

**The Desire to Act: Exploring Situational, Dispositional and Genetic Correlates
of a Fundamental Motivational State**

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Animals do not simply act to survive and maximize pleasure. They also act for the sake of action itself. Although such intrinsically motivated actions are ubiquitous throughout the animal kingdom, the mechanisms by which they are enacted remain poorly understood. Likewise, little is known in regard to what influences which actions an animal ultimately chooses. It has been speculated for some time that boredom signals our failure to satisfy this drive to act, and that it may play a crucial role in launching us into action. The goal of the current thesis was to investigate the role of boredom in mediating our desire to engage with our environment and to explore factors that influence how we interact with our environment. Chapter 2 tested whether boredom signals opportunities for action and makes us want to engage with such opportunities. Chapter 3 investigated whether different situations make us sensitive to distinct opportunities to act. Chapter 4 investigated whether a genetic variation predisposes us to be sensitive to specific opportunities to act. The results from this thesis highlight the importance of boredom in regulating our desire for action and provide novel insights into what factors make us act in specific ways. The last chapter situates these results within a broader self-regulatory framework.

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"Variety is the very spice of life, that gives it all its flavour."

- William Cowper

Chapter 1: Introduction

We prefer to be in a state of action. Inaction is dissatisfying and boring. What is this force that impels us to stay active and why do some actions serve as a cure for boredom while others are its cause? It has become increasingly apparent that animals have evolved to have a general motivational system meant to ensure their continual engagement with the environment – a drive to act (Hebb, 1955; Keynes, 1936; Woodworth, 1918; White, 1959). Although such a motive is ubiquitous and vital for life, the mechanisms that spur us into action have yet to be fully elucidated. Indeed, boredom was thought to be heavily implicated in regulation of this motive not long after formal recognition of the existence of this motive for action as an end in itself (Fenichel, 1951; White, 1959). Despite this, research examining the self-regulatory function of boredom has been sporadic until recent times (for review see Eastwood, Frischen, Fenske & Smilek, 2012; Westgate & Wilson, 2018). Perhaps an even greater challenge to the empirical study of motivation is to understand how an animal directs this unceasing need to act – that is, which actions do they ultimately choose? Understanding how animals choose to interact with their environment is stymied by the sheer complexity of the organisms, their environs and the dynamic interplay between the two. The goal of my thesis was to explore the role of boredom in mediating our desire to act and to investigate factors that influence the way we channel this desire.

1.1 Why do we act?

Historically the question of why animals act has had two prominent answers: in order to survive and in order to maximize pleasure (for review see Higgins, 2014). Survival or

satisfaction of biological needs more generally, is perhaps the most intuitive and evident driver of behaviours. It has been long documented that animals have an imperative to ensure their own survival (Woodworth & Schlosberg, 1954). However, this drive alone is insufficient to explain the full range of actions observed in animals. Perhaps the clearest critique against the idea that we act only in order to survive, is the fact that survival is silent on the matter of why we *want* to act. That is, survival revolves around need satisfaction and only motivates us when biological needs are unmet (Higgins, 2014). Although survival is without a doubt a major biological imperative, it fails to explain our desire to act when biological needs are met (White, 1959), and thus cannot account for the full suite of motivations to act.

Jeremy Bentham (1789/1988) suggested that animals follow a “principle of utility” by which an animal evaluates the extent to which a given action augments or diminishes one’s happiness. Bentham sees the notion of utility as a property of an action to promote benefit, advantage, good or pleasure, or to prevent pain or unhappiness. This notion of action for the purpose of maximizing pleasure and minimizing pain formed the basis of hedonic psychology and has reverberated in various forms since (for review see Higgins, 2014). Classic experiments demonstrate that such a hedonic principle may supersede survival. For instance, animals choose more pleasant food (i.e., sweet) even though a more physiologically beneficial food is available (Woodworth & Schlosberg, 1954). Animals push levers to activate pleasure processing areas of the brain despite having no biological need satisfaction and despite the fact that the behaviour may be detrimental to the animal’s well-being (Old &

Milner, 1954). Action for the purpose of maximizing pleasure and minimizing pain appears to be an important part of the story for why we act, but it still fails to explain a range of actions observed in animals. Indeed, the most clear-cut example of this is the fact that many people engage in a variety of activities that neither promote survival or pleasure (e.g., extreme sports, addiction). Indeed, such activities may even be quite painful and threaten survival (for review see Higgins, 2014)

