraging states that an animal's behaviour is best described according to three assumptions that the animal must

make: decision assumptions, currency assumptions, and constraint assumptions. Decision assumptions refer to the type of choice to be made by the animal, and generally consist of the animal deciding: which prey to consume, when to leave a patch, and where food is located within the environment (Stephens & Krebs, 1986). Currency assumptions refer to the evaluation of the costs (time or delays) and benefits (rewards) associated with a choice, and the rate or amount of reward to be gained. Further, it is assumed that the animal seeks to maximise its gains and minimise the associated costs. For example, when making a choice, an animal has to consider the amount of reward to be gained by spending a certain amount of time waiting for the reward. Constraint assumptions are the factors that limit and define the relationship between the currency and the decision variables (Stephens & Krebs, 1986). These factors assume that: a predator searches and exploits patches exclusively and cannot exploit a patch while in the process of searching for a new one; patches are encountered sequentially and randomly; and the foraging predator behaves as though it knows all the information relevant to exploring and exploiting its environment (Stephens & Krebs, 1986). Together, these assumptions provide a framework for which the optimisation of foraging behaviour, as exhibited by animals, can be systematically described.

A seminal paper in the literature (Schoener, 1971) comprehensively reviewed optimal foraging theories developed at the time. This paper outlined the factors integral to determining what comprises optimal foraging behaviour, which include the expenditure of energy, as well as the time required, for the pursuit, handling, and consumption of prey (Schoener, 1971). Further, optimal foraging is determined by the caloric content of food, the abundance of food, and the size of prey relative to that of

the predator, as the predator is thought to forage optimally when it maximises the net energy (or reward) intake. Despite the comprehensiveness of Shoener's (1971) review of optimal foraging theory, the temporal factor pertaining to the optimal feeding period was noted as being an important component in foraging theory; however a formal theory had not yet been proposed.

The Marginal Value Theorem

The optimal time when a predator should leave a reward patch to explore the environment had not yet been investigated when Shoener (1971) compiled and reviewed the evidence for optimal foraging behaviour in animals. An important contribution to optimal foraging theories that addressed this unexplored area was provided by the proposal of the Marginal Value Theorem (MVT) by Charnov (1976). This theorem directly addressed the temporal factor involved in determining the optimal point at which an animal decides to finish exploiting its current patch to move on and explore the next patch. It is important to note that the MVT predicts optimality in foraging by considering the average time an animal will spend traveling to different patches in an environment, and the average rate at which the patch resources are depleted in an environment. To this end, the MVT predicts optimal foraging behaviour based on the average delays and rewards within an environment.

Charnov's (1976) model of the MVT is such that the foraging environment contains resources clustered in individual 'patches,' which a predator needs to spend time travelling between and within. The key question, which the MVT attempts to model, is how long predators will exploit a current patch before moving on to the next.

Specifically, the MVT has three assumptions:

- 1) Decisions made by the animal are done so as to maximise the net rate of energy intake (Charnov, 1976).
- 2) If the environment is comprised of different types of patches, the patches are randomly distributed throughout the environment.
- 3) The rate of energy intake (reward gained) for a patch decreases as the amount of time the predator spends in that patch increases, as the predator diminishes the availability of resources to itself (Charnov, 1976).

For example, when a foraging predator first enters a patch, the rate at which reward (food) is gained is rapid as the resource (food) is readily available (Figure 1).

However, as time progresses the rate at which the predator gains reward gradually decays as the resources within the patch are depleted. The MVT states that the optimal amount of time that the predator should spend exploiting a particular patch depends on both the mean reward rate of that environment, and the time that the animal has spent travelling to reach patches within that environment. Thus, the optimal point at which an animal should leave the patch it is presently in is when the rate at which rewards are gained drops to the average rate for the environment (Charnov, 1976). A corollary of the MVT is that an animal should spend longer exploiting a patch which follows a longer travel time, or which is associated with a slower reward rate.

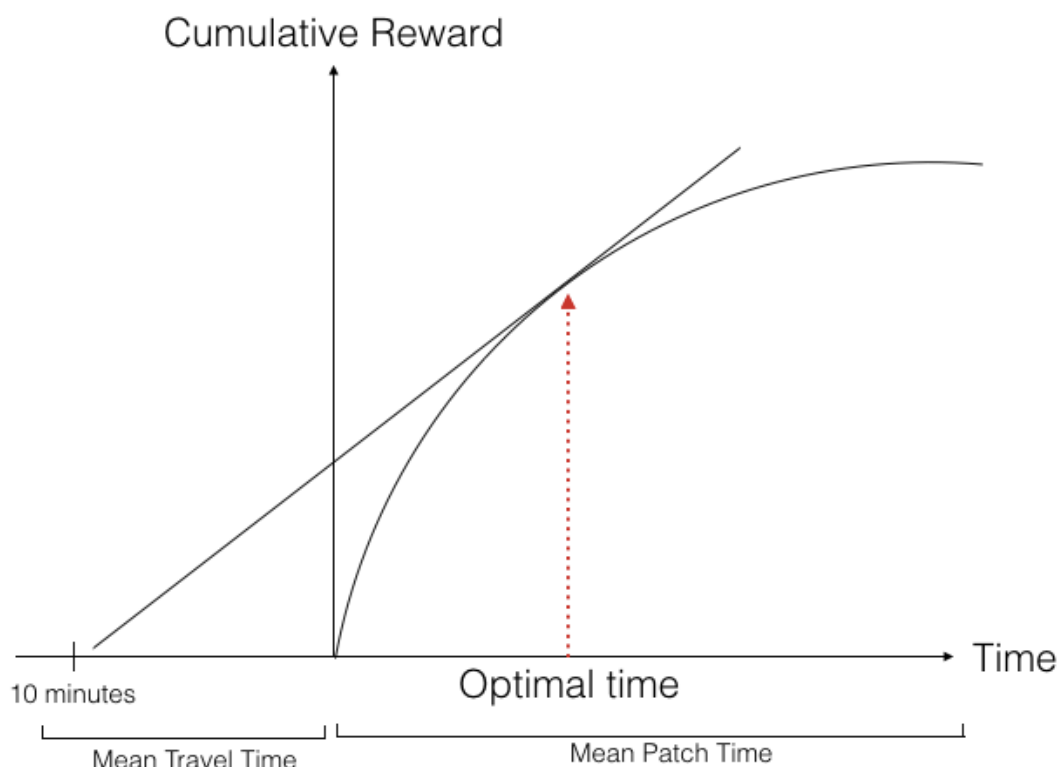


Figure 1. The Marginal Value Theorem (MVT), adapted from Charnov (1976). This figure depicts the optimal time when an animal should leave a patch, as predicted by the MVT. Within a patch, the rewards that an animal accumulates exponentially decrease over time, as the animal consumes the resources within the patch. The MVT predicts that the optimal dwell time for an organism within a patch should be when the rate of reward accumulation per unit of time (indicated by the tangent to the reward accumulation curves) equals the mean reward rate for the environment (taking into account the time spent travelling to the patch and the time spent within the patch)(i.e., when the marginal value of the patch approaches zero). Note that the MVT predicts optimal dwell times based on the average features (travel times and reward rates) of patches within an environment.

The MVT has evolved into a classical model of optimal foraging theory and has been applied to several qualitative and quantitative studies to establish predictions of animal behaviour when foraging (Cassini, Lichtenstein, Ongay, & Kacelnik, 1993; Marshall, Carter, Ashford, Rowcliffe, & Cowlshaw, 2013; Nonacs, 2001; Watanabe, Ito, & Takahashi, 2014). The MVT uses a hypothetical animal, which decides when to leave a patch based on its measure of the rate of gain in a patch comparative to the overall rate of gain within its environment. Importantly, the MVT does not serve as a

patch-leaving rule, or depend on the assessment of individual patches, but rather derives the best procedure for maximising the long-term reward gained from a known set of rules and information pertaining to the environment (Stephens & Krebs, 1986). Further, it has been noted that although the MVT is a valuable heuristic tool, there is a distinct separation between the model and the actual testing of foraging behaviour (Nonacs, 2001). The MVT thereby serves as a point from which foraging behaviour can be examined, however, deviations from the predictions of the MVT in testing must be attributed to the complexity of the natural environment in which foraging decisions occur. This is important to note as the MVT predicts the optimum of the temporal factor involved in foraging, utilising an objective and theoretical approach which incorporates a set of assumptions and constraints, in order to make the model functional. This does not imply that predators will perform optimally and adhere to the predictions of the MVT; rather, the MVT serves as a guideline that predicts optimal foraging behaviour. An important question then is: how well do animals perform relative to the optimum predicted by the MVT? Deviations from the optimal prediction must be accounted for by considering the influence of other factors (Schoener, 1971), in addition to accounting for the environmental factors specific to the study .

Alternative Theories of Optimal Foraging

Although the MVT is a prominent model of optimal foraging behaviour, its simplistic and deterministic nature has been criticised. Specifically, the optimal foraging behaviour predicted by the MVT denotes: that an animal has complete knowledge of the environment (including the capture rates of prey in the environment) (Watanabe et al., 2014); there are no limitations to the amount of time an animal has to forage for

reward; and the foraging behaviour of the animal is not effected by the variance (or volatility) within the environment. As a result, it is important to note other prominent theories that have provided accounts for the foraging behaviour of animals in a patchy habitat, which consider the environmental factors neglected by the MVT.

Hunting by Expectation. Gibb's (1966) proposed the 'hunting by expectation' hypothesis, based on his observations of the feeding habits of birds on larvae that had been laid in pinecones during the winter. The birds consumed fewer larvae when they encountered resource-rich pinecones (which contain many larvae), compared to when they encounter resource-poor pinecones with fewer larvae. Gibb (1966) attributed this behaviour to the birds' ability to learn to expect a certain amount of larvae within a pinecone. The hunting by expectation hypothesis is similar to the MVT as it considers the overall reward available in the environment, and is based on the foraging animal's complete knowledge of the environment. However, the hunting by expectation hypothesis is based on the animal's past foraging experience from which an expectation regarding the type of reward and amount of reward is derived (Hodges, 1981). This hypothesis has been widely scrutinised as it has not been widely observed in birds or other species, nor is it supported by the original data, but rather hinges on Gibb's interpretation of the results (Bateson & Klopfer, n.d.; Krebs, Ryan, & Charnov, 1974). Alternatively, it was proposed that the behaviour exhibited by the birds was instead indicative of the birds having developed a 'giving-up time' strategy (John R. Krebs et al., 1974).

Giving-Up Time. The 'giving-up time' (GUT) was an important contribution to the optimal foraging literature, and notably, is a concept derived purely from empirical

observations of behavioural responses to uncertainty, as opposed to mathematical models, such as the MVT (McNair, 1982; Tinbergen, Impekoven, & Franck, 1967). An important distinction of the GUT from the MVT is that it pertains to individual patches and is determined by the quality of different patches within the same environment, and is used to explain foraging behaviour a posteriori. Specifically, the GUT takes into account the quality of a patch and measures the amount of time that passes between the points at which the animal finds the last reward in a patch until it decides to leave the patch. The term ‘giving-up time’ was coined by Croze, who explained that the GUT “... is taken to be a quality of the [animal’s] persistence – and expression of the amount of effort the predator is willing to allot in pursuing one more of a particular prey” (as cited in McNair, 1982, pp. 512). Specifically, the GUT denotes that an animal will use its experiences of patches within the environment to determine how long to dwell in a patch based on when the last prey was captured within the patch; thereby establishing a temporal threshold. For example, if a giraffe has determined it can gain 80 acacia leaves (rewards) in 1 hour, it will remain searching for leaves to eat from the same acacia tree so long as it continues to gain 80 acacia leaves within that threshold of time. However, if an hour passes and the giraffe has not gained the expected 80 acacia leaves, it will leave the tree and move on to the next. Importantly, the GUT threshold is determined by the quality of patches within the same environment. The animal determines the quality of patches by evaluating the costs and benefits of an individual patch relative to that of other patches in the environment. That is, if the costs and benefits for one patch type (*A*) are comparatively better than those of other patch types (*B* and *C*), the GUT will be larger for *A* than it will be for *B* and *C* (McNair, 1982). Therefore, in an environment in which the rewards in patches have diminishing returns (as they do in the MVT), an

animal will “on average, spend more time in ‘good’ patches than poor ones” (McNair, 1982). Although some studies (John R. Krebs et al., 1974) have found the GUT to yield results consistent with the predictions of the MVT, an important distinction is that the GUT considers the quality of individual patches in an environment and does not assume the foraging animal to have complete knowledge of its environment. In light of this, some have posited that the use of a GUT may result in a foraging animal performing more optimally than the MVT predicts, as it is able to learn about changes in its environment and adapt its behaviour accordingly and efficiently.

The Stochastic Model. An element of learning is necessary for all circumstances under which a predator does not have complete information of its environment. Whereas the hunting-by-expectation hypothesis posited that birds learned to forage based on expectations derived from previous experiences, and the GUT was established through an animal’s previous experiences, another prominent contribution to optimal foraging theory is Oaten's (1977) stochastic model. In this model, the predator has incomplete information regarding its foraging environment, and thereby cannot predict the average reward available within the environment. This contrasts with the MVT, which assumes the animal is omniscient and thereby adheres to an optimal foraging procedure based on the average environmental features (i.e. average reward available). The stochastic model thereby posits that a predator will use its recent experiences of patch types and encounters with prey to inform its foraging decisions. Further, optimal foraging theory denotes an optimal predator to be seeking to maximise its long-term reward intake. Thus, a predator foraging in the stochastic model will use the information recently gained, such as past patch encounters, to deduce aspects of the patch distribution, and inform its decisions as they relate to

potential future decisions (Green, 1979; Oaten, 1977). As a result, the varied distribution of patches within an environment are thought to make the predator perform better in terms of maximising the reward gained, than if it adhered to the predictions of the MVT; given that foraging decisions are made based on the information specific to the types of patches comprising the environment as opposed to the average reward available in the environment (Green, 1979).

Foraging in a Variable Environment. An important consideration for optimal foraging theories has been the variance of rewards (or delays) within an environment, and the extent to which the variance influences the foraging behaviour of animals. Based on the predictions of the MVT, an environment comprised of different patch types that are randomly distributed should have no effect on the animal's foraging behaviour, as the animal is predicted to forage in accordance with the mean rate of reward or delay in the environment. However, studies have shown foraging behaviour to be different to that predicted by the MVT when the features in the environment are variable (Bateson & Kacelnik, n.d.; Bond, 1980). Given that the predictions of the MVT are based on the long-term rate-maximisation by using the mean reward within the environment, the variance of rewards in different patches should not have any affect on a forager's behaviour. However, the individual patches comprising an environment may be treated differently by a forager depending on the variance of reward or delay within a patch (Bateson & Kacelnik, n.d.). Specifically, when the mean rate of reward is the same for two reward options, but the variance of the reward options is differentiated, animals have demonstrated that the optimal choice is always the option with the smaller variance (Barnard & Brown, 1987; Barnard, Brown, Houston, & McNamara, 1985; Caraco, 1981).

Time Horizon. Optimal foraging theories assume an animal behaves so as to maximise its long-term reward gains while foraging. The predictions of the MVT propose a procedure for optimal foraging behaviour that will achieve this goal; however, the MVT does not consider limitations to the amount of time an animal has to do this. The ‘time horizon’ considers the foraging behaviour of animals in a naturalistic environment, in which the duration of daytime and approach of nightfall have been found to influence the foraging behaviour of animals (Barnard & Hurst, 1987; Caraco, 1980, 1981; Kolling, Wittmann, & Rushworth, 2014; John R. Krebs & Kacelnik, 1984). For example, during the day animals will pursue prey choices that will gradually help them meet their energy intake requirements for the day. However, as nightfall approaches, animals begin to pursue prey choices that are riskier but may yield more energy, particularly if the animal has not yet met its energy intake requirements necessary for them to survive the night. Therefore, deviations from the optimal foraging behaviour predicted by the MVT are probable when naturalistic time constraints are considered.

The MVT has been proven to be quite robust in its predictions of optimal foraging behaviour in animals with one of its main strengths being its simplicity (Cassini, Kacelnik, & Segura, 1990; Cassini et al., 1993; Cowie, 1977; Nonacs, 2001; Pyke, 1980; Walton, Ruxton, & Monaghan, 1998; Watanabe et al., 2014). Therefore, although the MVT was developed in 1976, it is still used today in various incarnations to describe optimal foraging. However, as can be seen in the aforementioned review, other theories provide accounts for the perceived shortcomings of the MVT; the most notable of which is the GUT theory as it is a posteriori measure of animal behaviour

for individual patches, and the behavioural response of animals to environmental variations. This then leads to question how the optimal foraging predictions of the MVT might hold in predicting human foraging behaviour.

How Humans Forage

Not unlike animals, humans exhibit foraging behaviour within their environment, with time and opportunity costs being constantly weighed. For example, farmers harvesting rice fields need to decide when to stop harvesting rice in one field and move on to the next, or individuals searching for information on the Internet must decide when sufficient information has been gained before moving on to the next page. In humans, foraging theory has been applied to decision-making in foraging-type tasks only within the last decade, and has been examined in eye-tracking studies of visual search and visual attention, though more predominantly, foraging theory has been applied to studies of humans foraging for information. In particular, Information Foraging Theory (IFT) was developed to examine the way in which individuals search, gather, and use information (Pirolli and Card (1999). Not unlike optimal foraging theories in animals, this theory assumes that individuals modify their search strategies so as to “maximise their rate of reward” gain, and investigates the foraging strategies used by individuals, depending on the constraints of their environment (Pirolli & Card, 1999). More recently, IFT has been used in collaboration with visual search and attention research, and several studies have demonstrated the ways in which information foraging is influenced by factors including size, shape, colour, and orientation, as noted in visual search studies (Buscher, Cutrell, & Morris, 2009; Cutrell & Guan, 2007; Duggan & Payne, 2011). As a result, accounting for the ways in which the aforementioned factors influence eye movements during visual search

would expedite the ways in which visual search and information foraging could potentially be optimised.

Furthermore, some studies have performed well-controlled experiments to examine human behaviour when foraging for reward; however, relatively little is known about this (Constantino & Daw, 2015; Kolling, Behrens, Mars, & Rushworth, 2012; Shenhav, Straccia, Cohen, & Botvinick, 2014). A study conducted by Constantino and Daw (2015) examined whether human participants learned the opportunity cost associated with gaining reward in such a way that was consistent with either the predictions of the MVT, or the temporal-difference learning model; which denotes incremental learning that occurs on a patch-by-patch basis. The task used a virtual simulation of apple picking, in which participants were presented with an apple tree and had to decide whether to harvest the apples (rewards) from the tree and incur a short delay, or move on to the next tree, which would incur a longer delay. The findings suggested the foraging behaviour of participants was consistent with the predictions of the MVT. However, the MVT does not involve learning, as the forager is assumed to have complete knowledge of its environment already.