The idea that we are only motivated to survive or maximize pleasure has been challenged since the inception of motivation as an area of formal study. Woodworth (1918, 1940) coined the term drive, defined as a state that disposes an individual to a specific set of behaviours and permits the use of energy for a specific purpose. It can also be regarded as a basic urge in need of satisfaction. Woodworth (1918) suggested that although action can result in satisfaction of a physical drive, for an activity to run freely and efficiently it needs to be running by its own drive, and thus action itself can be satisfying. This notion, that people are intrinsically motivated to act for the sake of acting – without an immediate external reward, has also been emphasized by the economist John Maynard Keynes. In his book, *General Theory of Employment, Interest, and Money* (1936), Keynes, states that:

The full consequence of [our decisions] will be drawn out over many days to come, can only be taken as a result of animal spirits – of a spontaneous urge to action rather than inaction, and not as the outcome of a weighted average of quantitative benefits multiplied by quantitative probabilities. (Keynes, 1936, p. 103)

The observation that animals do not always try to reduce drives (i.e., act in order to eliminate a homeostatic imbalance such as thirst) or maximize utility (i.e., act in order to attain a tangible benefit while minimizing costs) made the need for this “spontaneous urge to action rather than inaction” more apparent. Another reason for why people act is to have effective interactions with the environment – what White (1959) termed “effectance motivation”. White thought that such a motive is needed to explain two observations: First, animals are highly sensitive to opportunities to act and second, they display a high level of competence – a level that cannot be attained through drive satisfaction or pursuit of external rewards alone. In a sense, to satisfy the desire to have an effect on its’ environment, the organism needs to learn to do so (i.e., become competent) and is thus impelled to investigate, manipulate and master their environs. According to White (1959), to attain a high degree of mastery, an organism needs to be in a state of action most of the time, with most organisms having evolved to ensure just that. Therefore, an animal does not only have a goal of maintaining action, but is aware of the extent of its own engagement with the world and is sensitive to opportunities to be active. What is unique about this motive/drive is that it permits a type of exploratory behavior without a concrete end state. It is an unceasing motivational force, satisfaction of which lies in continued activity, while the failure to maintain action results in a dissatisfying state of unfulfilled potential.

1.2 Boredom as Signal to Act

Fenichel (1951) may have been the first to suggest that the unsatisfying state that is linked with the failure to maintain action is that of boredom – which he stated is

characterized by the paradoxical coexistence of the “need for action” and “action-inhibition”. White himself speculated that boredom is implicated in this motive: “Obviously there are no consummatory acts; satisfaction would appear to lie in the arousal and maintaining of activity rather than in its slow decline toward bored passivity” (White, 1959, p. 321). The most accepted definition of boredom today is that it is a state characterized by wanting but being unable to engage in a satisfying activity (Eastwood et al., 2012; Westgate et al., 2018). Functional theories of boredom suggest that the state of boredom informs us that we are dissatisfied with the current situation and are motivated to escape or alter the situation so as to better align it with our goals (Bench & Lench 2013; for review see Danckert, Mugon, Struk & Eastwood, 2018; Elpidorou, 2014, 2018). Based on these accounts, boredom has both a motivational component that reflects an individual’s desire to be engaged, and a situational component that reflects the inadequacy of the environment to fulfil this motive. This modern conception of boredom fits well with White’s notion of “bored passivity”, in which case what an individual wants is to be in a state of action but the current environmental affordances do not facilitate fulfilment of this desire. Likewise, Fenichel (1951) regarded boredom as a state of “drive-tension” – having the urge to act, coupled with the lack of “drive-aim” – an inability to direct this urge to act. Indeed, according to functional theories of boredom, boredom ought to motivate us to act on opportunities for action but does not dictate what those actions should be (Danckert et al., 2018; Elpidorou, 2014, 2018). Accordingly, two questions arise: 1) Which opportunities for action are we motivated to act on and 2) What determines our sensitivity to a particular opportunity to act?

1.3 How do we act?

Woodworth (1944) recognized that an organism is dependent on the environment not only for energetic needs but also for “stimulation” and “opportunity for activity”. However, an individual has many actions at their disposal and many stimuli impacting them simultaneously. In response, an individual needs to be highly selective in their action choices. Indeed, Woodworth (1944) suggests that an organism needs to have a selective “response” – meaning that it should produce one movement or action state at a time. Importantly, an organism also “shifts responses”. That is, although we direct our attention to the most “interesting” stimuli, presumably such interest decays and we change our responses in quick succession.

It has been theorized that our choices are guided by some combination of the subjective value of outcomes, as well as probabilities of their attainment, a concept that dates back to 18th century mathematician Daniel Bernoulli (1738/1954). However, when a choice is made between two alternatives, selecting only one option, by necessity, carries a cost equivalent to the value of the forgone option. This cost is also known as an opportunity cost – a term originally used by the economist Friedrich von Wieser (1911/1927). No area of study has benefited from this concept more than the examination of foraging behaviour in animals (for review see Charnov, 1976). The way an animal solves the problem of prioritizing tasks often relies on evaluating costs of staying in a patch of food (exploitation) versus leaving and searching for a new patch of food (exploration; Charnov, 1976; Cohen, McClure & Yu, 2007; Hayden, Pearson, & Platt, 2011). Another model, based on the notion that evaluation

of opportunity costs is an evolutionary adaptation, aimed to solve what has been termed the simultaneity problem (essentially Woodworth's problem of selectivity; Kurzban, Duckworth, Kable & Myers, 2013). This so-called "Opportunity Cost Model of Subjective Effort (Kurzban et al., 2013)", is the first to implicate an affective state – boredom – as a signal of opportunity costs. Furthermore, this model is the first to make the connection between boredom and opportunities to act since it has been proposed that boredom may arise from the failure to ensure constant activity (Fenichel, 1951; White 1959).

Considering that the desire to engage and its behavioural manifestations are so pervasive, understanding this motivational system and the mechanisms by which it operates is of great importance. The goal of this thesis was to broadly explore the situational, behavioural and genetic correlates of the desire to act. Chapter 2 investigates whether boredom signals opportunity costs pushing us to engage in alternative activities. Chapter 3 looks at the role of difficulty on perceived boringness, and investigated whether boredom arising from different circumstances makes people sensitive to distinct opportunities for action. Chapter 4 explores how genes affect the types of opportunities we prioritize and ways in which we choose to regulate our engagement with them. Chapter 5 concludes with discussion of the implications of the current research and situates boredom and the desire for action within a broader self-regulatory framework.

Chapter 2: Exploring the Role of Opportunity Costs in the Experience of Boredom¹

2.1 Introduction

Boredom is a ubiquitous human experience. Indeed, research suggests that a typical high-school student will experience some level of boredom up to 36% of the time in any given day (Goetz, 2013), and that 91% of North American youth experience boredom (The National Center on Addiction and Substance Abuse, 2003). In addition, boredom is a consequential experience linked to a slew of negative cognitive, affective, and behavioural outcomes, with inattention, depression, and substance use forming just the tip of the iceberg (Amos, Wiltshire, Haw, & McNeill, 2006; Carriere, Cheyne, & Smilek, 2008; Farmer & Sundberg, 1986; German & Latkin, 2012; Goldberg, Eastwood, LaGuardia, & Danckert, 2011; LePera, 2011; Malkovsky, Merrifield, Goldberg, & Danckert, 2012; Wiesner, Windle, & Freeman, 2005). A thorough understanding of boredom and its antecedents is essential in the development of methods by which the consequences of boredom might be minimized, and hence, identifying such antecedents is of practical, as well as theoretical importance. In the present study, the aim was to examine the recently theorized—yet currently untested—hypothesis that boredom is more likely to result when opportunity costs are high; that is, when there is a high potential value of engaging in activities other than one’s current activity (Charnov, 1976; Gomez-Ramirez & Costa, 2017; Kurzban, et al., 2013).

Boredom is commonly characterized as a state of wanting to engage with a satisfying activity, coupled with an inability to do so (Eastwood et al., 2012). Eastwood and colleagues

¹ A version of this chapter is under consideration at *Psychonomic Bulletin and Review*.

(2012) theorized that boredom arises when we fail to sustain attention, and attribute this failure to the environment (i.e., the environment is not sufficiently engaging). In support of this view, research has demonstrated that failures of sustained attention may lead to increased reports of boredom (Damrad-Frye & Laird, 1989; Fisher, 1998) and, moreover, failures of attention have been shown to be positively associated with the tendency to experience boredom (Carriere et al., 2008; Hunter & Eastwood, 2018; Malkovsky et al., 2012). Although an abundance of experimental findings have supported this attention-failure view of boredom, it has recently been argued that this view is incomplete insofar as it largely ignores the reasons that lead to attention failures (and thus, boredom) in the first place. Functional accounts of boredom aim to bridge this gap (for review see Westgate & Wilson, 2018).