Further, a seminal fMRI study conducted by Kolling et al. (2012) sought to examine the neural correlates of human decision-making while foraging for reward. The task itself required participants to make a choice to either exploit the current reward option or move on to an alternative option, for which the reward was unknown. The results showed the ventromedial prefrontal cortex (vmPFC) and the anterior cingulate gyrus (ACC) to be involved in evaluating the cost of foraging when making a decision between two choices. Specifically, Kolling et al. (2012) purported that their findings

were indicative of the vmPFC being involved in encoding the value of well-defined options, whereas the ACC was involved in encoding the value of the average environment relative to the cost of foraging. By replicating the study, Shenhav et al. (2014) challenged the findings of Kolling et al. (2012), arguing that the activity observed in the ACC during the foraging task was instead attributable to the difficulty of the task decision. The two conflicting results have instigated an on-going debate pertaining to the role of the ACC and whether its activity is due to the average value of a foraging environment, or the difficulty of foraging decisions. However, although these studies concern human foraging decisions, the predictions of the MVT were not applied or tested to determine the optimality of human foraging decisions. Thus, it cannot be said how well the foraging behaviour of humans in a task adhere to – or deviate from – the optimal foraging behaviour predicted by the MVT.

Summary

The Marginal Value Theorem (MVT) – as applied to behavioural ecological research – has been found to be a good predictor of optimal foraging behaviour as animals aim to maximise their long-term reward gains. However, the MVT is limited by some of its assumptions and is notably not intended to be an accurate predictor of actual behaviour, but rather a tool utilised to determine the optimality of foraging behaviour. Deviations from the optimal predictions of the MVT have been accounted for by other theories – such as the GUT and stochastic models – which consider the limitations of the MVT predictions as they pertain to the constraints of the naturalistic environment, including the quality of different patches comprising an environment, foraging with incomplete information pertaining to the environment, the variance of the environment, and the influence of time horizons on an animal's foraging behaviour.

However, these other theories consider foraging behaviour on a patch-by-patch basis and do not necessarily consider the overall environmental features, as the MVT does.

Although the MVT has been extensively tested in studies of ecological behaviour, the temporal factor involved in optimal foraging, as predicted by the MVT, paves a way to determine the extent to which human decision-making in a foraging-type task adheres to the predictions of the MVT. Thus far, studies involving the application of the MVT to human foraging behaviour are few and far between. Therefore, the question is: do the predictions of the MVT regarding optimal foraging decisions apply to humans? Specifically, do humans consider the mean features of the environment when making foraging-type decisions, or do humans behave in accordance with the quality of individual patches? If the former is true, then the MVT is applicable to predicting the foraging decisions of humans; if the latter is true, the GUT provides a better explanation for human foraging decisions.

In this research, I use four experiments, each of which comprises a different time-based foraging task. Each task is similar in that points represent the reward gained, and are used as incentive, and the duration of the trial imposes a temporal constraint. Importantly, to remain consistent with the assumptions of the MVT in this study, I ensure that participants have complete knowledge of the task environment in order to eliminate learning, as the MVT assumes the forager has complete knowledge of its environment. I then ask participants to make decisions about how long to stay in a patch and gain reward, given that there was a delay in reaching that patch, and the reward is gained at an exponentially declining rate. Further, in light of the temporal factor of the MVT's predictions, I ask participants to complete the Barratt Impulsivity

Scale (BIS-11) questionnaire, as previous studies have examined impulsivity as it pertains to rewards and delays, and found that traits of impulsivity result in the discounting of delayed rewards (Grecucci et al., 2014; Mobini, Grant, Kass, & Yeomans, 2007; Patton, Stanford, & others, 1995; Sinha, Manohar, & Husain, 2013).

I predict that participants will dwell longer in patches following longer delays or slower reward rates. I also calculate the optimum behaviour – based on the MVT – and compare the actual behaviour to the predicted optimum. I further predict that participants with BIS-11 scores indicative of impulsive traits will have shorter dwell times in the task, with strong correlations between the BIS-11 score and their dwell times. In addition, I examine whether the GUT provides a posteriori account for deviations of participant performance from the MVT predictions of foraging behaviour

Chapter 2: Experiment One

Introduction

The Marginal Value Theorem (MVT) is a simple, deterministic model that accounts for the widely observed optimal foraging behaviour of animals. Specifically, the MVT signifies that the optimal time to dwell within a patch is determined by the duration of time taken to travel to the patch (delay), and the point at which the rate rewards are gained within the patch diminishes below that of the average rate of reward available in the environment (Figure 1) (Charnov, 1976). This model consistently predicts the optimality of the decisions made by foraging animals regarding how long to exploit a patch for reward before moving on to explore the next patch. Given that this type of decision is regularly encountered by humans, to what extent are human decisions in a foraging task optimal?

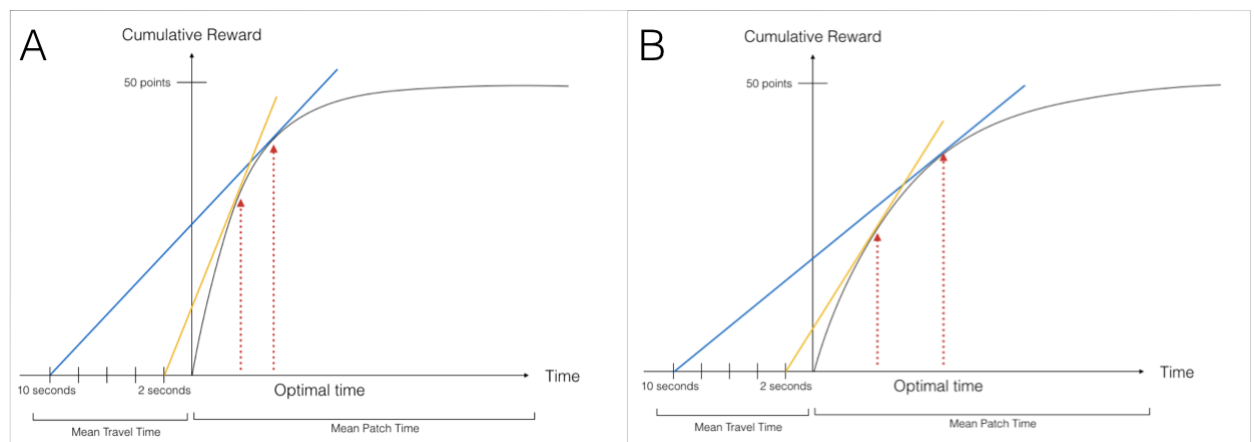


Figure 2. Predictions of the MVT as applied to Experiment 1 for (A) Fast reward rates, and (B) Slow reward rates. Note that a general prediction of the MVT is that longer mean travel times should lead to longer mean dwell times within a patch (A). In addition, patches with slower reward rates should similarly result in longer dwell times than patches with faster reward rates (B compared to A).

In this experiment, I utilise the predictions of the MVT to determine to what extent human decisions in a time-based foraging task are optimal. The MVT predicts that

individuals will dwell longer following longer delays, or with slower reward rates (Figure 2). Therefore, I examined the optimality of participants' dwell times when presented with either a longer or a short delay, which represents the time animals take to travel to a patch; and a fast or slow rate of reward, which represents the different rates at which reward is accumulated by animals in a patchy environment.

Additionally, I examined the extent to which the dwell times of participants deviated from the predicted optimum. Furthermore, I examined the variance of participant dwell times to determine if dwell times vary as a function of the foraging task condition, and if participants change their strategy over the course of a trial.

Methods and Materials

Subjects. Twenty-one healthy participants volunteered for the first experiment, of which 6 were male and 15 were female. Ages ranged from 17 to 31 years ($M = 20.24$, $SD = 3.02$). All participants were right-handed ($N = 21$). Three additional participants completed the experiment but were excluded from the analysis due to technical issues and incomplete data. Participants were pre-screened to ensure they had a good command of the English language. Participants were recruited from the Psychology Participant Pool at Macquarie University in return for course credit, in addition to the possibility of winning a small amount of money based on their performance in the task. The Ethics Committee of Macquarie University approved this study, and all participants provided informed consent.

Stimuli. The experiment was implemented on Presentation® software (Version 18.3, www.neurobs.com). In addition, participant completed the Barratt Impulsiveness Scale (BIS-11) prior to commencing the experiment (Patton, Stanford, et al. 1995).

Experimental Design. In this experiment, participants' primary goal was to earn as many points as possible. To motivate their performance, they were informed that, if their scores were the highest of the preceding 5 participants, they would earn a \$10 bonus (for the first five participants, the comparison scores were based on pilot data). This additional reward was in addition to the two course credits they received for participation.

Each *trial* of this task comprised *multiple* 'patches' of reward, in each of which participants had the opportunity to earn a maximum of 50 points. These points were accrued automatically according to an exponentially decreasing function (Figure 2):

$$\text{(Equation 1)} \quad R(t) = A \cdot (1 - e^{-\rho t})$$

where $R(t)$ is the cumulative reward at time t ; A is the maximum reward available in that trial (which in Experiments 1-4 was set at 50); and ρ is the reward rate (which was set at 0.05 vs. 0.1 in Experiment 1). The cumulative rewards were displayed as a vertical bar on the right side of the screen, which gradually filled up to indicate the number of points accumulated in that patch. To accumulate the maximum reward of 50 points in each patch, participants would have had to wait 14.4 seconds when the reward rate was 0.05, and 11.5 seconds when it was 0.1. Based on these exponentially decreasing rewards, participants' were instructed to indicate by button press when they felt it was no longer worth remaining in the current reward patch, and when they wished to move to the following patch.

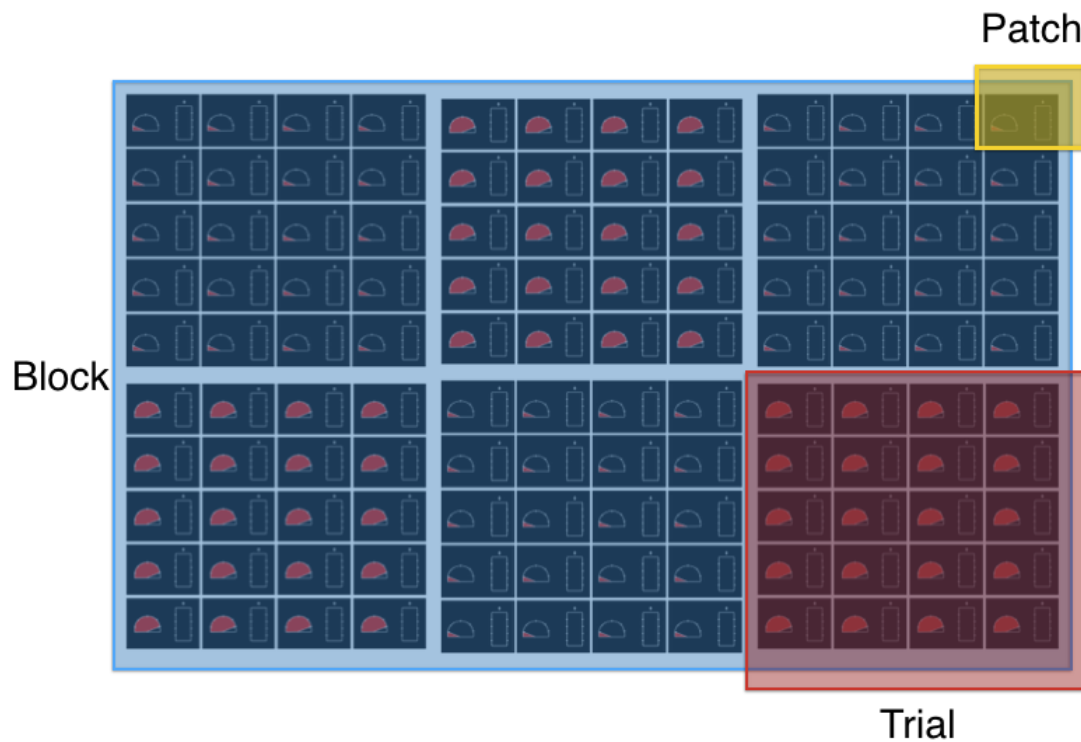


Figure 3. Each block comprised multiple *trials*. Each *trial* comprised multiple *patches*, and lasted between 105 and 135 seconds. Participants' goal was to maximise their winnings on each trial. Trial conditions (e.g., mean travel time) were varied across blocks, but kept constant within blocks, in order to convey to participants the impression of a stable reward environment within blocks.

Critically, however, at the beginning of each patch, a temporal delay was imposed before any rewards could be accumulated (Figure 4). This delay was displayed in the form of a semi-circular timer with two-second gradations from 0-seconds to 12-seconds. In Experiment 1, the possible delays were either 2-seconds or 10-seconds. In each case, red shading on the timer would indicate the imposed delay, and an arrow would gradually revolve anti-clockwise from the starting position (2s, 10s) to 0-seconds. At the conclusion of this delay, the reward bar would automatically begin to fill with accumulated rewards.

Participants were asked to base their decisions of how long to remain in a particular patch based on two factors: the delay that was imposed at the beginning of that patch, and the exponentially decreasing reward rate. The cumulative reward gained throughout the trial was displayed above the reward bar in each patch.

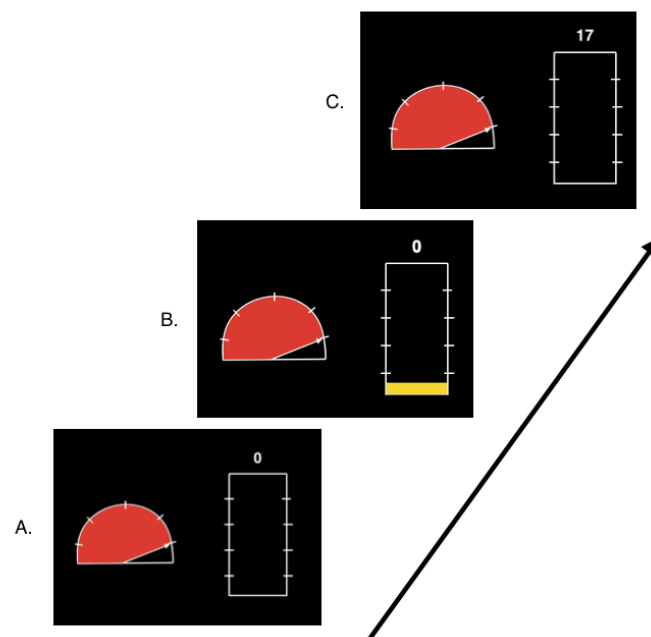


Figure 4. Sequence of events within a patch. (A) Each patch begins with a timer on the left of the screen, which indicates in red the delay imposed in that patch (the ‘travel time’) before rewards can be accrued. The timer is divided into 2s increments, ranging from 2s to 10s. The display dynamically changes as the arrow counts down from the imposed delay (6s in the displayed example). (B) Once the imposed delay has elapsed, participants automatically begin accruing rewards in an exponentially decreasing fashion, with the cumulative reward displayed as the height of a yellow bar on the right side of the screen. The maximum reward available on each trial is 50. Participants indicated by button press when they are satisfied with the rewards they have accumulated in that patch, and were ready to move to the next patch. [(C) is not necessary here] (D). Participants then progress instantly to the next patch, with their cumulative reward in the patches to that point displayed above the reward bar on the right.

In Experiment 1, I manipulated the rate of reward accumulation (0.05 ('slow') vs. 0.01 ('fast')), and the duration of the imposed delay occurring before reward accumulation (2s v 10s). Each of these four conditions was tested across separate blocks, with block order randomised across participants. Participants were informed as to which condition they were going to complete prior to commencing a block, and all participants undertook a two-minute practice trial prior to each block. Each block was divided into five trials of approximately two minutes duration, and each trial comprised multiple patches (the precise amount was determined by participants' decisions). The duration of each trial varied randomly from 1 minute 45 seconds, to 2 minutes 15 seconds, to ensure that participants could not strategise their responses based on the precise duration of each trial. Participants thereby had no indication of how much time remained in a trial. Upon termination of the trial the screen stopped, or 'cut off', at whatever point the patch within the trial was at – whether it be the delay count down or the accumulation of rewards. At the end of each trial, participants' total winnings for that trial were displayed on the screen.

Results

Mean Dwell Times. To test the hypothesis that dwell times should increase with greater delays and slower reward rates, I ran a within-subjects repeated measures analysis of variance (ANOVA) on the factors of Reward Rate (fast, slow) and Delay (2s, 10s) on mean dwell times for each patch. This analysis showed a significant main effect of Reward Rate, $F(1, 20) = 11.565, p = .003$, such that the dwell times were longer for the slow Reward Rate, $M = 11.57s, SD = 4.25s$, relative to the fast Reward Rate, $M = 9.58s, SD = 3.41s$. Further, the main effect of Delay was significant, $F(1, 20) = 23.545, p < .001$, such that the dwell times were longer for the long Delay, $M =$

11.94s, $SD = 3.81s$, relative to the short Delay, $M = 9.20s$, $SD = 3.66s$. There was no significant interaction, $F(1, 20) = 1.334$, $p = .262$. This demonstrates that participants were willing to dwell for longer periods of time when presented with longer delays, and slower reward rates.

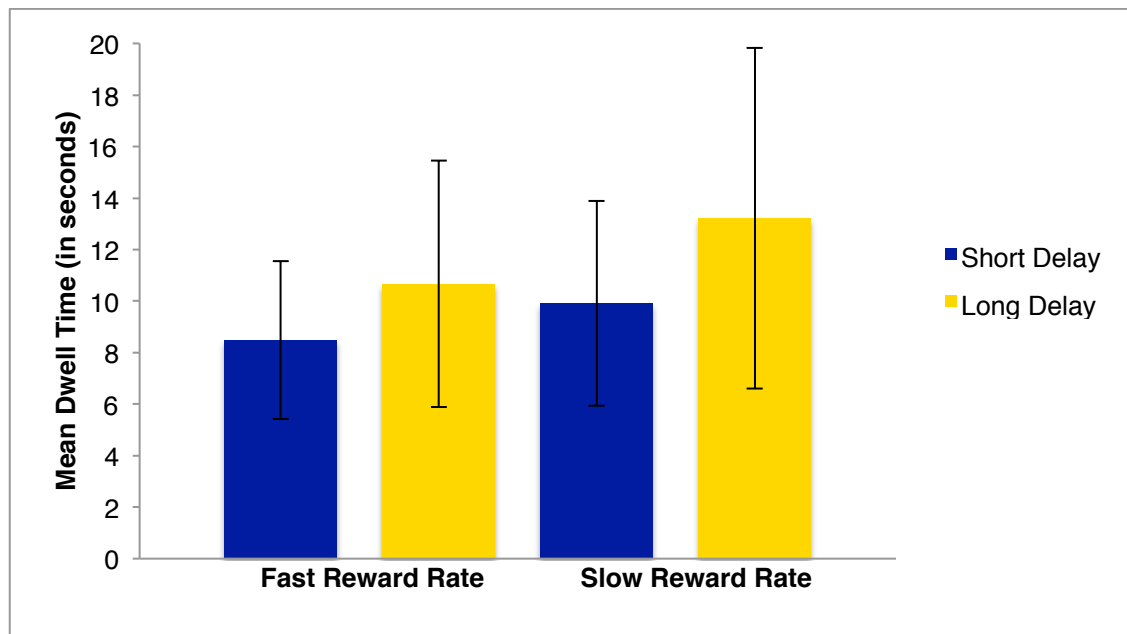


Figure 5. Mean dwell time (± 1 standard deviation) as a function of condition. Dwell times were shorter for the short vs. long delay, and for the fast vs. slow reward rate.