Functional accounts of boredom suggest there is more to the experience of boredom than merely attentional errors (Bench & Lench, 2013; Danckert et al., 2018; Elpidorou, 2014). Broadly speaking, these accounts suggest that boredom serves two functions. First, boredom informs us that the current situation is unsatisfactory in some way; second, it motivates us to pursue new, potentially more-satisfactory goals (Elpidorou, 2014, 2018). According to this perspective, a situation is unsatisfactory (and hence, boring) when it is associated with *opportunity costs* (Kurzban et al., 2013); that is, the uncomfortable feeling of boredom signals that the potential value of engaging in alternative activities is higher than current activity. Thus, according to the opportunity-cost framework, boredom is not solely a failure to attend, but is also a self-regulatory signal that indicates that we could be more optimally engaged if we completed some other activity. In the present studies, I sought to test

Kurzban et al.'s (2013) opportunity-cost theory by determining whether simply exposing participants to potential, but unattainable, affordances promotes the experience of boredom. Specifically, I wanted to test whether boredom is high when there are salient but unavailable opportunities for action, whereas boredom should be low when there are either no salient options for action or when there are salient and available opportunities.

2.2 Study 2.1

In Study 2.1, participants were seated in one of two environments, an empty room or a room containing various objects that afforded meaningful engagement (affordances condition). In the empty room participants were told to occupy their time with only their thoughts. Whereas participants who were seated in the engaging room were either told to occupy their time with only their thoughts (just as the participants in the empty room were instructed; hereafter labelled the affordances –ve condition) or they were told that they could freely engage with the environment (hereafter labelled the affordances +ve condition). It was predicted that participants who were asked to occupy themselves with their own thoughts in the engaging room (affordances –ve) would report higher levels of boredom than those placed in the engaging room in which they were allowed to engage (affordances +ve), essentially reaffirming the notion that constraint is boring (Troutwine & O’Neal, 1981). My novel hypothesis is that participants placed in the engaging room in which they were prevented from engaging with any potential avenues for action (affordances –ve) would report higher levels of boredom than those placed in an empty room, presumably because such environments dramatically increase the opportunity costs associated with the primary task. Furthermore, given that boredom has been characterized as a state of wanting, I tested whether the exposure to different environments would also affect people’s state of wanting to engage. It was hypothesized that environments with many affordances would elicit a greater desire for engagement (i.e., increased wanting) than environments with no affordances. Finally, since people were prevented from engaging in their environments, there was the real

possibility that this manipulation would lead to feelings of frustration. However, it was believed that the study manipulation would primarily affect boredom – a state characterized by a failure to launch into goal pursuit (Mugon, Struk, & Danckert, 2018). In contrast, frustration is a state that arises when we encounter obstacles during goal pursuit (Dollard, Miller, Doob, Mowrer & Sears, 1939). Thus, feelings of frustration were measured with the prediction that there would be no differences in frustration between any of the study conditions as none explicitly impede a goal already in progress.

2.3 Study 2.1 Methods

Participants

One hundred and sixty-one undergraduates (103 females, mean age = 19.79 (1.76) years) participated in exchange for partial course credit. Ethnicity data was not collected in the Fall 2015 sample ($n = 72$). In the remainder of the sample ($n = 89$), 39.3% identified as White/Caucasian, 31.5% as East Asian, 10.1% as South Asian, 6.7% as Southeast Asian, 4.5% as Black/African, 3.4% as Middle Eastern, 1.1% as West Indian/Caribbean, 1.1% as Hispanic, 1.1% as Aboriginal (First Nations), with 1.1% of the sample responding ‘other’ or declining to indicate the ethnicity they identified with. Participants were randomly assigned to one of three experimental conditions. Data were collected throughout Fall of 2015 and 2016 academic year. It was decided a priori that data collection will go on until at least $n = 50$ was attained for each of the three conditions. This study received ethics clearance from University of Waterloo Office of Research Ethics.

Procedure and experimental setup

Participants were seated in either (1) an empty room – in which there was only a chair, an empty bookshelf, a chalk board with no chalk, a filing cabinet, and a desk (Figure 2.1) – or (2) a room with affordances (affordances -ve) – in which, in addition to the items in the empty room, there were numerous objects with which participants could normally interact: chalk was added to the chalk board, a laptop computer in Firefox web-kiosk mode and a Google front page were opened, and a partially completed Lego car puzzle, a partly

completed jig-saw puzzle, three sheets of blank paper, and a set of crayons were placed in the room (Figure 2.2). In both conditions participants were instructed to “stay seated, remain awake, and entertain themselves with their thoughts for the 10-minute period”. In a third condition (3) participants were seated in a room with the same affordances but were told that they were “free to engage with the environment or entertain themselves with their own thoughts” (affordances +ve). Prior to the researcher’s departure, participants were required to give their backpack and electronic devices to the researcher for the duration of the study (Wilson et al., 2014). After the 10-minute period, the researcher returned to administer a brief questionnaire on a laptop computer. Participants responded to the three questions presented in the fixed order as follows. “Rate how bored you were over the last 10-minute period”; “Rate how much you wanted to do something over the last 10 minute period.”; “Rate how frustrated you were over the last 10 minute period”; Participants responded to all questions on a Likert scale ranging from, 1 (“Not At All”) to 9 (“Extremely”). Prior to departure, the experimenter asked each participant an open ended question: “What did you do to occupy your time during the experiment?” and recorded their response. Next, participants were informed of the purpose of the experiment and thanked for their participation.



Figure 2.1 Experimental room (Empty Room condition)

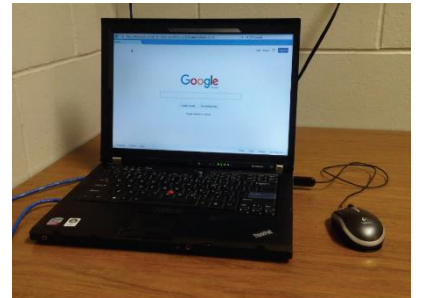
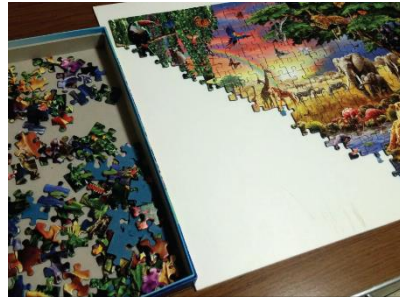


Figure 2.2 Additional objects present in the Affordances condition. In clockwise order: Lego car puzzle, jigsaw puzzle, laptop in kiosk mode, chalk board with chalk, paper with crayons.

2.4 Study 2.1 Results

Normality

All data analyses were conducted in R (R Core Team, 2015). Shapiro-Wilks tests of normality (Shapiro & Wilk, 1965) indicated that none of the study variables were normally distributed (all $ps < 0.05$). As such, non-parametric comparisons were conducted throughout. Independent-samples non-parametric comparisons were conducted using Wilcoxon's rank-sum test (Wilcoxon, 1945). When more than two groups were present non-parametric comparisons were conducted using Kruskal-Wallis rank-sum test (Hollander & Wolfe, 1999). For all comparisons, medians, Mann-Whitney-Wilcoxon U statistics were employed and non-parametric effect sizes were reported as a point-biserial correlation r ; p-values are based on two-tailed tests (Cohen, 1988; Fritz, Morris, & Richler, 2012).