Standard Deviation of Dwell Times. Another important question is how reward rate and delay influenced the variability of participants' responses. To determine the variability of participants' responses, the standard deviation of dwell times within each patch was calculated for each Reward Rate (fast, slow) and Delay (2s, 10s). These standard deviations were then subject to the analogous 2x2 within-subjects repeated measures ANOVA, as in the analysis on mean dwell times. The main effect of Reward Rate was significant, $F(1, 20) = 14.436$, $p = .001$, and showed less variability in dwell times for the fast Reward Rate, $M = 3.92s$, $SD = 1.66s$, compared to the slow Reward Rate, $M = 5.31s$, $SD = 2.60s$. Further, this analysis showed a

significant effect of Delay, $F(1, 20) = 49.153, p < .001$, such that there was less variance in dwell times for the short Delay, $M = 3.53s, SD = 1.68s$, relative to the long Delay, $M = 5.70s, SD = 2.32s$. There was no significant interaction, $F(1, 20) = 2.228, p = .100$. In summary, faster reward rates and shorter delays led, not only to shorter dwell times, but correspondingly less variance, compared to conditions with slower reward rates or longer delays.

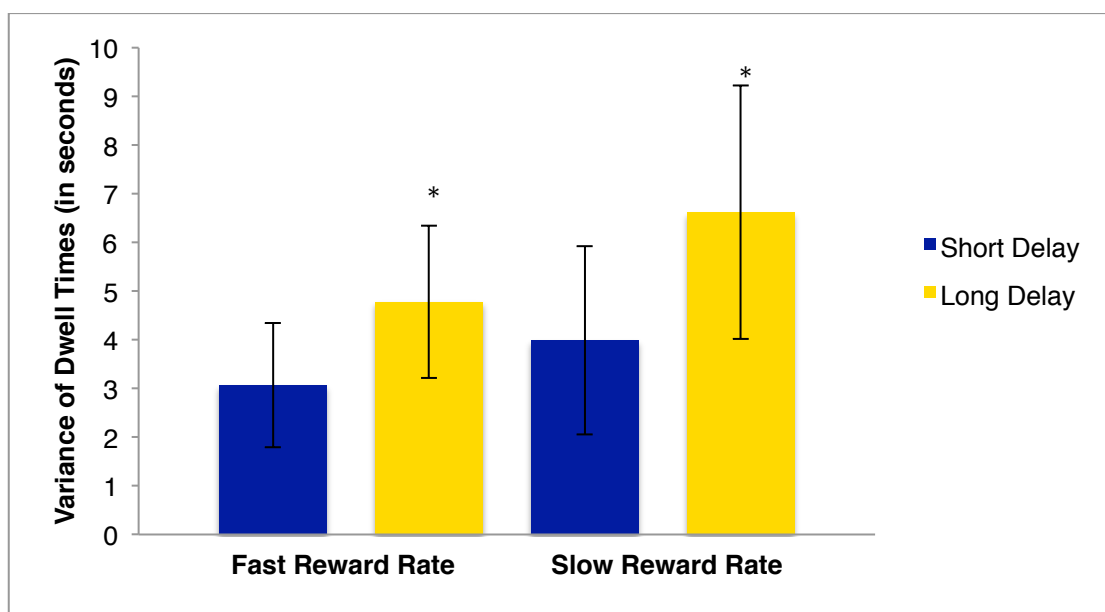


Figure 6. Mean variance of dwell time (± 1 SD) for each trial. The variances of dwell times were greater for longer delays and slower rewards (*, $p < .05$).

Changes in Strategy Across an Individual Trial. Recall that the MVT predicts optimal performance based on mean patch delays and mean reward rates of each trial. However, there is evidence that animals may change their foraging behaviour as they approach a fixed deadline (e.g., sundown) (Bateson & Kacelnik, n.d.; Kirk, Esler, & Boyd, 2007; Krebs & Kacelnik, 1984a; Shettleworth, 1985). Do dwell times in this task change as a function of trial time? The dwell times for the first and last patches

within each trial were calculated to determine if there were changes in trial strategy as a function of trial time. . Importantly, the last patch was considered to be the patch preceding the patch during which the trial terminated. This circumvented any confounds pertaining to the dwell time being interrupted and cut short by the termination of the trial. I ran a within-subjects repeated measures ANOVA on Reward Rate (Fast, Slow), Delay (2s, 10s), and Patch Position (first, last) on dwell times for each trial. The main effect of Patch Position was significant, $F(1, 20) = 16.065, p = .001$, and showed longer dwell times for the first patch, $M = 11.80s, SD = 5.31s$, compared to the last patch, $M = 9.39s, SD = 5.05s$, in a trial. This analysis also revealed main effects of Reward Rate, $F(1, 20) = 17.378, p = .000$, and Delay, $F(1, 20) = 46.668, p = .000$, which were all qualified by a significant interaction between Delay and Patch Position, $F(1, 20) = 4.694, p = .043$, as well as a significant three-way interaction, $F(1, 20) = 39.983, p = .000$. Decomposing this three-way interaction with Bonferroni-adjusted comparisons revealed that dwell times were significantly shorter in the first relative to the last patch only for the extreme conditions – that is, for the fastest reward rate at the shortest delay (first patch, $M = 9.20s, SD = 4.22s$; last patch, $M = 3.9s, SD = 2.20s$), and at the slowest reward rate at the longest delay (first patch, $M = 15.66s, SD = 5.91s$; last patch, $M = 12.73, SD = 4.67s$). However, there were no differences in dwell times between the first and last patch for the intermediate conditions (fast reward rate, long delay: first patch, $M = 11.71s, SD = 3.90s$; last patch, $M = 11.15s, SD = 3.67s$; slow reward rate, short delay: first patch, $M = 11.02s, SD = 5.40s$; last patch, $M = 10.16s, SD = 4.33s$) [Figure 7].

This demonstrates that there is a change in participant behaviour as the dwell time in a patch is dependent on how much time has elapsed for the trial, but only for the extreme conditions.

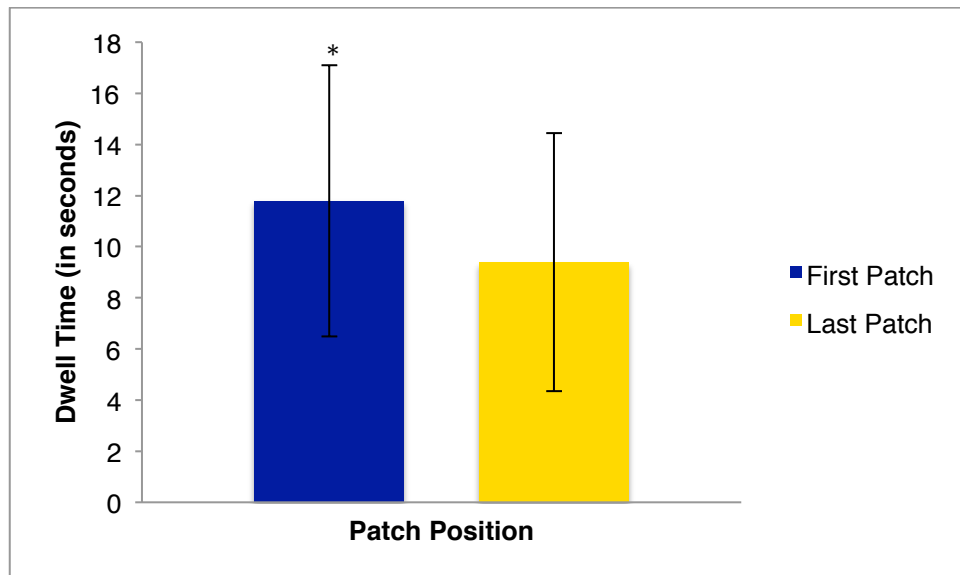


Figure 7. Mean dwell times (± 1 standard deviation) collapsed across trials for the first compared to the last patch in a trial. Dwell times were longer for the first patch than the last patch (*, $p < .05$).

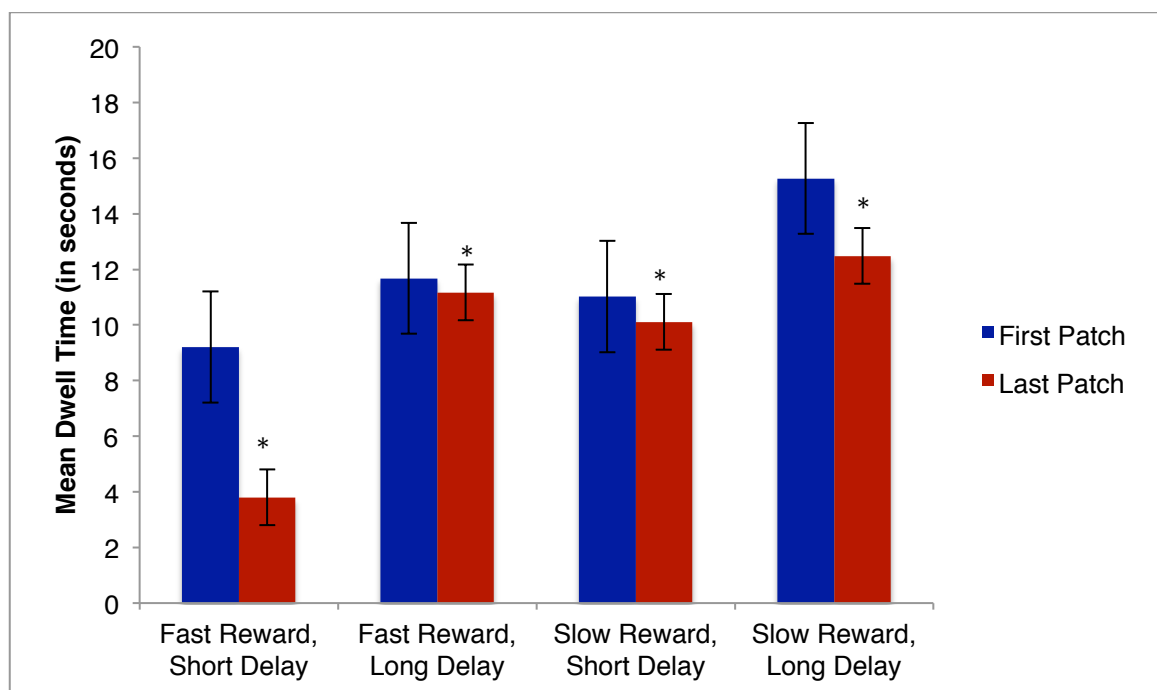


Figure 8. Mean dwell times (± 1 standard deviation) collapsed across trials for first v. last patch in each condition. Dwell times were shorter for the last patch in a trial compared to the first patch (*, $p < .05$).

Performance Relative to Optimal. Given the precise predictions that the Marginal Value Theorem (MVT) posits on optimal dwell times, it is possible to derive the optimal dwell time for each condition of this experiment (Figure 9). In order to determine the optimum time to leave each patch, we need to determine when the rate of reward accumulation falls below the patch average given the mean delay. The point at which these two functions intersect is given by solving the following equation:

$$\text{(Equation 2)} \quad \frac{1}{e^{\rho t}}(t + d) = 1 - \frac{1}{e^{\rho t}}$$

where d = the delay in each patch, ρ is the reward rate, and t is the dwell times in seconds. Solving this equation for t given each d and ρ gives the following optimal dwell times:

d	ρ	Optimal Dwell Time
2	0.1	5.27s
2	0.05	27.4s
10	0.1	11.5s
10	0.05	33.6s

To determine whether optimal dwell-times were significantly different to the optimum, I ran Bonferonni-corrected one-sample t-tests, comparing the mean dwell times in each of the four conditions against the optimal dwell time for those conditions (adjusted p-value = $0.05/4 = 0.0125$; Figure 9). For the fast Reward Rate,

there was no difference between participants' dwell times and the optimum when the delay was long ($p = .236$, $M = 10.67s$, $SD = 3.12s$), but participants dwelled significantly longer than optimal when the delays were short ($p = .001$, $M = 8.49s$, $SD = 3.40s$). In contrast, however, the mean dwell times for the slow Reward Rate were significantly less than optimum for the short ($p = .000$, $M = 9.92s$, $SD = 3.85s$) and long Delay ($p = .000$, $M = 12.21s$, $SD = 4.07s$). Overall, this indicates that the Marginal Value Theorem was mostly poor at predicting participant performance, with participants dwelling either significantly shorter or longer than would be optimal under most conditions.

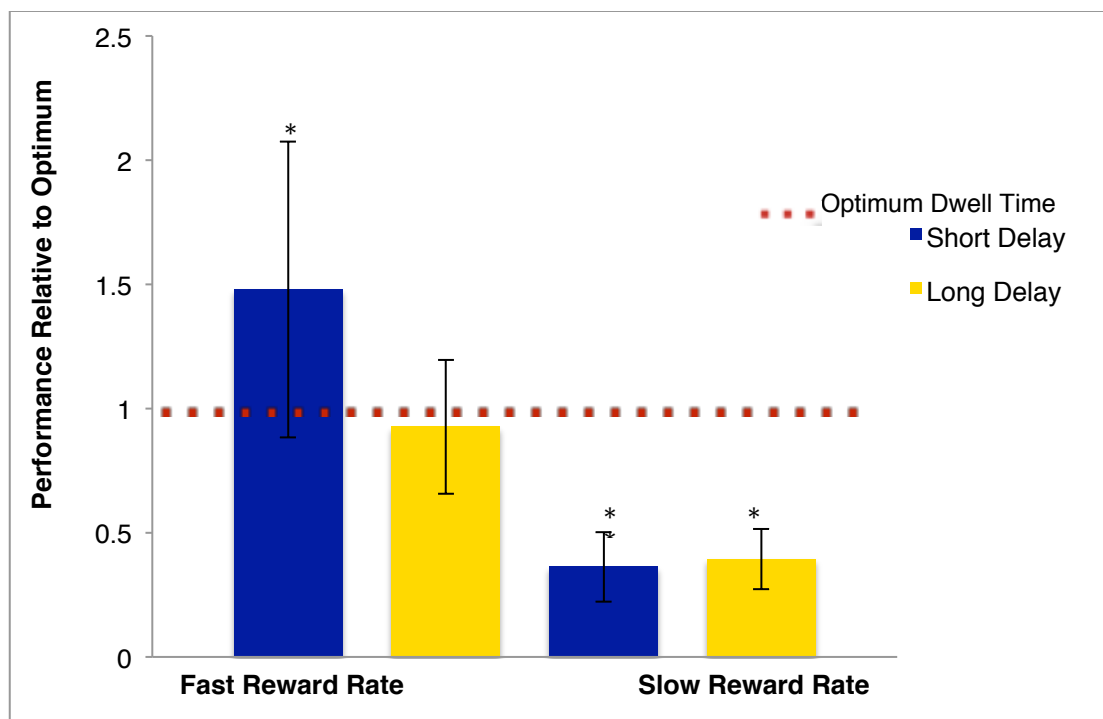


Figure 9. Performance relative to optimum. Optimal dwell time for each condition, as predicted by the MVT, represented by the red dotted line. Standard deviation bars that are >1 indicates participants dwelled longer than optimum; <1 indicates participants dwelled less than optimum (*, $p < .05$).

Correlations. Using the scores attained from the Barratt Impulsivity Scale (BIS-11), I ran bivariate correlations between the overall experiment duration (comprised of the sum of participant dwell times and patch delays), and the first- and second-order subscales, and results of the BIS-11 questionnaire. Importantly, the foraging task in this experiment was comprised of temporal components to which participants were required to respond to. Further, traits of impulsivity are denoted by variations in temporal responses to stimuli (Bonnelle et al., 2015; Grecucci et al., 2014; Patton et al., 1995; Radakovic & Abrahams, 2014). For this reason, the overall experiment duration was used as it provided a comprehensive measure of participants' engagement with the temporal requirements of the task: delay and dwell time. However, the results yielded no significant correlations (Appendix A).

Discussion. In this experiment, I examined the extent to which human decision-making in a foraging task adheres to – or deviates from – the predictions of the Marginal Value Theorem (MVT), and thereby, the extent to which foraging decisions are optimal. The key results of this task were that dwell times were shorter and less variable with shorter delays and faster reward rates. Overall, this is consistent with the predictions of the MVT. Further, these results show that participants changed their behaviour as they approached a deadline, and tended to dwell for shorter periods of time as they approached the deadline. However, this behaviour was only observed in the extreme conditions (fast reward rate, short delay; slow reward rate, long delay). Furthermore, participants' performance was optimal only in an 'intermediate' condition (fast reward rate, long delay), but not in the others. This suggests a possible framing effect in participants' responses.

Recall that the MVT predicts dwell times based on the average features of the environment (e.g., the average reward rate and patch delays). Experiment 1 provides evidence broadly consistent with the MVT, but in the special case in which the mean delays and reward rates of each patch were identical across entire trials and across each block. A stronger, more ecologically valid, test of the MVT would be to compare behaviour across environments (or trials) which differ according to their *mean* patch delays, but within which individual patch delays differ. This will be the subject of Experiment 2.

Chapter 3: Experiment Two

Introduction

The Marginal Value Theorem (MVT) denotes that the optimal point to leave each patch is determined by the *average* reward available within the environment.

Therefore, the dwell times for each condition should be relative to the mean delay of each environment. Having established that behaviour in Experiment 1 was largely consistent with the predictions of the MVT in the particular case when patch delays were constant, Experiment 2 aimed to test the prediction that dwell times are determined by the *average* environmental features (e.g., dwell times), rather than features of individual patches. In order to provide enough power for the analyses, both the reward rate and the delay could not be varied, so I chose to fix the reward rate and vary the patch delay; however, varying the reward rate is an equally valid manipulation that could be looked at in future experiments.

Experiment 2 involved comparing dwell times across trials, which differ in their *mean* patch delays (4 vs 8 seconds). Unlike Experiment 1, however, patches within each trial varied within a range of ± 2 seconds of the trial mean. Specifically, when the mean patch delay for a condition was 4 seconds, the possible patch delays were 2, 4, and 6 seconds. In contrast, when the mean patch delay for a condition was 8 seconds, the possible delays were 6, 8, and 10 seconds.

Two important features of this design are worth noting. First, the 6-second patch delay was used in both trial types, and therefore allowed me to distinguish the effect of mean delays on the patches with identical delays. Second, this experimental design allowed me to examine the effect of mean trial delay (mean of 4s versus mean of 8s)

on dwell times, while holding constant the variability of trial delays (the range for both trial types is +/- 2 seconds).

Methods and Materials

Subjects. A total of 21 healthy participants volunteered for Experiment 2, of which 4 were male and 17 were female. Ages ranged from 19 to 40 ($M = 21.29$, $SD = 5.35$). All participants were right-handed ($N = 21$). Inclusion criteria were identical to those of Experiment 1.

Experiment Design. This experiment was similar to that of Experiment 1, with two main differences: The Reward Rate was set at $\rho = 0.1$ in order to increase the power of this experiment by increasing the number of trials, and patch Delays were varied within each trial. In Experiment 1, all patches within a trial involved the identical delay (i.e., either 2 seconds or 10 seconds). In Experiment 2, I manipulated the mean delay in each trial while varying the specific delays of individual patches.

Specifically, each trial in this experiment either had a *mean* delay of 4 seconds or 8 seconds. Trials themselves were composed of patches with delays that were either equal to the mean trial delay, or 2 seconds longer or faster than the mean delay. Thus, trials with a mean delay of 4-seconds comprised patches that had delays of 6, 8, or 10 seconds. The experiment was divided into four blocks, with two blocks containing trials with mean delays of 4-seconds, and the remaining two containing trials with mean delays of 8-seconds, counterbalanced in A B A B or B A B A fashion. It is important to note that the two conditions of this experiment vary the mean delay of each trial, while holding the delay variance constant (the range in both conditions is

+/- 2 seconds from the mean). This allowed me to examine the effect of manipulating mean delay independent of variance.

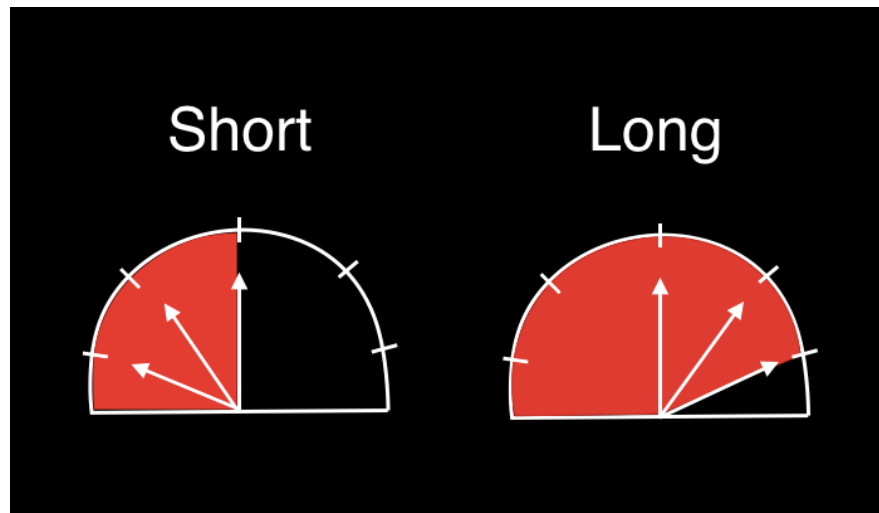


Figure 10. Possible patch delays for each trial (+/- 2s) relative to the mean trial delay, as presented to participants when the task was explained. Each block comprised multiple trials. Each trial comprised multiple patches with different delays according to the trial type (short or long). A block of 'short' trials would have several patches with 2, 4, or 6s delays. A block of 'long' trials would have several patches with 6, 8, or 10s delays.

Results

Mean Dwell Times. I ran a within-subjects repeated measures ANOVA on Mean Trial Delay (4s, 8s) and Patch Delay (less than, equal to, or greater than the trial mean) on mean dwell times in each patch. This analysis showed a significant main effect of Mean Trial Delay, $F(1, 20) = 8.347, p = .009$, such that dwell times were longer for the long Mean Trial Delay, $M = 9.46s, SD = 3.23s$, than for the short Mean Trial Delay condition, $M = 7.55, SD = 2.98s$. Mauchly's Test indicated that the assumption of sphericity had been violated for the factor of Patch Delay, $\chi^2(2) = 15.151, p = .001$, and was thereby corrected using Greenhouse-Geisser estimates of sphericity, $\epsilon = .645$. However, there was no significant main effect of Patch Delay,

$F(1.291, 25.815) = 4.161, p = .43$, or interaction, $F(1.812, 36.231) = .142, p = .848$.

Importantly, this confirmed and extended the findings from Experiment 1 and the predictions of optimal foraging, by showing that longer delays resulted in longer dwell times, and shorter delays resulted in comparatively shorter dwell times.

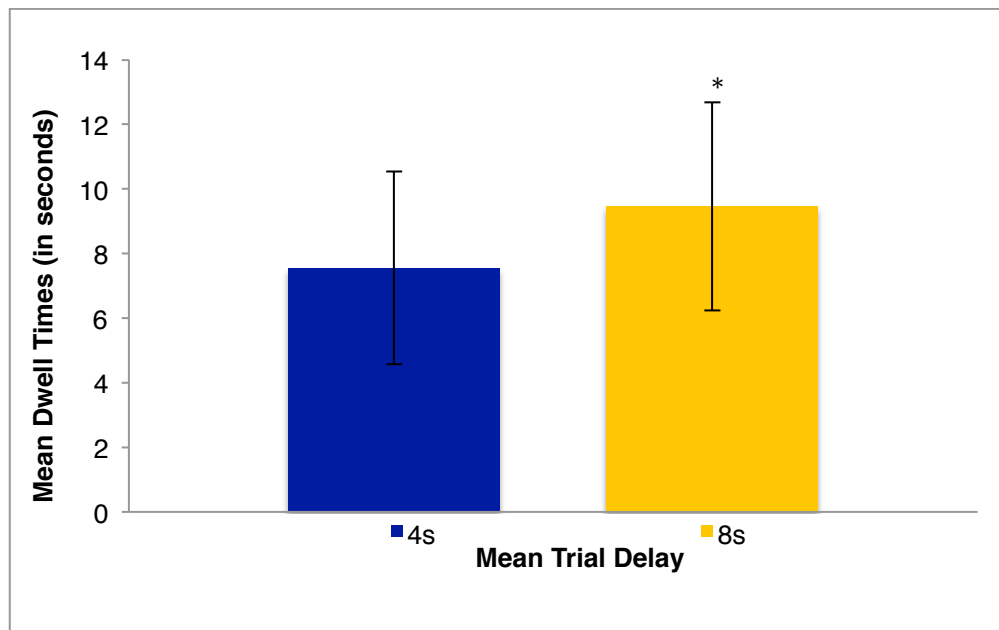


Figure 11. Mean dwell time (± 1 SD) collapsed across patches within a trial. Each trial is comprised of patches that impose either a short (mean of 4s) or long (mean of 8s) initial delay. Participants dwelled significantly longer in trials comprising mean patch delays of 8s vs. 4s (*, $p < .05$).

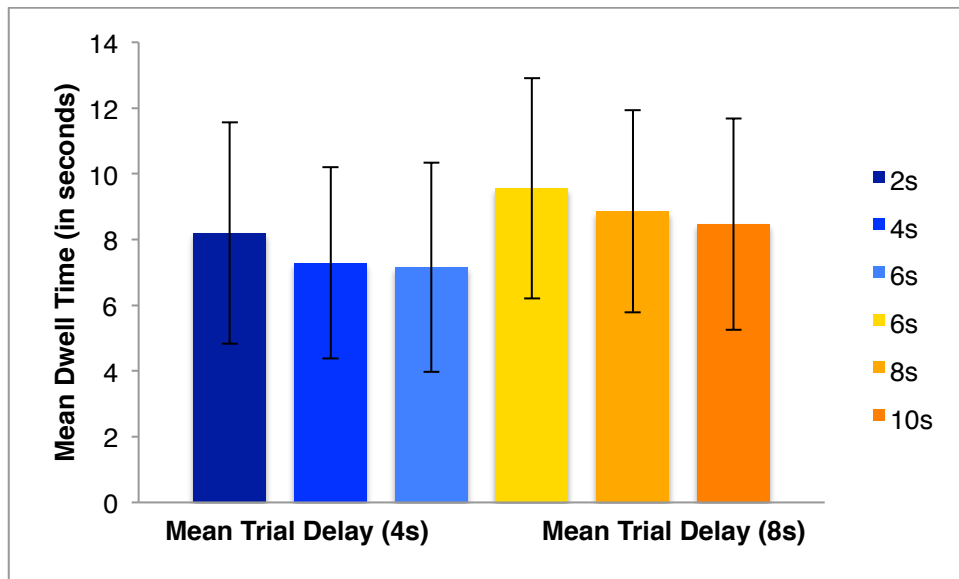


Figure 12. Mean dwell time (+/- 1 SD) for each patch within a trial. Each trial is comprised of patches that impose either a short (mean of 4s, in blue) or long (mean of 8s, in orange) initial delay. Each patch within a trial involved a delay that was either equal to the mean, or 2s longer or shorter than the mean.

Standard Deviation of Dwell Times. As in Experiment 1, I examined variability in dwell times by calculating the standard deviation for each trial type, and subjected this to a within-subjects repeated measures ANOVA on Mean Trial Delays (short, 4s; long, 8s) and Patch Delays (less than, equal to, or greater than the trial mean). This analysis showed a significant main effect of Mean Trial Delay, $F(1, 20) = 4.596, p = .045$, such that there was less variance of dwell times for the short Mean Trial Delay ($M = 3.67s, SD = 1.48s$) than for the long Mean Trial Delay ($M = 4.97, SD = 2.74s$). There was no significant main effect of Patch Delay, $F(2, 40) = 1.815, p = .176$, or interaction, $F(2, 40) = .070, p = .933$. The lower variance in dwell times for trials with shorter mean delays is in keeping with the shorter mean dwell times for that condition, and is consistent with the findings from Experiment 1.

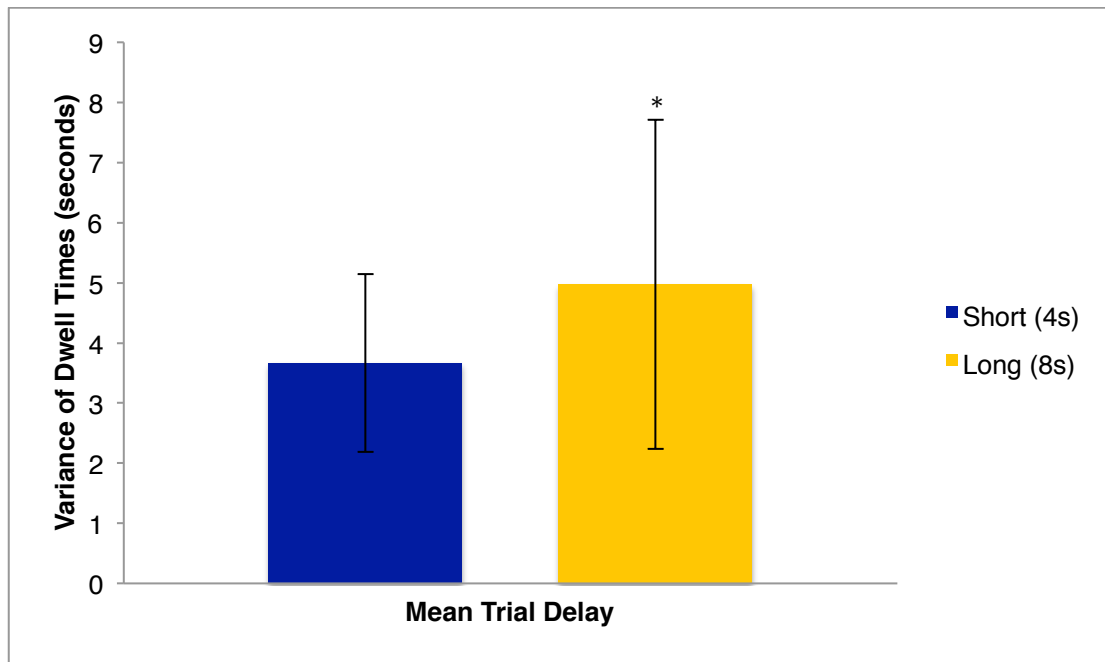


Figure 13. Mean variance of dwell time (+/- 1 SD) for mean trial delays. Variance of mean dwell times were greater for mean trial delays 8s vs. 4s (*, $p < .05$).

Changes in Strategy Across an Individual Trial. As in Experiment 1, this analysis showed a significant main effect of Patch Position, $F(1, 20) = 16.050$, $p = .001$, such that dwell times were longer for the first patches in a trial ($M = 9.52s$, $SD = 3.93s$) compared to the last patches ($M = 8.34s$, $SD = 3.23s$). Furthermore, in line with the mean dwell time results, the main effect of Mean Trial Delay was significant, $F(1, 20) = 6.848$, $p = .017$, such that dwell times were longer for the long Mean Trial Delay (8s) ($M = 9.65$, $SD = 2.98s$) and shorter for the short Mean Trial Delay (4s) ($M = 8.21s$, $SD = 3.15s$). Importantly, neither the main effect of Patch Delay, nor any of the higher order interactions were significant (Mean Trial Delay, $F(1, 20) = 1.436$, $p = .245$; Patch Delay, $F(1, 20) = .226$, $p = .799$; three-way interaction, $F(1.516, 30.322) = .240$, $p = .726$). These results show participants to dwell for shorter periods of time in the last patches of a trial compared to the first patches of a trial.

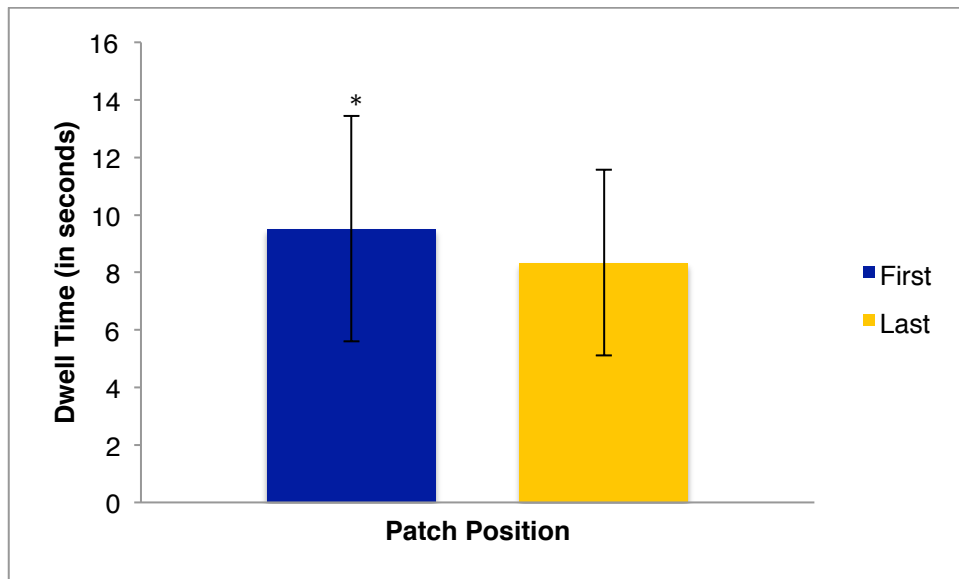


Figure 14. Mean dwell times (± 1 SD) collapsed across trials for the first compared to the last patch in a trial. Dwell times were longer for the first patch than the last patch (*, $p < .05$).

Performance Relative to Optimum. As in Experiment 1, the optimum dwell time for each patch given the mean patch delays can be calculated using Equation 2.

Solving Equation 2 for t given $d = 4$ or 8 s gives the optimal dwell time as:

d	ρ	Optimum
4s	0.1	7.79s
8s	0.1	10.46s

Based on the predictions of the MVT, the mean dwell times for each condition should be a function of the mean delay of each environment. I conducted one-sample t-tests comparing participant dwell times for each trial in each condition to the optimal dwell time for that condition. Bonferroni-correction for multiple comparisons was applied to prevent false positive results, with the critical p -value being $0.05/2 = 0.025$. With this

correction, participant dwell times were not significantly different from the optimum for the short (4s) Mean Trial Delay ($p = .838$, $M = 7.93s$, $SD = 3.18s$) or for the long (8s) Mean Trial Delay ($p = .166$, $M = 9.48s$, $SD = 3.12s$). This suggests that participant performance in each condition was not significantly different to the predictions of the MVT.

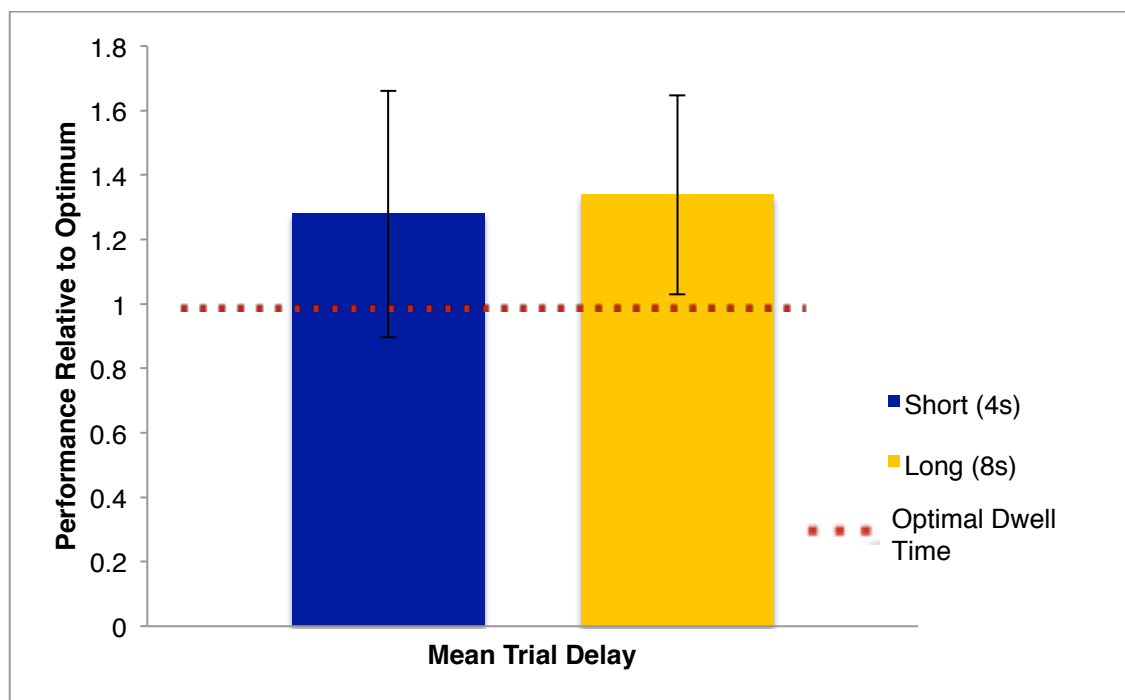


Figure 15. Performance relative to optimum. Optimal dwell time for each condition, as predicted by the MVT, represented by the red dotted line. Standard deviation bars that are >1 indicates participants dwelled longer than optimum; <1 indicates participants dwelled less than optimum.

Correlations. Congruent with the correlations conducted in Experiment 1, the scores attained from the Barratt Impulsivity Scale (BIS-11) were used to determine if there were any correlations between traits of impulsivity and the overall experimental duration; which was comprised of the total sum of dwell time and delay time over the course of the experiment for each participant. I ran bivariate correlations between the overall experiment duration and the first- and second-order subscales and results of

the BIS-11 questionnaire. However, the results yielded no significant correlations ($r_s > .02, p > .05$) [Appendix B].

Discussion. In this experiment, I examined the extent to which human decision-making adheres to – or deviates from – the predictions of the Marginal Value Theorem (MVT) in a foraging task where the mean delay is varied for each condition, while the variance of delays remains the same. The results showed participants to dwell longer for reward when presented with longer delays, and dwell comparatively shorter for reward when presented with shorter delays. Further, the variance of dwell times in each condition showed participant dwell times to be less varied in the short delay condition relative to the long delay condition. These findings are largely congruent with the results in Experiment 1.