Rule Breakers

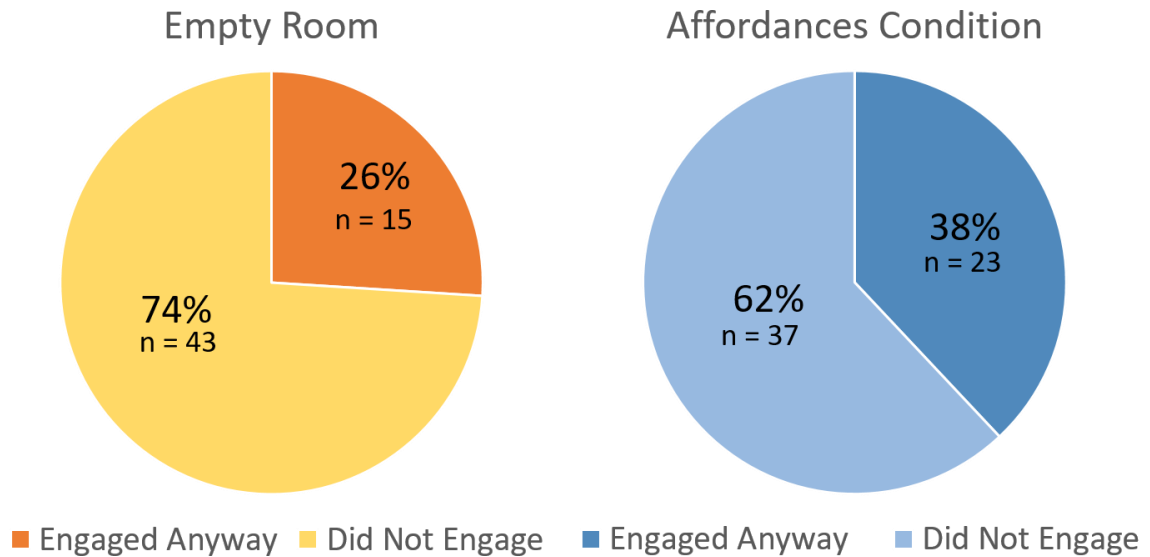


Figure 2.3 Proportion of rule breakers (engaged anyway) versus rule compliers (did not engage).

Because a valid test of the study hypothesis required that participants followed instructions, prior to analyzing group differences, groups were separated by virtue of compliance with instructions. Participants were marked as rule breakers if they reported that they did not remain seated, fell asleep or interacted with the environment. Of 57 participants in the empty room, 15 (26%) broke the rules, while for the 60 participants in the affordances –ve condition, 23 (38%) broke the rules (Figure 2.3). This trend towards more rule breakers in the affordances –ve condition did not reach significance ($\chi^2(1) = 1.57, p = 0.210$).

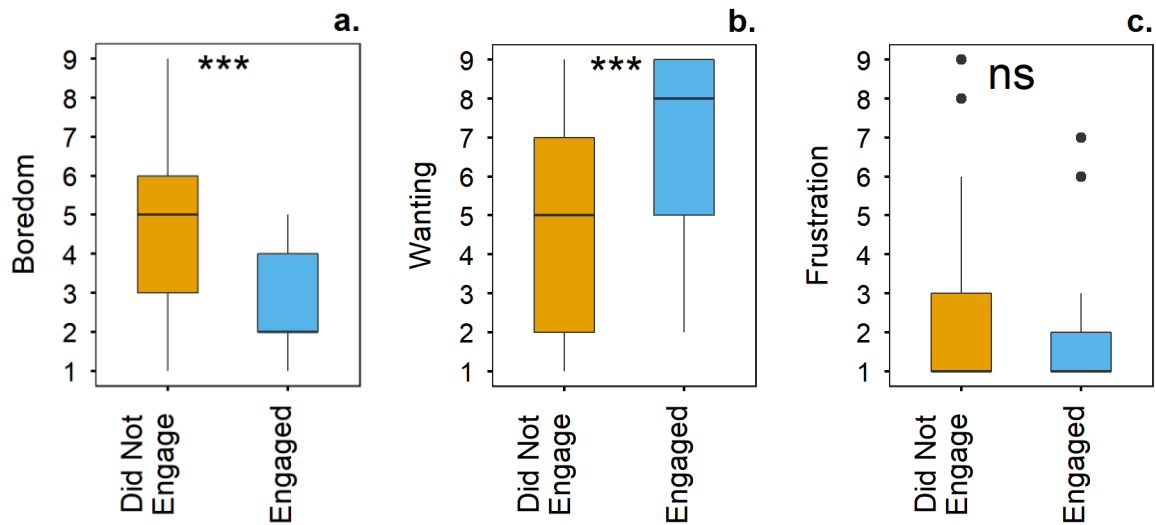


Figure 2.4 Boxplots of study variables for rule compliers and non-compliers for affordance –ve condition. *** = significant point bi-serial correlation at $\alpha < 0.001$

Given that participants could not be randomly assigned to either comply or break rules, the number of rule breakers versus non-rule breakers was highly uneven, and none of the study variables were normally distributed, an appropriate factorial analysis could not be conducted. Instead, a number of point-biserial correlations between rule breaking and the study variables were conducted for each condition (*Family-wise* $\alpha = 0.05/6 = 0.008$). In the empty room, none of the variables differed among rule breakers versus rule followers (*all ps* > 0.202). In the affordance –ve condition (Figure 2.4), relative to rule followers, rule breakers tended to report higher levels of wanting ($r = 0.46, p < 0.001$) and less boredom ($r = 0.42, p < 0.001$), but did not differ in terms of frustration ($r = 0.17, p = 0.072$). Finally, rule breakers were marginally higher in boredom ($r = 0.38, p = 0.017$; *Family-wise* $\alpha = 0.05/3 = 0.017$) and lower in wanting ($r = 0.35, p = 0.033$) in the empty room than affordance -ve

condition, but there was no difference across these conditions in terms of in terms of frustration ($r = 0.00$, $p = 0.995$).

Condition Differences

Rule-Compliers

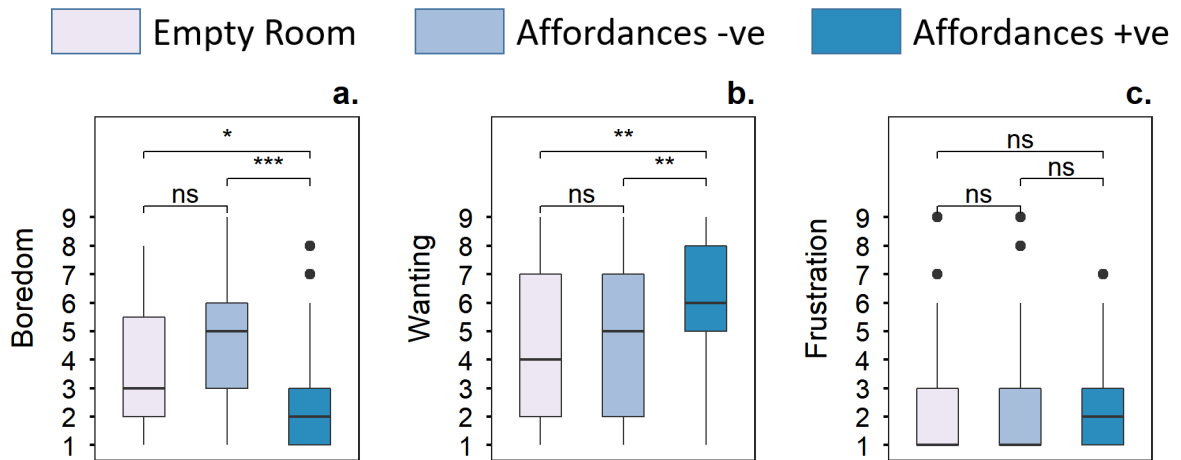


Figure 2.5 Boxplots of all conditions and variables in the trimmed sample (rule compliers only). For comparisons unadjusted Wilcoxon ranked-sum significance values are used: * = $p < 0.05$, ** = $p < 0.01$

Since a valid test of the study hypothesis required that participants follow the instructions, rule compliers were analysed first (Figure 2.5). As predicted, there was a significant difference in boredom scores across the three conditions ($\chi^2(2) = 14.18$, $p < 0.001$). Participants reported significantly lower levels of boredom in the affordances +ve condition ($Mdn = 2$) than in the affordances -ve condition ($Mdn = 5$; $U = 1171.5$, $r = 0.411$, $p < 0.001$) and the empty room ($Mdn = 3$; $U = 1167$, $r = 0.230$, $p = 0.033$). There was a

marginally significant difference in boredom between the affordances –ve condition ($Mdn = 5$) and the empty room ($Mdn = 3$; $U = 606$, $r = 0.206$, $p = 0.066$). Furthermore, there was a significant difference in wanting scores across the three conditions ($\chi^2 (2) = 11.18$, $p = 0.003$). Participants reported significantly lower levels of wanting in the empty room ($Mdn = 4$) than the affordances +ve condition ($Mdn = 6$; $U = 559$, $r = 0.343$, $p = 0.002$) but not in the affordances –ve condition ($Mdn = 5$; $U = 736$, $r = 0.065$, $p = 0.566$). There was also a significant difference in wanting between the affordances –ve condition ($Mdn = 5$) and the affordances +ve condition ($Mdn = 6$; $U = 524$, $r = 0.295$, $p = 0.008$). As predicted, there were no significant differences in frustration scores across the three conditions ($\chi^2 (2) = 0.253$, $p = 0.881$).