Critical differences in this experiment pertain to the presence of different delays in each condition (environment), and the way in which this element tested the predictions of the MVT by determining if participants performed optimally based on the average delay for each condition. In this experiment, participant performance relative to the predicted optimal dwell time for each condition showed participants to be dwelling nearly optimally. Interestingly, this suggests that behaviour within each patch was determined by the overall trial mean – not the individual patch delay. In addition, the dwell time for the 6-second delay was longer for the longer Mean Trial Delay (8s) than for the shorter Mean Trial Delay (4s).

Together, Experiment 1 and Experiment 2 have both provided evidence in favour of the MVT predictions; that is, the predictions indicate that dwell times are determined

by the mean environmental features. In this experiment, the mean delay was varied for each condition, while the variance of delays varied equally by 2-seconds (less than, equal to, or greater than the mean delay). The results are compelling as participants' dwell according to the predictions of the MVT, and thereby largely confirm the results from Experiment 1. The MVT implies that the variance of an environment does not influence dwell times. However, there is evidence that environmental variance (or volatility) should make a difference (Bond, 1980; McNamara & Houston, 1992). Therefore, in order to further examine the adherence of human foraging decisions to the predictions of the MVT successively, the mean in each condition should be kept constant while the variance of the corresponding delays differs in each condition. This will be the subject of Experiment 3.

Chapter 4: Experiment Three

Introduction

The results from Experiment 1 and Experiment 2 were consistent with the optimal foraging predictions of the MVT, as participants dwelled longer when mean trial delays were longer. Specifically, Experiment 2 showed participants adhered to the predictions of the MVT when the variance of delays, relative to the mean trial delay, was held constant (± 2 -seconds). However, the MVT provides no predictions regarding optimal dwell time when the environmental delays are varied, but rather maintains that it is the mean rewards or delays in an environment that are pertinent to a forager's decisions. Therefore, Experiment 3 aimed to examine the extent to which human decisions in a time-based foraging task adhere to the MVT predictions of optimal foraging. Further, Experiment 3 aimed to determine if the variance of delays in each environment changed the performance of participant dwell times relative to the optimal predictions of the MVT.

The results from Experiment 1 and Experiment 2 confirmed the optimal foraging predictions of the MVT, as participants dwelled longer when mean trial delays were longer. Experiment 2 examined the effect of altering mean patch delays across a trial, while varying the individual delays within each patch. Importantly, in Experiment 2, the mean patch delays across a trial were varied, but the range of patch delays was held constant (± 2 seconds of the mean patch delay). Although the mean delay is the basis on which the predictions of the MVT are made, other studies have contended that foraging behaviour is not only determined by the mean delay in an environment, but also the extent to which patch delays within the environment are varied (M.

Bateson & Kacelnik, n.d.; Caraco, 1980, 1981; Caraco, Martindale, & Whittam, 1980;

J. R. Krebs, Kacelnik, & Taylor, 1978). Thus, Experiment 3 aimed to determine if the extent to which the delays are varied in an environment changed the dwell times relative to the optimal predictions of the MVT.

Experiment 3 involved comparing dwell times across trials, which differed in their variance of patch delays such that one trial type was comprised of patches with delays that were ± 2 -seconds from the mean trial delay, and the other with patches that were ± 4 -seconds from the mean trial delay. Unlike Experiment 2, however, the mean trial delay for both trial types was held constant at 6-seconds. Specifically, when the variance of patch delays was ± 2 -seconds, the possible patch delays were 4, 6, and 8 seconds. In contrast, when the variance of patch delays was ± 4 -seconds, the possible patch delays were 2, 6, and 10 seconds. An important feature of this design worth noting is the constant mean trial delay, which allowed me to distinguish the effect of patch delay variance from the mean (± 2 s or ± 4 s) on dwell times. This could potentially inform the predictions of the MVT regarding optimal foraging predictions in a patchy environment with low or high variance in delays for each patch.

Methods and Materials

Subjects. A total of 22 healthy participants volunteered for Experiment 3, of which 7 were male and 15 were female. Nineteen were right-handed, and 3 were left-handed. Ages ranged from 18 to 36 ($M = 21.3$, $SD = 3.87$). Inclusion criteria were identical to the preceding experiments.

Stimuli. The stimuli for this experiment were identical to those in Experiments 1 and 2.

Experimental Design. This experiment was similar to Experiment 2, except that, here, I manipulated the variance of delays within each trial, while holding the mean of each trial type constant. For all trials in this experiment, the mean trial delay was set at 6s. However, in one condition, the delay variance in each trial was low (with patch delays of ± 2 seconds, i.e. 4s, 6s, or 8s), and in the other, the delay variance was high (with patch delays of ± 4 seconds, i.e. 2s, 6s, or 10s). As in Experiment 2, there were four counterbalanced blocks of trials, with the Low and High Delay Variance conditions run over two blocks each.

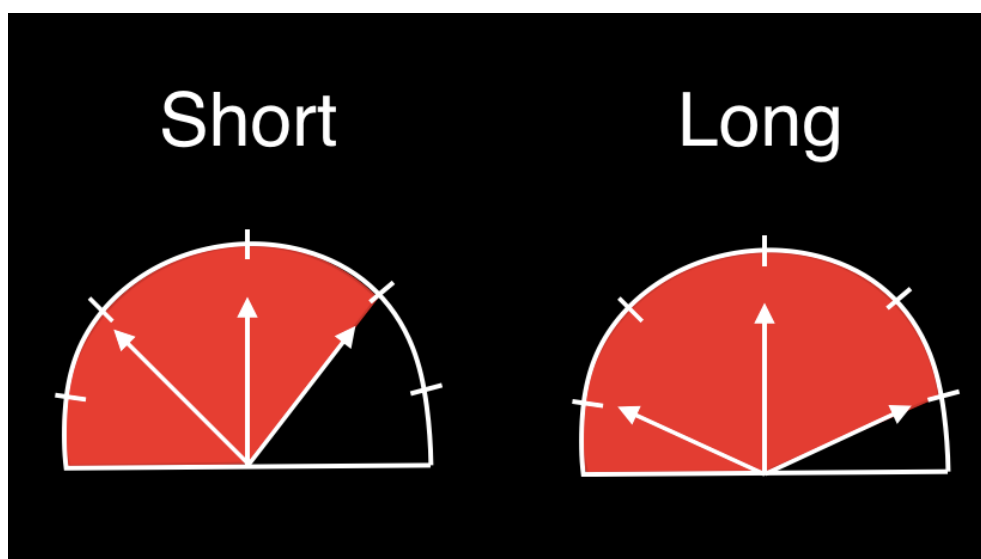


Figure 16. Possible delays for each patch in a trial. The possible patch delays (± 2 s or ± 4 s) relative to the mean trial delay, as presented to participants when the task was explained. Each block comprised multiple trials. Each trial comprised multiple patches with different delays according to the trial type (short or long). A block of 'short' trials would have several patches with 4, 6, or 8s delays. A block of 'long' trials would have several patches with 2, 6, or 10s delays.

Results

Mean Dwell Times. I ran a within-subjects repeated measures ANOVA on the Trial Delay Variance (high, +/- 4s; low, +/- 2s) and the Patch Delay (less than, equal to, or greater than the mean) on mean dwell times within each patch. This analysis showed no significant main effect of Trial Delay Variance, $F(1, 21) = .111, p = .743$.

Mauchly's Test indicated that sphericity had been violated for the factor of Patch Delay, $\chi^2(2) = 24.814, p = .000$, and was corrected with the Greenhouse-Geisser estimate, $\epsilon = .585$. There was a significant main effect of Patch Delay at the $p < .05$ level, $F(1.169, 24.550) = 11.860, p = .001$, which Bonferonni-corrected t-tests in a post-hoc analysis showed that patch dwell times progressively decreased with increasing patch delays, such that dwell times for patch delays less than the mean ($M = 10.21s, SD = 3.52s$) were longer than the dwell times for patch delays equal to the mean ($M = 8.66s, SD = 3.40s$), and greater than the mean ($M = 7.71s, SD = 2.95s$) (less vs. equal, $p = .003$; less vs. greater, $p = .006$; equal vs. greater revealed a trend at $p = .066$). There was no significant interaction, $F(2, 42) = 1.420, p = .253$. These results indicate that the extent to which the delays were varied in each condition had no effect on participant dwell times.

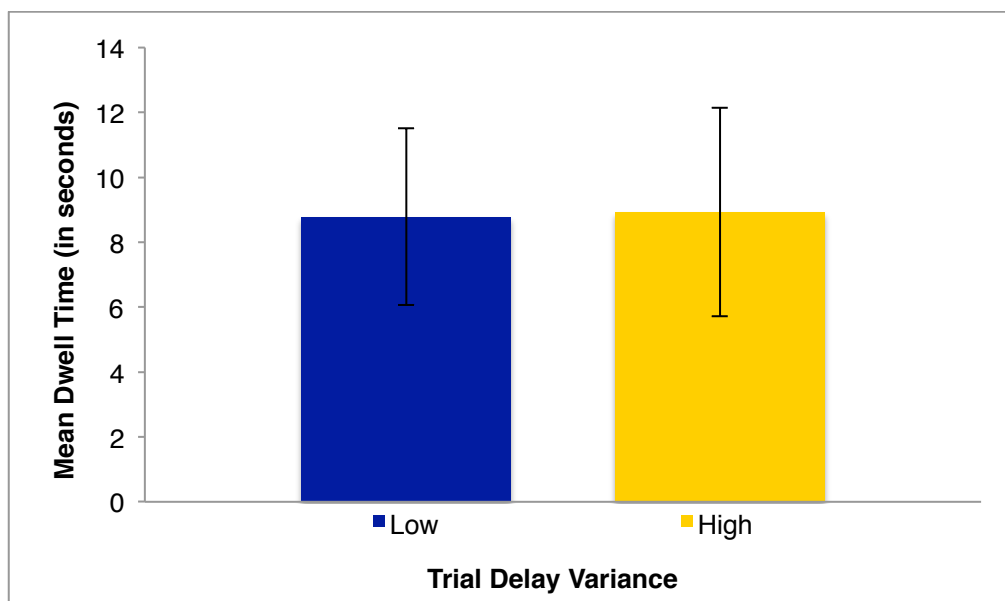


Figure 17. Mean dwell time (± 1 standard deviation) collapsed across patches within a trial. Each trial is comprised of patches that impose either a delay of low variance (± 2 s) or high variance (± 8 s) initial delay.

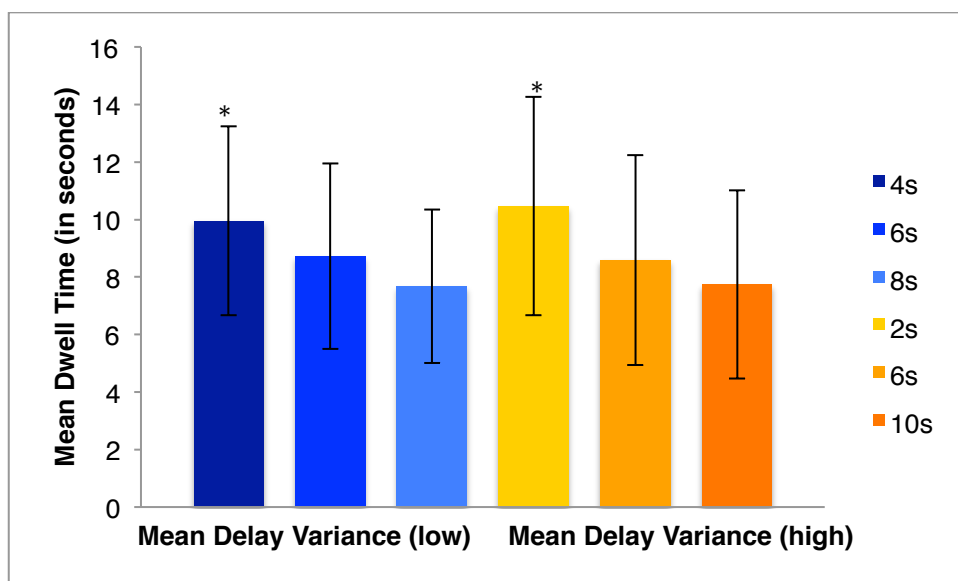


Figure 18. Mean dwell time (± 1 standard deviation) for each patch within a trial. Each trial is comprised of patches that impose either a low (± 2 s, in blue) or high (± 8 s, in orange) mean delay variance. Each patch within a trial involved a delay that was either equal to the mean, less or greater than it. Participants dwelled significantly longer in trials comprising patch delays that were less than the mean trial delay (*, $p < .05$).

Standard Deviation of Mean Dwell Times. In order to examine the extent to which participant dwell times differed in each condition, I ran a within-subjects repeated measures ANOVA on Trial Delay Variance (Low, High) and Patch Delays (less than, equal to, or greater than the trial mean) on the standard deviation of the dwell times. This analysis showed no significant main effect of Trial Delay Variance, $F(1, 21) = .678, p = .420$, such that the variance of dwell times for each Trial Delay Variance were not significantly different for the Low Trial Delay Variance condition ($M = 3.74s, SD = 1.08s$) or the High Trial Delay Variance condition ($M = 3.97s, SD = 1.56s$). Mauchly's Test indicated the assumption of sphericity had been violated for Patch Delay, $\chi^2(2) = 8.250, p = .016$, and was corrected for with the Greenhouse-Geisser estimate, $\epsilon = .747$. There was no significant main effect of Patch Delay, $F(1.495, 31.390) = 1.462, p = .245$, or interaction, $F(2, 42) = .643, p = .531$. Overall, this shows no effect on patch delay variability on the standard deviation of responses.

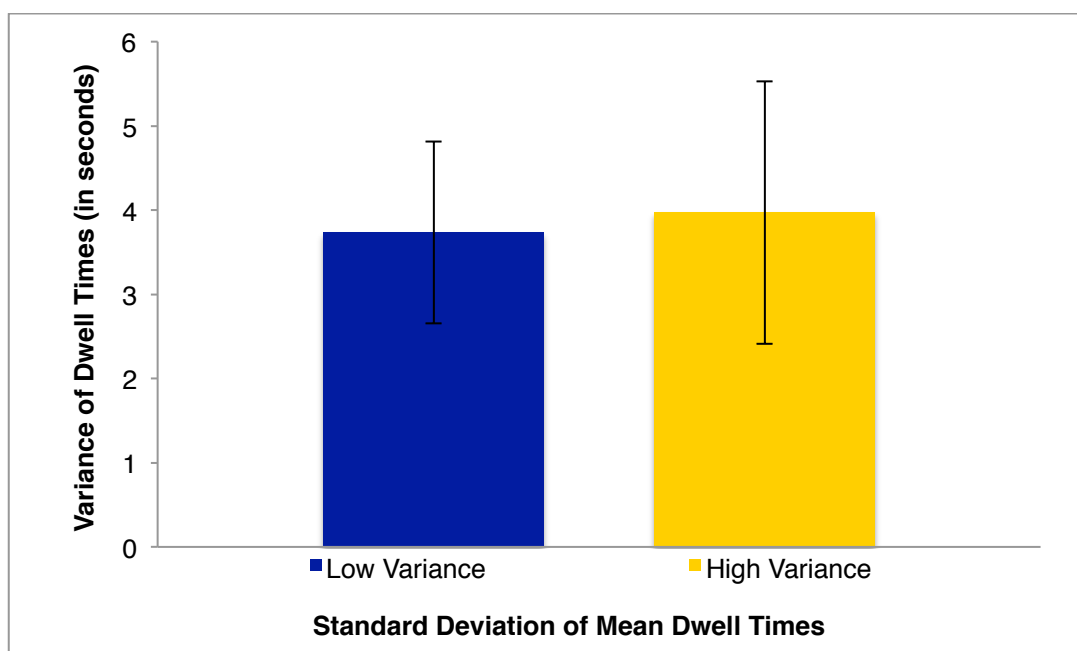


Figure 19. Difference of mean dwell time (+/- 1 standard deviation) for each trial.

Changes in Strategy Across an Individual Trial. To determine whether behaviour changed over the course of a trial, I compared the first and last patches with the analogous ANOVA to Experiments 1 and 2, on the factors of Mean Delay Variance (low, high), Patch Delay (less than, equal to, or greater than the mean), and Patch Position (first, last) on dwell times for each trial. This analysis showed a significant main effect of Patch Position, $F(1, 21) = 8.402, p = .009$, such that dwell times were longer for the first patches in a trial ($M = 9.95s, SD = 3.90s$) compared to the last patches ($M = 8.89s, SD = 3.24s$). Mauchly's Test indicated the assumption of sphericity had been violated for Patch Delay, $\chi^2(2) = 20.438, p = .000$, and was thereby adjusted for with Greenhouse-Geisser estimate, $\epsilon = .610$. There was a significant main effect of Patch Delay which was consistent with the analysis on Mean Dwell Times, $F(1.219, 25.608) = 6.316, p = .014$, showing that dwell times were longest for patch delays that were less than the mean ($M = 10.52s, SD = 3.61s$) and became progressively shorter for patch delays that were equal to ($M = 9.31s, SD = 3.45s$) and greater than ($M = 8.43s, SD = 3.53s$) the mean. There was no significant main effect of Mean Delay Variance, $F(1, 21) = .157, p = .696$, or interactions of Patch Position with Mean Delay, $F(1, 21) = 2.231, p = .150$, Patch Delay, $F(1.167, 24.517) = .764, p = .410$, or three-way interactions, $F(1.233, 25.889) = 2.412, p = .128$. As in the preceding experiments, these results showed participants to dwell for shorter periods of time in patches closest to the trial deadline, relative to longer dwell times for patches at the beginning of the trial.

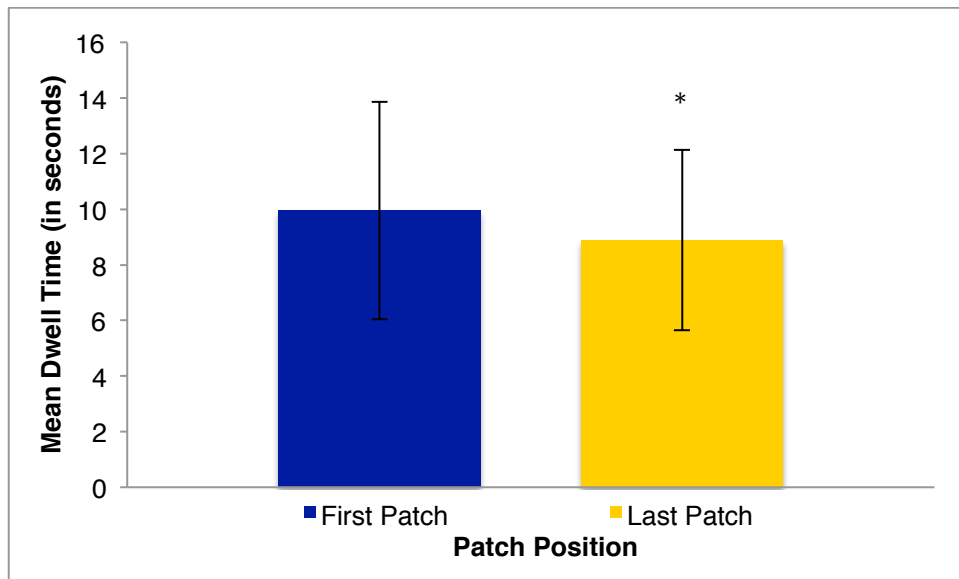


Figure 20. Mean dwell times (± 1 standard deviation) collapsed across trials for the first compared to the last patch in a trial. Dwell times were longer for the first patch than the last patch (*, $p < .05$).

Performance Relative to Optimal. Using a similar mathematical approach to Experiments 1 and 2, solving Equation 2 where $d = 6s$ and $\rho = 0.1$ gives an optimal dwell time of 9.27 seconds. The MVT predicts the dwell times for each type of trial (condition) should be relative to the mean delay of each environment. To determine the mean dwell time for each trial type relative to the optimum (for mean delay of 6s for both trial types), I conducted one-sample t-tests comparing participant dwell times for each condition to the optimal dwell time (determined by the mean trial delay of 6s). Bonferroni-correction for multiple comparisons was applied to prevent false positive results, with the critical p -value being $0.05/2 = 0.025$. With this correction, participant dwell times were not significantly different from the optimum for the Low Trial Delay Variance condition ($p = .655$, $M = 9.01s$, $SD = 2.66s$) or for the High Trial Delay Variance condition ($p = .926$, $M = 9.20s$, $SD = 3.29s$). This thereby indicates that participants were performing in accordance with the predictions of the MVT regarding optimal foraging behaviour.

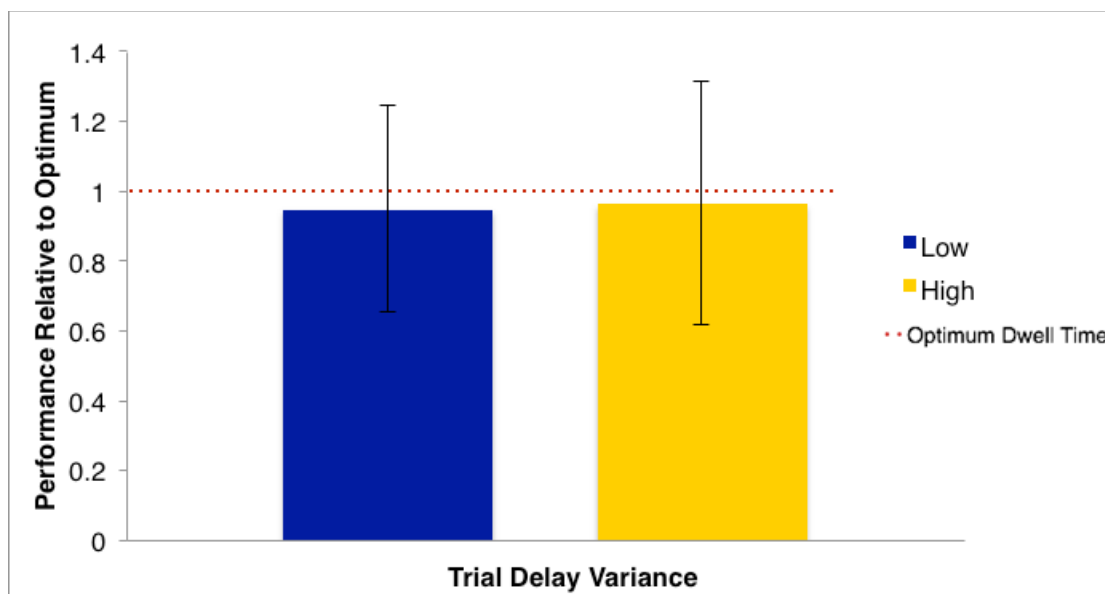


Figure 21. Performance relative to optimum. Optimal dwell time for each condition, as predicted by the MVT, represented by the red dotted line. Error bars that are >1 indicates participants dwelled longer than optimum; <1 indicates participants dwelled less than optimum.

Correlations. Correlations between total experimental duration and measures of the BIS-11 revealed no significant correlations (all $r_s > .007$; all $p > .05$) [Appendix C].

Discussion. In this experiment, I examined the effect of altering the variance of patch delays within a trial, while holding the mean patch delay of those trials constant. The results showed mean dwell times were not affected by the variance in patch delays. Given that the optimal dwell time predictions of the MVT are based on the mean environmental delays, the findings from this experiment are consistent with the predictions of the MVT in this regard. Furthermore, these results are in line with the predictions made based on the findings from Experiment 2, which showed the mean delay of the environment to be a determinant of participant dwell times. In

Experiment 3, the mean delay was found to determine participants' dwell times in each patch, and further demonstrated the variance of delays to have no effect; and thereby is consistent with the findings from Experiment 2.

In this experiment, I examined the effect of varying patch delays on participant dwell times by manipulating the *range* of delays ($\pm 2s$ vs $\pm 4s$), while holding the mean patch delays constant. The results showed the dwell times for each condition to be consistent with the predictions of the MVT, and thereby adhere to the mean delay of the environment. However, ecological studies have shown that animals have a tendency to be sensitive to the variance of patches throughout an environment (Bateson & Kacelnik, n.d.; McNamara & Houston, 1992; Smith, 1974). In particular, the variance of patches in an environment does not only pertain to the range of patch delays, but also to the volatility of patch delays in an environment. The volatility of patch delays in an environment thereby denotes the extent to which the next patch delay is consistent with the current patch delay, and therefore stable.

Thus, another way to examine the effect of varying patch delays is by manipulating the variance of delays – in terms of the frequency with which patch delays change or remain the same over the course of a trial – while holding the mean and the range of the delays constant. This will be the subject of Experiment 4.

Chapter 5: Experiment Four

Introduction

Ecological studies of foraging behaviour have found animals to be sensitive to the variance of patches throughout an environment (M. Bateson & Kacelnik, n.d.; Caraco, 1981; McNamara & Houston, 1992; Pyke, 1984). The MVT does not make predictions regarding the volatility or variance of reward rates (or delays) within an environment; and only refers to the variance of an environment to ascertain that different patch types should be randomly distributed throughout the environment (Charnov, 1976). However, several studies have contended that – in addition to the mean of the environment – the variance of reward rate (or delay) across patches in an environment is critical to an animal's foraging decisions (Caraco, 1980; Green, 1979; Iwasa, Higashi, & Yamamura, 1981; McNair, 1982; Oaten, 1977; Pyke, 1984; Schoener, 1971; Stephens & Charnov, 1982)

As established in Experiment 2 and Experiment 3, the dwell time for each condition is determined by the mean delay of each environment and is consistent with the predictions of the MVT; which denotes the dwell time within a patch is dependent on the average reward or delay in the environment. Importantly, Experiment 3 showed that dwell time is not determined by the variance of patch delays relative to the mean. However, another way to examine the effect of varying patch delays on dwell times is by manipulating the variance of delays, in regards to the frequency with which patch delays changes or remain the same in an environment, while holding the mean and the range of the delays constant.

In this experiment, each trial was either ‘stable’, comprising infrequent changes in patch delays, or ‘volatile’, in which changes in patch delays were more frequent.

Methods and Materials

Subjects. A total of 22 healthy participants volunteered for the fourth experiment, of which 2 were male, and 20 were female. Fifteen participants were right-handed and 7 were left-handed. Ages ranged from 18 to 23 ($M = 19.6$, $SD = 1.7$). Inclusion criteria were identical to Experiments 1-3.

Stimuli. The stimuli for this experiment replicates those used in previous experiments.

Experimental Design. This experiment was similar to Experiment 3, except that here I manipulated the volatility of delays within each trial while maintaining the mean delay constant. For all trials in this experiment, the mean trial delay was set at 6 seconds. However, in one condition the volatility of the patch delays was low (comprised of 4s and 8s delays that alternated every 5 or 6 patches, with 50% probability), and in the other, the volatility of the delay was high (comprised of 4s and 8s delays that alternated every 1 or 2 patches, with 50% probability). As in Experiment 3, there were four counterbalanced blocks of trials, with the Low Volatility and High Volatility conditions run over two blocks each, in A B A B or B A B A fashion.

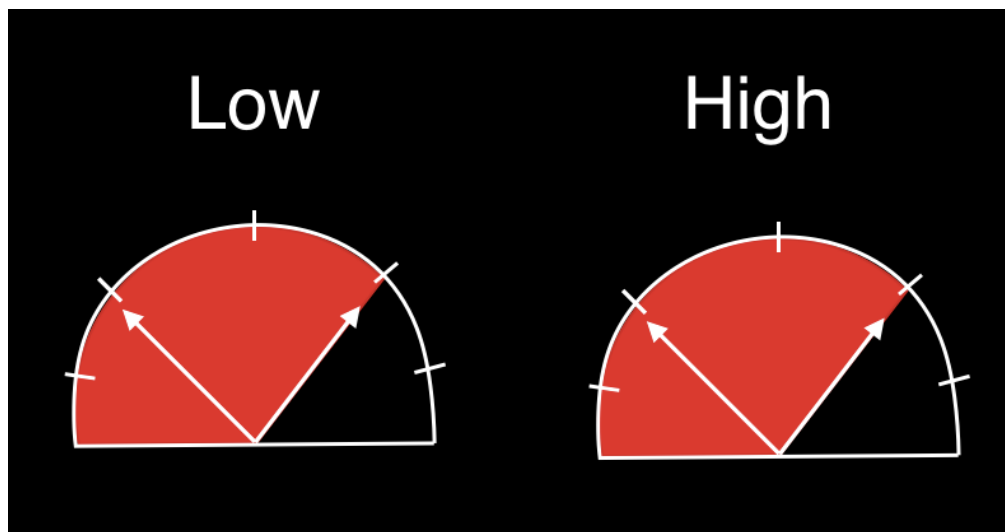


Figure 22. Possible delays for each patch in a trial. The possible patch delays (± 2 s or ± 4 s) relative to the mean trial delay, as presented to participants when the task was explained. Each block comprised multiple trials. Each trial comprised multiple patches with different delays according to the trial type (short or long). A block of ‘short’ trials would have several patches with 4, 6, or 8s delays. A block of ‘long’ trials would have several patches with 2, 6, or 10s delays.

Results

Mean Dwell Times. I ran a within-subjects repeated measures ANOVA on the Delay Volatility (high, low) and the Patch Delay (4s, 8s) on mean dwell times within each patch. This analysis showed no main effect of Delay Volatility, $F(1,17) = .006, p = .937$. This analysis did show a significant main effect of Patch Delay, $F(1,17) = 10.540, p = .005$, such that the dwell times were longer after a shorter delay of 4-seconds ($M = 9.84s, SD = 2.83s$) and comparatively shorter after a longer delay of 8-seconds ($M = 7.76s, SD = 1.78s$). There was no significant interaction, $F(1,17) = 2.020, p = .173$. This demonstrates that the volatility of delays did not have an effect on participant dwell times, however participants were dwelling longer for reward when presented with a short delay (4s), and dwelling less for reward when presented with a long delay (8s).

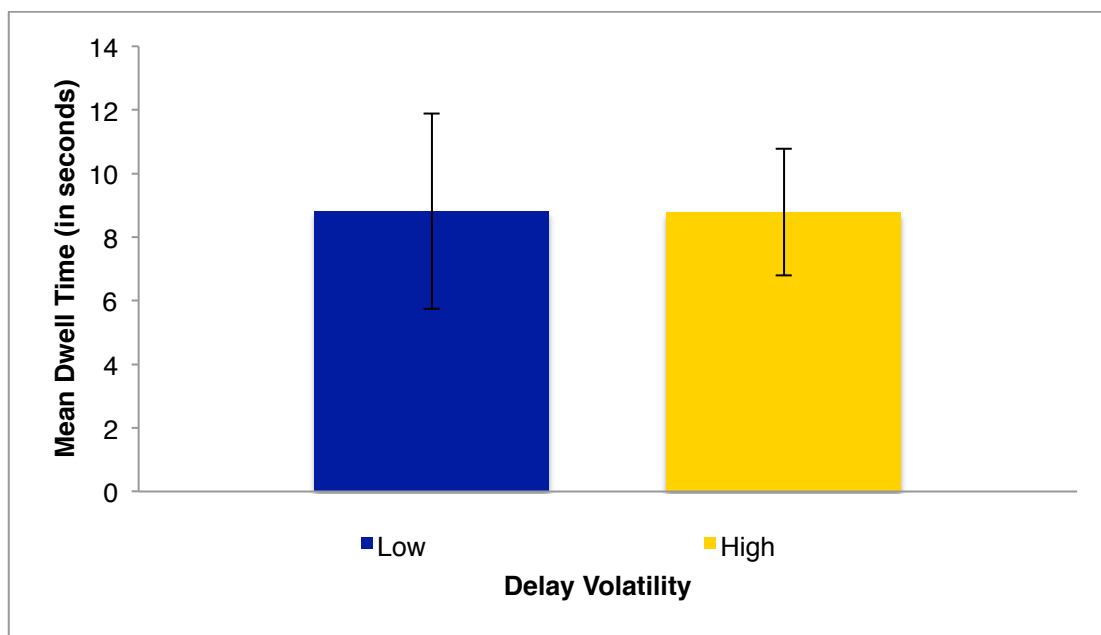


Figure 23. Mean dwell times (± 1 standard deviation) as a function of condition. Dwell times were not significantly different.

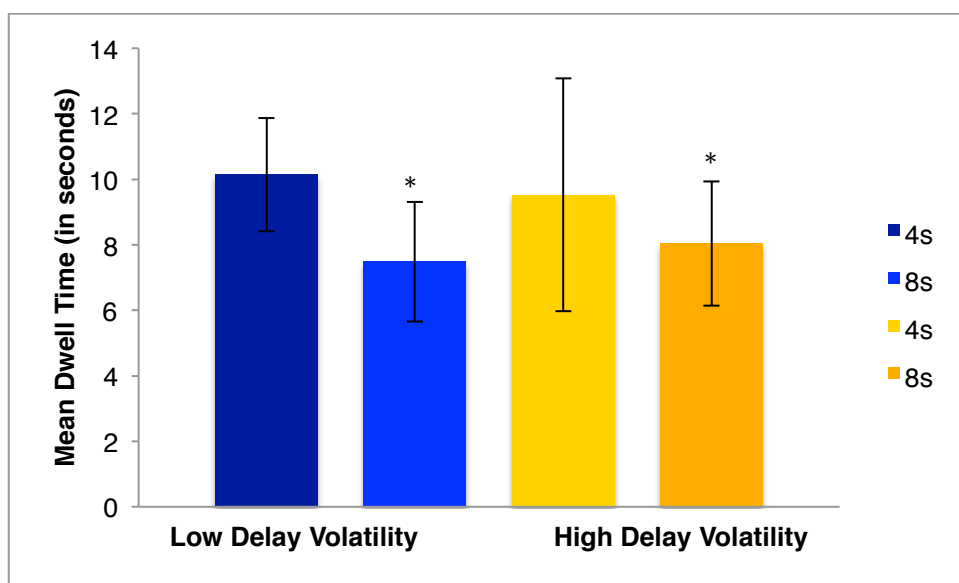


Figure 24. Mean dwell time (± 1 standard deviation) for each patch within a trial. Each trial was comprised of patches that impose a delay (4s or 8s) that changed frequently (high volatility; orange) or infrequently (low volatility; blue). Dwell times were shorter for the 8s patch delays compared to the 4s patch delays for each trial condition (*, $p < .05$).

Standard Deviation of Dwell Times. As in previous experiments, I examined variability in dwell times by calculating the standard deviation for each trial type, and subjecting this to a within-subjects repeated-measures ANOVA on the conditions of Delay Volatility (Low, High) and Patch Delay (4s, 8s) on the standard deviations of the dwell times. This analysis showed no significant main effect of Delay Volatility, $F(1,17) = .871, p = .364$, or of Delay, $F(1, 17) = .583, p = .456$. There was no significant interaction, $F(1,17) = .545, p = .470$. This demonstrates that the amount of time participants spent dwelling in each patch did not vary significantly between conditions or between patch delays.

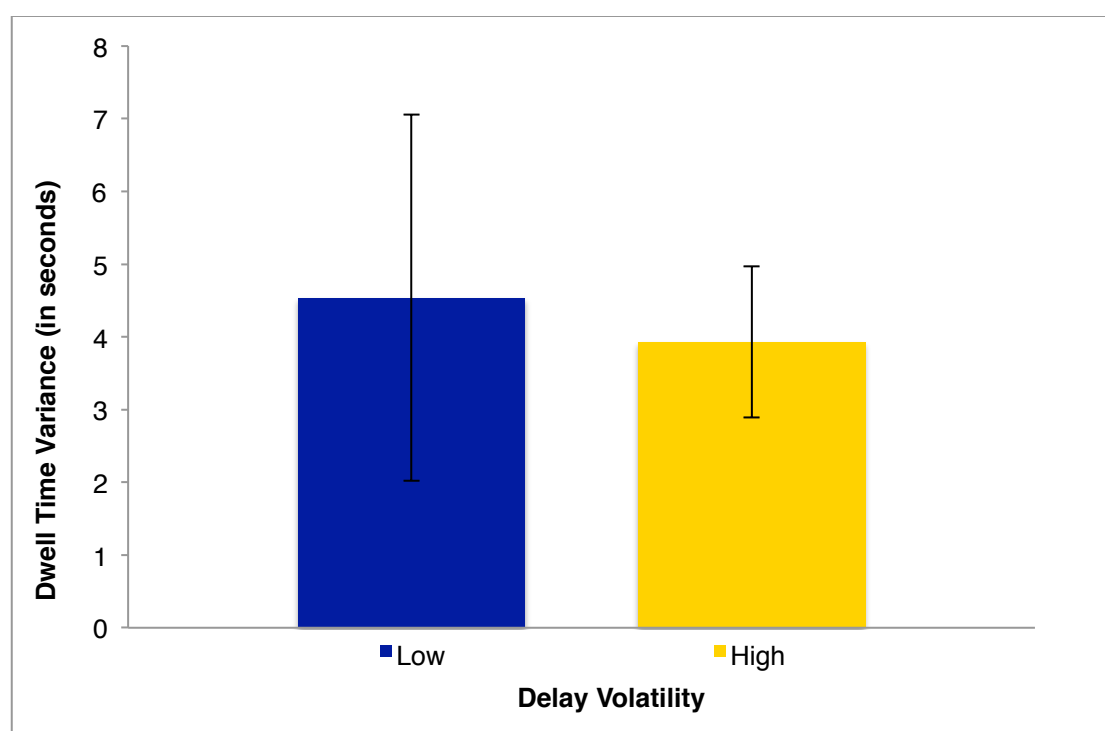


Figure 24. Variance of mean dwell times (± 1 standard deviation). Less variance for trials with greater volatility than trials with low volatility in delays.

Changes in Strategy Across an Individual Trial. I ran a within-subjects repeated measures ANOVA on Delay Volatility (high, low), Patch Delay (4s, 8s), and Patch Position (first, last) on dwell times for each trial. This analysis showed a significant

main effect of Patch Position, $F(1, 16) = 6.269, p = .023$, such that dwell times were longer for the first patches ($M = 10.22s, SD = 4.56s$) compared to the last patches in a trial ($M = 9.22s, SD = 2.99s$). Consistent with the analysis on mean dwell times, there was a significant main effect of Patch Delay, $F(1, 16) = 5.735, p = .029$, such that dwell times were longer for 4-second patch delays ($M = 10.61s, SD = 4.66s$) and shorter for 8-second patch delays ($M = 8.41s, SD = 2.35s$). There was no significant main effect of Delay Volatility, $F(1, 16) = .150, p = .704$, or interactions of Patch Position and Delay Volatility, $F(1, 16) = 2.070, p = .170$, Patch Delay, $F(1, 16) = 1.756, p = .204$, or three-way interaction, $F(1, 16) = .017, p = .897$. These results showed participants dwelled shorter for reward in patches near the end of a trial compared to longer dwell times in patches at the beginning of a trial.

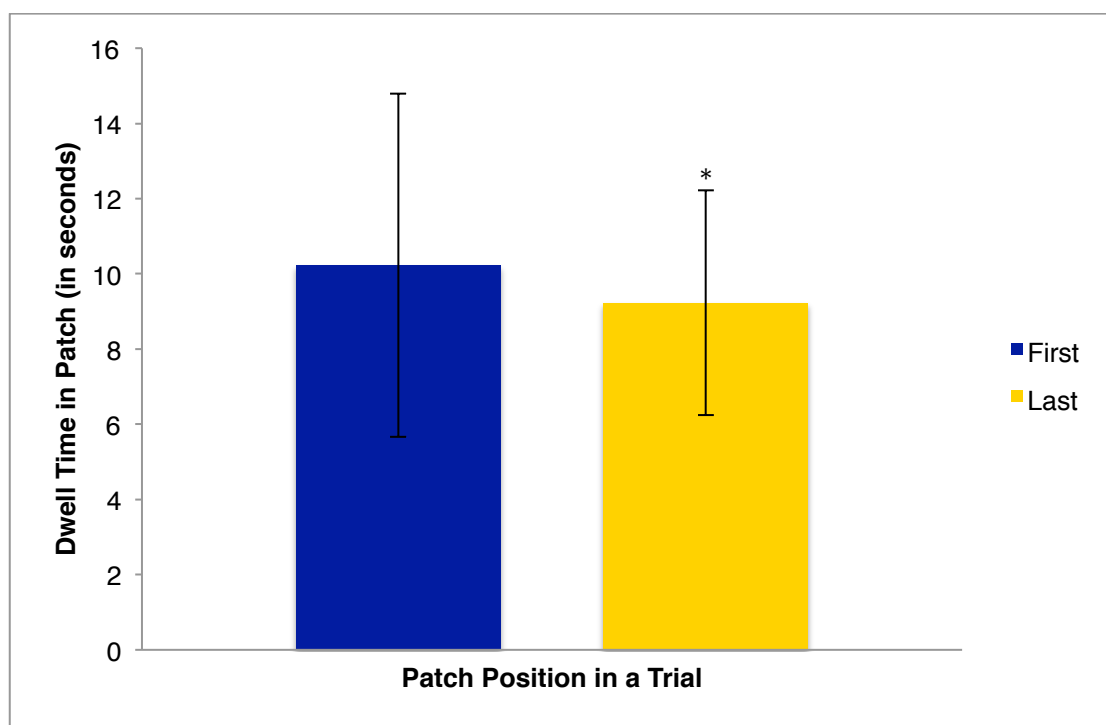


Figure 25. Dwell times (± 1 standard deviation) were longer for the first patch compared to the last patch in a trial (*, $p < .05$).

Performance Relative to Optimum. Using a similar mathematical approach to Experiments 1, 2, and 3, solving Equation 2 where $d = 6s$ and $\rho = 0.1$ gives an optimal dwell time of 9.27s. To determine the mean dwell time for each condition relative to the optimum (6s), I conducted one-sample t-tests comparing participant dwell times for each condition to the optimal dwell time. Bonferroni-correction for multiple comparisons was applied to prevent false positive results, with the critical p -value being $0.05/2 = 0.025$. With this correction, participant dwell times were not significantly different from the predicted optimum for the low Delay Volatility condition ($p = .406$, $M = 10.29s$, $SD = 5.09s$), or for the high Delay Volatility condition ($p = .646$, $M = 9.07s$, $SD = 1.75s$). This suggests that participant performance in each condition was not different to the predictions of the MVT.

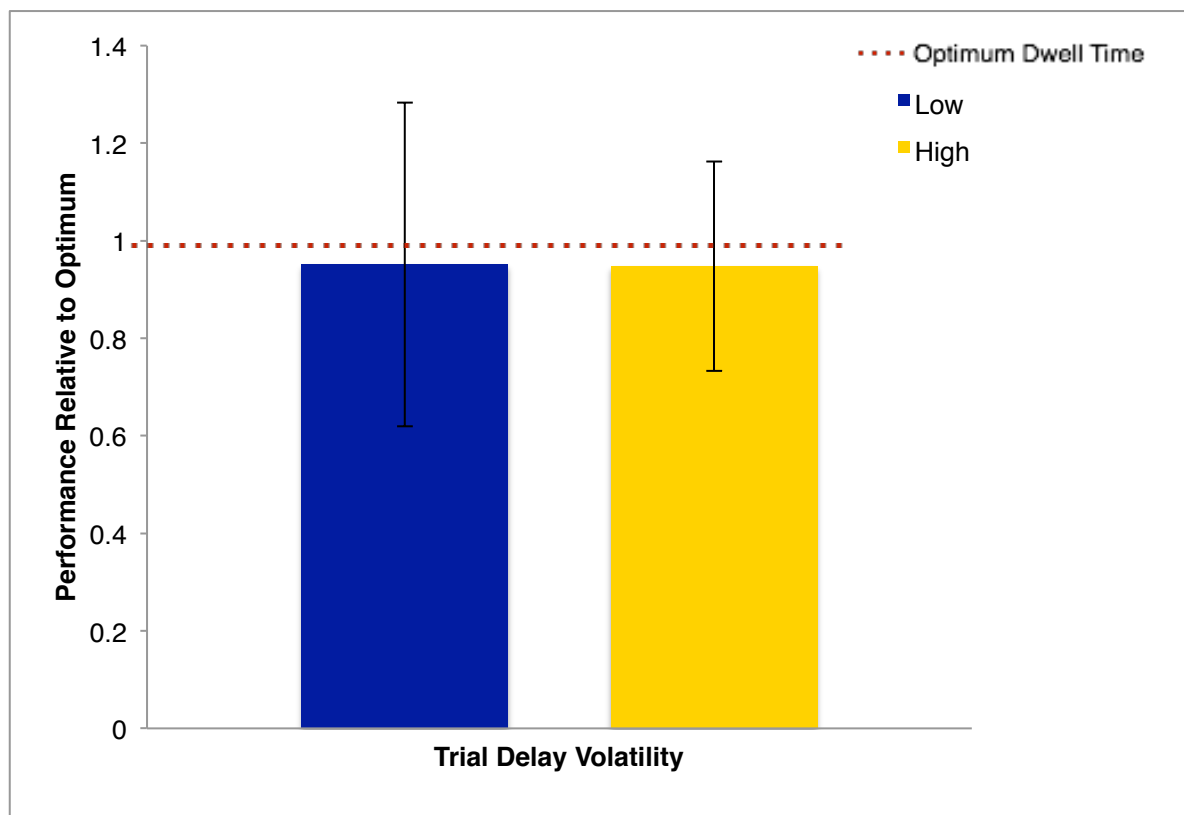


Figure 26. Performance relative to optimum. Optimal dwell time for each condition, as predicted by the MVT, represented by the dotted line. Standard error bars that are >1 indicates participants dwelled longer than optimum; <1 indicates participants dwelled less than optimum.

Correlations. Consistent with the correlations conducted in the previous experiments, I ran bivariate correlations between the overall experiment duration (total sum of dwell time and delay time) and the results of the BIS-11 questionnaire. The results yielded no significant correlations ($r_s > .006, p > .066$) [Appendix D].

Discussion. This experiment varied the volatility of patch delays within each trial, in order to further examine the effect of variance on participant dwell times relative to the optimal dwell times predicted by the MVT. The results showed no difference between the volatility and stability of patch delays in a trial, and thereby indicate that participants performed in accordance with the predictions of the MVT. Importantly, this result is consistent with the findings from Experiment 2 and Experiment 3.

Further, the results from this experiment showed participants dwelled longer in patches with a 4-second delay, and dwelled comparatively shorter in patches with 8-second delays. This pattern of patch behaviour is consistent with the findings from Experiment 2 and Experiment 3, in which participants dwelled longer for patch delays that were less than the mean delay for each condition, and dwelled progressively shorter for patch delays that were equal to, or greater than the mean delay for each condition. However, the results from this experiment show participants were performing according to optimal for each trial, even though this result was driven by longer dwell times in the patches with 4-second delays. Notably, the MVT bases its predictions of optimal foraging on the average rate of reward – or delay – in the environment, and thereby does not predict behaviour on an individual patch level (Charnov, 1976).

Chapter 6: Discussion

In this research, the primary goal was to test the directional predictions of the Marginal Value Theorem (MVT), and a secondary goal was to examine the performance of participants relative to the optimum. Each task examined the extent to which human foraging decisions adhered to – or deviated from – what the MVT had predicted to be optimal, and further examined the effect that different variables had on participants' performance. The variables examined included: fast and slow reward rates coupled with short or long delays (Experiment 1); delays varied relative to the mean trial delay (Experiment 2); different degrees of delay variance from the mean trial delay (Experiment 3); and different frequencies (volatility) at which the delay changed in a trial (Experiment 4).

Trial Times Decided by Mean Trial Delays

The main goal of this study was to test the prediction of the MVT, which indicated individuals should dwell longer in trials (environments) associated with longer delays or slower reward rates. This was confirmed in Experiment 1. Experiment 2 further confirmed the predictions of the MVT, which noted that these findings should be relative to the mean features of the trial environment, rather than the individual features of the patches comprising that environment. This is consistent with the findings of ecological studies, in which the average dwell time of an animal foraging in an environment corresponded to the optimal dwell time predicted by the MVT (Cassini et al., 1993; J. N. M. Smith & Sweatman, 1974). Furthermore, participants in this study were informed of all the relevant features for the experiments, and thereby had complete information on which to base their decisions. Given this, the findings

from Experiment 1 and Experiment 2 are also consistent with the predictions of other optimal foraging theories – such as hunting by expectation, giving-up time (GUT), and stochastic models – which predict that an omniscient animal will forage more optimally than a naïve animal (Gibb, 1966; Green, 1979; Hodges, 1981; McNair, 1982).

The variance and volatility of patch delays did not result in changes in dwell time. Although the MVT makes specific predictions about performance relative to the mean trial environment, it remains agnostic about whether the variance or volatility of features within a trial should affect behaviour. Experiments 3 and 4 found that behaviour in the foraging task was not significantly altered by the variance or volatility of patch delays. These results suggest that participants used the information about the task that was provided, in addition to their knowledge of the trial features gained through their experience of trials, to determine the optimal method that maximised their reward gain.

Interestingly, in many circumstances, there is evidence that the variance or volatility of a trial environment affects decisions (Barnard et al., 1985; Caraco et al., 1980; Dukas & Real, 1993; Sutherland & Anderson, 1987). Animals have been found to be sensitive to factors of environmental variance or volatility which results in foraging behaviour that deviates from the predictions of the MVT (Bateson & Kacelnik, n.d.; Caraco, 1981; Real & Caraco, 1986). Further, when the animal is foraging with limited knowledge or experience of the environment, the environmental variance or volatility further impedes the rate at which it is able to learn about the mean

environmental features; such as the extent to which delays or rewards vary, or the frequency with which they change (McNamara & Houston, 1992).

However, there are also instances in which decisions are not affected by variance and volatility (Gibb & Betts, 1963; Iwasa, Higashi, & Yamamura, 1981; Krebs, Kacelnik, & Taylor, 1978; Krebs, Ryan, & Charnov, 1974). In such instances, the foraging animal has complete information of the mean environmental features and is thereby able to behave in accordance with the mean reward rate, or mean delay, and circumvent the hindrance that would otherwise be imposed by the variability or volatility of the environment.

The findings of Experiments 3 and 4 are therefore consistent with the latter body of evidence, and is overall consistent with the MVT which states that the major determinant of foraging behaviour are the mean features (delays or reward rates) of an environment.

Mean Trial Performance Relative to Optimum

To further test the predictions of the MVT, which denoted that participants would dwell longer after long delays and slower rewards rates, the mean trial performance of participants was compared to the predicted optimal dwell time for each condition. The findings from Experiment 1 showed that in the extreme conditions – where short delays were coupled with fast reward rates, and long delays were coupled with slow reward rates - participant performance deviated from the predicted optimum.

This finding is consistent with that of some ecological studies in which the quality of an environment resulted in dwell times that were longer or shorter than the MVT predicted to be optimal (Cassini et al., 1990; Munger, 1984; Pyke, 1978; Tome, 1988). The quality is determined by evaluating the mean costs (delay) and benefits (rate at which reward is gained) of an environment (trial) compared to that of others, given that the goal is to maximise the reward gained. Thus, in Experiment 1, the trial that was comprised of short delays and fast reward rates would be of better quality than the trial with long delays and slow reward rates. The random counterbalanced sequence in which participants completed the conditional blocks might have caused a framing effect, which thereby would have enabled participants to assess the comparative costs and benefits of each trial to determine the trial quality. The trade-off of the costs and benefits for each of the four trial blocks would have been further instigated if participants were attempting to maximise the reward gained over the course of the entire experiment, as opposed to maximising the reward gained within each trial, or trial block.

The two intermediary conditions in Experiment 1 – comprised of short delays and slow rewards, or long delays and fast rewards – show the foraging behaviour of participants to be consistent with the optimum, as predicted by the MVT. The foraging behaviour of participants was also consistent with the MVT predictions for Experiment 2, Experiment 3, and Experiment 4.

Variance of Mean Trial Times

Although the findings showed dwell times to be consistent with the predictions of the MVT, another important consideration pertains to determining how the trial features

influenced the variability of participants' responses. The results showed that dwell times in Experiment 1 and Experiment 2 were less varied for conditions (trials) that consisted of fast reward rates or short mean trial delays, than for trials with slow reward rates or long mean trial delays. This finding is consistent with the mean trial dwell times, which showed that dwell times were shorter for conditions with fast rewards or short mean trial delays. Given that the mean dwell times were shorter for these trials, it follows that there was less variance in dwell times for the same conditions.

The results from Experiment 3 and Experiment 4 showed that the dwell times were not significantly different for the conditions (trials) that consisted of high or low delay volatility or delay variance. This finding is consistent with the corresponding mean trial dwell times, which showed that the mean volatility or variance of trial delay determined participants' dwell times. Importantly, in Experiment 3 and Experiment 4, the mean trial delay was 6-seconds for the two types of trials (conditions) comprising each task.

Therefore, these findings suggest that when the mean environmental (trial) features (delay or reward rate) are identical for each patch in a trial, there is greater variance in dwell times – particularly for conditions in which patches consist of longer delays or slower reward rates (Experiment 1). However, when the mean is the same but the types of patches comprising the trial are varied, there are less variance, or no significant difference, in dwell times (Experiment 2, 3, and 4). Importantly, these results are consistent with the predictions of the MVT, which denotes that the mean features of the environment are integral to foraging decisions.

Individual Patch Behaviour

Although the MVT provides good directional predictions about dwell times relative to mean trial features, it does not provide any indication of how individuals should behave in individual patches. Interestingly, in Experiment 3 and Experiment 4, although there were no differences in the mean dwell times across trials with low and high variance or volatility, individuals dwelled longer in patches within a trial that were associated with short delays as opposed to longer delays.

The ‘giving-up’ time (GUT) is a foraging theory derived a posteriori from empirical observations, which assesses the amount of time that passes between the point at which the animal finds the last reward in a patch until it decides to leave the patch. This term was coined by Croze, who explained that the “The Giving-Up Time... is taken to be a quality of the [animal’s] persistence – and expression of the amount of effort the predator is willing to allot in pursuing one more of a particular prey” (as cited in McNair, 1982, pp. 512). Specifically, the GUT denotes that an animal will use its experiences of patches within the environment to determine the quality of the patch, and how long to dwell in the patch based on its established temporal threshold. For example, if a giraffe has determined it can gain 8 acacia leaves (rewards) in 10 minutes from a single branch, it will remain searching for leaves to eat from the same branch so long as it continues to gain 8 acacia leaves within that threshold of time. However, if 10 minutes passes and the giraffe has not gained the expected 8 acacia leaves, it will leave the current branch and move on to the next. Importantly, based on this, the GUT is predicted to be longer for patches of better quality. The quality of a patch is determined by evaluating the costs and benefits of a patch, relative to that of

other patches in the environment. That is, if the costs and benefits for one patch type (*A*) are comparatively better than those of other patch types (*B* and *C*), the GUT will be larger for *A* than it will be for *B* and *C* (McNair, 1982).

Several studies have examined optimal foraging behaviour using the GUT to determine the point at which the animal will cease searching for prey in the current patch and move on to the next, and provided empirical evidence that supports the GUT as a measure of optimal foraging behaviour (Brunner, Kacelnik, & Gibbon, 1992; Cook & Hubbard, 1977; Krebs et al., 1974; Smith & Sweatman, 1974; Townsend & Hildrew, 1980; J. A. van Gils & Tijssen, 2007; van Gils, Schenk, Bos, & Piersma, 2003; Wildhaber, Green, & Crowder, 1994; Ydenberg, 1984). Specifically, the use of a GUT has shown that animals are able to adapt their foraging behaviour in response to changes in the environment, and still perform optimally. This has been found to occur as a result of the animal assessing the quality of different patches as it forages within its environment. The GUT is thereby determined by the animal's assessment of patch quality, with resource-rich patches entailing longer GUT, and shorter GUT in patches that are resource-poor (McNair, 1982).

Notably, the mean trial dwell times were consistent with the predictions of the MVT, however the results from Experiment 3 and Experiment 4 showed patch behaviour to be longer after short delays, and shorter in long patch delays, relative to the mean delay. The MVT uses the mean environmental features as the basis for its predictions, and thereby does not claim to predict foraging behaviour in individual patches; nor does it account for the variance or volatility of an environment. Therefore, I purport that the GUT provides an account for the unpredicted patch behaviour in Experiment

3 and Experiment 4, as it considers the quality of individual patches and uses the forager's knowledge of the environment to determine the GUT. Whereas the GUT denotes patch quality to be determined by evaluating the costs and benefits for each patch relative to other patches in the environment, the tasks for Experiment 3 and Experiment 4 were comprised of equal rewards (benefits) accrued at the same diminishing rate. Thus, the associated temporal costs was the key determinant of patch quality. It follows then that patches with short delays were perceived to be 'better' patches, and patches with longer delays were 'poor' patches. Therefore, participants dwelled longer in 'better' patches and shorter in 'poorer' patches. With this logic, the GUT provides an account for the observed behaviour in individual patches for Experiment 3 and Experiment 4. Although the GUT adequately explains patch behaviour, particularly when the environment is variable or volatile, it does not make predictions of foraging decisions that are based on the mean environmental features; whereas the MVT does. The primary goal of the tasks used in Experiment 3 and Experiment 4 was to determine if environmental variability or volatility effected mean dwell times relative to the predictions of the MVT.

An alternative explanation might be provided by the use of heuristics, or 'rules of thumb', in which participants used compensatory processes to trade-off the amount of time spent traveling to a patch (delay) relative to the rate of reward gain (Hutchinson & Gigerenzer, 2005; Iwasa et al., 1981; Kurz-Milcke & Gigerenzer, 2007). In the foraging tasks for Experiment 3 and Experiment 4, each 'patch' had both the delay (travel time) and the reward bar present. The use of simple heuristics thereby denotes that participants compensated for the differences in patch delays within a trial by ensuring that approximately the same amount of time was spent in

each patch; longer delays would yield shorter dwell times, to result in the same mean dwell time in a patch.

Therefore, the use of simple heuristics or the application of the ‘giving-up’ time theory present adequate accounts for the foraging behaviour observed in individual patches for Experiment 3 and Experiment 4, as the MVT does not make predictions of patch behaviour. However, these experiments were designed to examine the MVT predictions of foraging behaviour relative to the mean environmental features, and to determine if environmental variability or volatility effected the mean performance.

The Effect of Trial Time on Behaviour

The MVT predicts mean dwell times across a trial environment. However, as previously discussed, it does not predict performance within individual trials. Here, I showed that performance across patches differed significantly as a function of trial duration, such that dwell times in the first patch of each trial were significantly longer than dwell times in the last patch. This is consistent with a large body of evidence, which suggests animals will change their foraging behaviour based on the time horizon (Bateson & Kacelnik, n.d.; Bateson & Klopfer, n.d.; Caraco, 1980, 1981; Kolling, Wittmann, & Rushworth, 2014; Krebs & Kacelnik, 1984; McNamara & Houston, 1992). For example, during the day animals will pursue prey choices that will gradually help them meet their energy intake requirements for the day. However, as nightfall approaches, animals begin to pursue prey choices that are riskier but may yield more energy, particularly if the animal has not yet met its energy intake requirements necessary for them to survive the night. The four experiments presented in this study had an imposed delay, after which reward was gained at a diminishing

rate; this thereby denotes that reward was accrued rapidly to begin with. Thus, as the time horizon approached, participants made ‘riskier’ foraging decisions and switched to a replenished patch rather than remaining in a patch with depleting resources in an effort to maximise their reward within a small timeframe. This resulted in the observed effect of time horizons on participant dwell times in patches across trials, which is consistent with this larger body of work.

One feature of this research, which differs from more naturalistic accounts of foraging, is that the features of the trial environment were declared to participants at the beginning of each block of trials. Thus, individuals had explicit knowledge of the possible delay times and reward rates for each trial of that block. Therefore, although the results of this research are largely in keeping with the predictions of the MVT, they apply in the particular circumstance in which individuals had complete knowledge of each trial environment, which is not always the case in real life.

The features of the trial environment in this study were declared to participants to eliminate learning during the trial and to determine whether the predictions of the MVT were sustained. As a result, future studies can examine how behaviour changes as more information is learnt. This can be done, for example, by examining whether there is an effect of the preceding trial on behaviour in the current trial when environmental features are uncertain.

Limitations

In most cases, comparing participants’ mean dwell times in a trial to the optimum predicted by the MVT revealed no significant differences (e.g., Experiments 2-4).

Although this indicates that participants' performance in these experiments is thereby consistent with the predictions of the MVT, this data should be interpreted with caution given that it rests on a null difference between performance and the predicted optimum. It is unlikely that the reason for the null difference in Experiments 2-4 was due to insensitivity of the paradigm to detect any differences from the optimum, as Experiment 1 showed deviations from the optimum at extremes of the feature space (long delay, slow reward rate; short delay, fast reward rate). Future studies may provide further insight into behaviour relative to the optimum by incorporating a larger range of delay and reward rates into a single experiment, with the aim of computationally modelling participants' behaviour and comparing it to the dwell times predicted by the MVT.

Furthermore, in this study, participants completed the Barratt Impulsivity Scale (BIS-11) questionnaire (Patton, Stanford, & others, 1995). The findings from previous studies of impulsivity, as it pertained to rewards and delays, suggested that traits of impulsivity would result in discounting of delayed rewards, and thereby yield shorter dwell times in the task (Grecucci et al., 2014; Housden, O'Sullivan, Joyce, Lees, & Roiser, 2010; Mobini et al., 2007; Sinha et al., 2013). The scores obtained from this questionnaire were used to determine if there was a correlation between traits of impulsivity and dwell times; however the results yielded no significant correlations. This result is attributed to the small sample sizes for each experiment, in which there were approximately 20 participants for each. However, given that the data shows participant behaviour to be relatively consistent with the predictions of the MVT, testing more participants in the future would increase the sample size so that a significant correlation could be found, if there is one.

Future Research

Although the tasks used in this study have been set up as foraging tasks, there is a temporal element in that the delays and the exponentially declining reward rate impose a temporal cost on each patch. Future studies could aim to model the behaviour with a temporal discounting model to determine if foraging behaviour in this task could simply be explained as a behaviour resulting from delay discounting.

Temporal discounting models have also been used as a measure of decision-making in clinical studies, which have shown increased discounting of delayed rewards in patients with cognitive, neurological, and motivational disorders; substance abuse and addiction; and brain trauma (Ahn et al., 2011; Bickel et al., 2007; Grecucci et al., 2014; Housden et al., 2010; McHugh & Wood, 2008; Mobini et al., 2007; Pulcu et al., 2014; Scheres, Lee, & Sumiya, 2008). Thus, foraging tasks similar to those used in this study could potentially be used as a measure of decision-making in a clinical population; based on the extent to which dwell times adhere to – or deviate from – the predictions of the MVT. These results could then potentially be contrasted to a control group, which has been established by the results obtained from healthy participants in this study.

In future studies, the neural correlates of foraging might also be explored. At present, few studies have done so and consequently, very little is known regarding the underlying mechanisms of when and how people make a decision to explore or exploit.

Over the course of the last decade, functional magnetic resonance imaging (fMRI) studies have determined that there is a large network of neural areas responsible for reward valuation in decision tasks. This network is comprised of the anterior cingulate cortex (ACC), ventromedial prefrontal cortex (vmPFC), orbitofrontal cortex (OFC), insula, amygdala, and the ventral striatum (VS). Specifically, these areas have been found to consistently show increased blood-oxygen-level dependent (BOLD) signal in response to decisions regarding the gain or loss of rewards in a task. Importantly, this was determined through numerous studies in which decision tasks involving the gain or loss of reward were used to examine the corresponding increase of blood-oxygen-level dependent (BOLD) signal in the brain (Clithero & Rangel, 2014; Glascher, Hampton, & O'Doherty, 2009; Izuma, Saito, & Sadato, 2008; Kable & Glimcher, 2007; Knutson, 2005; Levy & Glimcher, 2012; C. Padoa-Schioppa, 2009; Camillo Padoa-Schioppa & Assad, 2006; Pessiglione & Delgado, 2015; Rushworth, Kolling, Sallet, & Mars, 2012; Sescousse, Redoute, & Dreher, 2010). Further support for these findings was provided by meta-analytical studies which found that these areas consistently showed increased BOLD signal responses to the decision tasks (Bartra, McGuire, & Kable, 2013; Guillaume Sescousse, Caldú, Segura, & Dreher, 2013). However, relatively little is known about how these areas respond to foraging decisions; in particular, how these areas are modulated by the approach to a time horizon.

A seminal study conducted by Kolling, Behrens, Mars, and Rushworth (2012) set in motion investigations into the neural correlates of foraging. Kolling et al. (2012) reported that the anterior cingulate cortex plays a key role in encoding the average value of the foraging environment and the cost of foraging. Importantly, this finding

was consistent with a previous primate study which had found the dorsal anterior cingulate cortex (dACC) to encode the value of the foraging environment (Hayden, Pearson, & Platt, 2011). However, Shenhav, Straccia, Cohen, and Botvinick (2014) challenged the findings of Kolling et al., (2012) by replicating their study and asserting that the results instead provided evidence for the engagement of the dACC being reflective of decision difficulty as opposed to the value of foraging. As a result, a debate has ensued and consumed much of the existing literature pertaining to foraging decisions in humans.

Therefore, an interesting question for future studies is how the areas responsible for reward valuation – the ACC, vmPFC, VS, OFC, insula, and amygdala – are able to keep track of the features for individual patches, and trial environment features, in order to mediate decisions in a foraging task. Further, these investigations could establish a benchmark on which both cognitive and physical effort involved in a foraging-task could be determined. The time course of events in effort-based decision-making during a foraging task could be determined due to the temporal resolution of the MEG, which would be complemented by the spatial resolution of the fMRI. Further, as it is not yet possible to measure disorders of motivation or reward-sensitivity objectively in patients (eg. Parkinson's Disease), the proposed future studies could establish an objective measure on which to determine the extent of a motivational deficit in patients.

Conclusion

The present data provides directional evidence in favour of the general framework of the MVT, and performance that is largely consistent with the predicted optimal. The

findings from this study thereby indicate that the MVT is applicable to other studies of human decisions, and paves the way for further research into the components of choice behaviour. Specifically, this study examined the temporal component of foraging costs relative to the predictions of the MVT, and determined that sequential human decision-making predominantly adheres to its predictions.

In the animal kingdom, costs are not merely temporal, but also energetic. In humans, this has not been well explored. In particular, the role of effort in foraging has not been examined. Within the last five years, effort has gained a lot of attention in human research due to the potential relationship effort has with apathy.

Naturalistically, foraging involves both temporal and effort costs. Effort in humans has recently been the focus of much interest and has generated a great deal of insight regarding the computational and neural mechanisms effort-based decisions. However, many of these studies examine isolated decisions, as opposed to the more ecologically valid sequential decisions one would encounter in a natural foraging context.

Incorporating an effort-based component to these foraging tasks would increase the ecological validity, as sequential decisions and an energetic component would be involved, and additionally provide a way in which the connection between time and effort costs could be determined.

In humans, effort can be perceived in both cognitive and physical domains. Physical effort has been extensively researched due to the quantifiably overt manner in which physical effort is exerted. Contrarily, cognitive effort is implicitly exerted and has resulted in theories pertaining to the functions of cognitive effort being put forth.

Notably, the research conducted by Kahneman (2011) in which cognitive effort is

governed by two systems—System 1 being automatic and intuitive, whereas System 2 is deliberate and analytical—has drawn attention to the notion of cognitive effort.

However, the question remains as to whether cognitive and physical effort costs have the same behavioural and neural effects on foraging decisions.

In light of the fact that neural correlates of foraging have only recently been explored, there remains a great deal to still be understood about the underlying mechanisms of when and how people make a decision to explore or exploit. In addition, the neural correlates of foraging pertaining to effort costs are yet to be investigated. This would complement the existing literature on effort-based decision-making and extend it to examine sequential decisions, as opposed to the currently literature, which examines isolated decisions.

Importantly, it is not yet possible to measure disorders of motivation or reward-sensitivity objectively in patients. Disorders comprised of motivational deficits, such as apathy, are diagnosed with questionnaires with a Likert-type scale. The subjective reporting presents a prominent issue with these questionnaires. For example, if asked to rate a feeling (for our purposes: happiness) on a scale of 1-7, one person's perception of what each number on the scale represents varies drastically to that of another person's perception. An objective metric of a motivational disorder, such as apathy, is yet to be developed. By evaluating the performance of patients with PD in a temporal and effort-based foraging task, the results could be compared and contrasted to the results from a control group in addition to the predictions made by the MVT. Further, the scores on the apathy questionnaires could be correlated with the performance on the objective measures of the foraging task. On this basis, future

studies have the potential to provide a way in which motivational disorders can be objectively measured.

Discovering the neurobiological mechanisms underlying foraging behavior in regards to temporal or effort costs could help us understand the neural basis for disorders of decision-making in patient populations. For example, patients with Parkinson's disease (PD) have disorders of effort- and reward- based decision-making, though the precise mechanisms involved are yet to be clarified. It has been proposed by some (Chong et al., 2015; Martinez-Horta et al., 2014) that apathy – which is a common motivational disorder in PD – may represent a disorder of effort-based decision-making. Therefore, to more precisely quantify this, the aforementioned paradigms pertaining to foraging and effort in decision-making could be used collaboratively to provide a metric for these impairments.

The data from the current study provides empirical evidence in favour of the general framework of the MVT, as human decisions in the four foraging tasks used were consistent with the optimal behaviour predicted by the MVT. Therefore, this study paves the way for further research into the components of decision-making that may be pathologically altered in patients with motivational disorders, such as Parkinson's disease.

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Appendix A: Experiment 1 - Correlations

			Experiment Duration
Spearman's rho	Experiment Duration	Correlation Coefficient	1.000
		Sig. (2-tailed)	.
		N	21
	First Order: Attention	Correlation Coefficient	-.302
		Sig. (2-tailed)	.184
		N	21
	First Order: Cognitive Instability	Correlation Coefficient	-.069
		Sig. (2-tailed)	.765
		N	21
	First Order: Motor	Correlation Coefficient	-.020
		Sig. (2-tailed)	.932
		N	21
	First Order: Perseverance	Correlation Coefficient	.050
		Sig. (2-tailed)	.831
		N	21
	First Order: Self-Control	Correlation Coefficient	.103
		Sig. (2-tailed)	.656
		N	21
	First Order: Cognitive Complexity	Correlation Coefficient	-.085
		Sig. (2-tailed)	.713
		N	21
	Second Order: Attention	Correlation Coefficient	-.279
		Sig. (2-tailed)	.220
		N	21
	Second Order: Motor	Correlation Coefficient	-.007
		Sig. (2-tailed)	.978
		N	21
	Second Order: Non-Planning	Correlation Coefficient	.034
		Sig. (2-tailed)	.884
		N	21
	Total BIS-11 Score	Correlation Coefficient	.001
		Sig. (2-tailed)	.998
		N	21

Appendix B: Experiment 2 - Correlations

			Experiment Duration
Spearman's rho	Experiment Duration	Correlation Coefficient	1.000
		Sig. (2-tailed)	.
		N	21
	First Order: Attention	Correlation Coefficient	-.285
		Sig. (2-tailed)	.211
		N	21
	First Order: Cognitive Instability	Correlation Coefficient	-.316
		Sig. (2-tailed)	.162
		N	21
	First Order: Motor	Correlation Coefficient	.208
		Sig. (2-tailed)	.365
		N	21
	First Order: Perseverance	Correlation Coefficient	.031
		Sig. (2-tailed)	.895
		N	21
	First Order: Self-Control	Correlation Coefficient	-.258
		Sig. (2-tailed)	.259
		N	21
	First Order: Cognitive Complexity	Correlation Coefficient	.150
		Sig. (2-tailed)	.516
		N	21
	Second Order: Attention	Correlation Coefficient	-.400
		Sig. (2-tailed)	.072
		N	21
	Second Order: Motor	Correlation Coefficient	.201
		Sig. (2-tailed)	.382
		N	21
	Second Order: Non-Planning	Correlation Coefficient	-.043
		Sig. (2-tailed)	.853
		N	21
	Total BIS-11 Score	Correlation Coefficient	-.088
		Sig. (2-tailed)	.705
		N	21

Appendix C: Experiment 3 - Correlations

			Experiment Duration
Spearman's rho	Experiment Duration	Correlation Coefficient	1.000
		Sig. (2-tailed)	.
		N	22
	First Order: Attention	Correlation Coefficient	-.223
		Sig. (2-tailed)	.320
		N	22
	First Order: Cognitive Instability	Correlation Coefficient	.196
		Sig. (2-tailed)	.381
		N	22
	First Order: Motor	Correlation Coefficient	.039
		Sig. (2-tailed)	.862
		N	22
	First Order: Perseverance	Correlation Coefficient	.005
		Sig. (2-tailed)	.982
		N	22
	First Order: Self-Control	Correlation Coefficient	-.080
		Sig. (2-tailed)	.724
		N	22
	First Order: Cognitive Complexity	Correlation Coefficient	-.191
		Sig. (2-tailed)	.395
		N	22
	Second Order: Attention	Correlation Coefficient	-.115
		Sig. (2-tailed)	.609
		N	22
	Second Order: Motor	Correlation Coefficient	.052
		Sig. (2-tailed)	.818
		N	22
	Second Order: Non-Planning	Correlation Coefficient	-.182
		Sig. (2-tailed)	.417
		N	22
	Total BIS-11 Score	Correlation Coefficient	-.128
		Sig. (2-tailed)	.569
		N	22

Appendix D: Experiment 4 - Correlations

			Experiment Duration
Spearman's rho	Experiment Duration	Correlation Coefficient	1.000
		Sig. (2-tailed)	.
		N	18
	First Order: Attention	Correlation Coefficient	-.442
		Sig. (2-tailed)	.066
		N	18
	First Order: Cognitive Instability	Correlation Coefficient	-.038
		Sig. (2-tailed)	.881
		N	18
	First Order: Motor	Correlation Coefficient	-.072
		Sig. (2-tailed)	.778
		N	18
	First Order: Perseverance	Correlation Coefficient	.014
		Sig. (2-tailed)	.956
		N	18
	First Order: Self-Control	Correlation Coefficient	.006
		Sig. (2-tailed)	.980
		N	18
	First Order: Cognitive Complexity	Correlation Coefficient	-.314
		Sig. (2-tailed)	.204
		N	18
	Second Order: Attention	Correlation Coefficient	-.327
		Sig. (2-tailed)	.186
		N	18
	Second Order: Motor	Correlation Coefficient	-.086
		Sig. (2-tailed)	.734
		N	18
	Second Order: Non-Planning	Correlation Coefficient	-.246
		Sig. (2-tailed)	.325
		N	18
	Total BIS-11 Score	Correlation Coefficient	-.307
		Sig. (2-tailed)	.216
		N	18

Re: Ethics Amendment to Ref 5201300103

APPROVED

By Fran Thorp at 9:34 am, Feb 02, 2016

Trevor Chong <trevor.chong@mq.edu.au>

Thu 28/01/2016 10:44

To: Ethics Secretariat <ethics.secretariat@mq.edu.au>;

Fran Thorp

1 attachment (119 KB)

Chong_2016_AddStudents.docx

Dear Fran,

Marion Aitchison is a Masters student starting with me this year, and I was wondering if you could please add her on to my existing ethics application (5201300103). Please find attached an HREC amendment request.

Many thanks,
Trevor

On 25 August 2015 at 16:23, Trevor Chong <trevor.chong@mq.edu.au> wrote:

Dear Fran,

Many thanks for this, and for the quick turnaround of the request.

Best wishes,
Trevor

On 25 August 2015 at 16:21, Ethics Secretariat <ethics.secretariat@mq.edu.au> wrote:

Dear Trevor

Thank you for your email and amendment request.

The addition of the interns has been approved, effective 25 August 2015. Please find attached an approved copy of the amendment request form for your records.

Please do not hesitate to contact the Ethics Secretariat if you have any questions.

Kind regards
Fran

On 18 August 2015 at 13:14, Trevor Chong <trevor.chong@mq.edu.au> wrote:

Dear Ethics Secretariat,

Please find attached a request for additional personnel to be added to HREC 5201300103 ('Response inhibition in health and disease'). The four students to be added are undergraduate psychology students undertaking a three month student internship under my supervision as part of the subject PSY 399. As this is a short-term placement, I would appreciate it if the addition of their names to my ethics is expedited.

With thanks and kind regards,
Trevor Chong

--

Dr. Trevor T-J Chong
NH&MRC (Australia) Neil Hamilton Fairley Early Career Fellow
Department of Cognitive Science
Macquarie University
Sydney NSW 2109
Australia