Full Sample

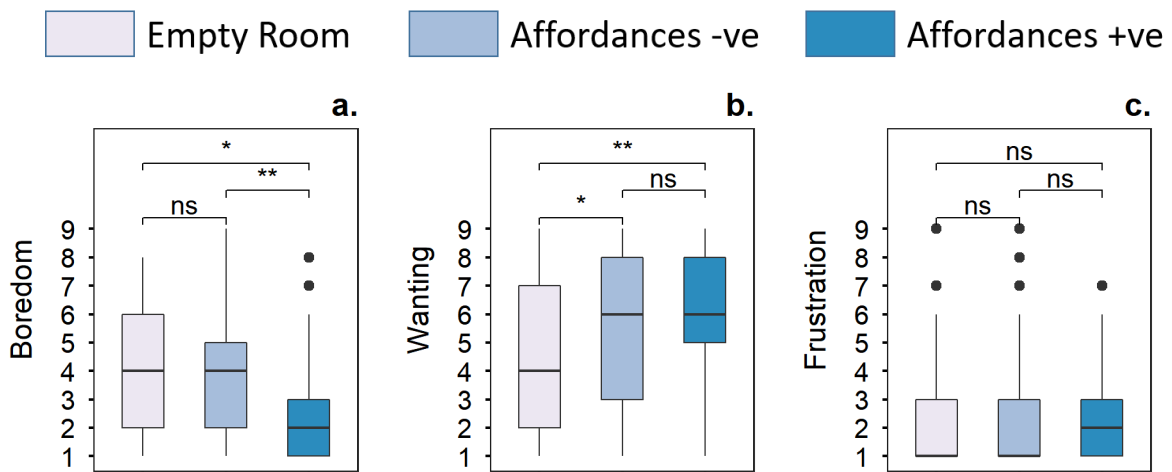


Figure 2.6 Boxplots of all conditions and variables in the full sample (rule compliers and non-rule compliers). For comparisons unadjusted Wilcoxon ranked-sum significance values are used: * = $p < 0.05$, ** = $p < 0.01$

For transparency the entire sample was also analysed (Figure 2.6). Consistent with the study predictions and findings observed in rule compliers, there was a significant difference in boredom scores across the three conditions ($\chi^2(2) = 9.44, p = 0.009$). Participants reported lower levels of boredom in the affordances +ve condition ($Mdn = 2$) than in the affordances –ve condition ($Mdn = 4; U = 1712.5, r = 0.286, p = 0.004$) and the empty room ($Mdn = 4; U = 1616.5, r = 0.256, p = 0.010$). However, contrary to my central prediction and the rule-compliant sample, there was no significant difference in boredom between the affordances –ve condition ($Mdn = 4$) and the empty room ($Mdn = 4; U = 1702, r = 0.019, p = 0.838$). Furthermore, there was a significant difference in wanting scores across the three conditions ($\chi^2(2) = 8.64, p = 0.013$). Participants reported lower levels of wanting in the empty room ($Mdn = 4$) than in the affordances –ve condition ($Mdn = 6; U = 1375, r = 0.182, p = 0.048$) and the affordances +ve condition ($Mdn = 6; U = 829.5, r = 0.287, p = 0.004$). There was no significant difference in wanting between the affordances conditions ($Mdn = 6; U = 1157, r = 0.088, p = 0.378$). As predicted, there were no significant differences in frustration scores across the three conditions ($\chi^2(2) = 0.725, p = 0.700$).

Gender differences

Given that males are typically more prone to boredom (i.e., trait boredom proneness; Farmer & Sundberg, 1986; Isacescu, Struk, & Danckert, 2017), differences across gender on all study variables while collapsing across conditions were examined. Gender proportions were marginally different across conditions (Empty Room: 74% Female; Affordances –ve

condition: 63% Female; Affordances +ve condition: 51% Female; $\chi^2(2) = 5.67, p = 0.059$). Females ($Mdn = 4$) reported significantly higher levels of state boredom than males ($Mdn = 2.5; U = 2369.5, p = 0.028, r = 0.17$). There was no difference in wanting level between females ($Mdn = 6$) and males ($Mdn = 5; U = 2786, p = 0.478, r = 0.06$). There were no differences in reported frustration levels between females ($Mdn = 2$) and males ($Mdn = 1; U = 2466.5, p = 0.100, r = 0.13$).

2.5 Study 2.1 Discussion

Constraint in the form of prohibiting participants from engaging with their environment effectively elevates boredom. This conceptually confirms prior theories of boredom (Troutwine & O'Neal, 1981). In my sample 32% of participants failed to comply with the rules of the task. That is, despite being told to sit quietly with only their thoughts to occupy them, many chose to either interact with objects in the room (affordances –ve) or did things like stand up from the chair, explore desk drawers, or even do squats in the empty room (all indicated via self-report at the end of the task). Such a large number of non-compliant participants was not anticipated. Indeed, it was found that non-compliers benefited from disobeying the rules in the engaging room, reducing their experience of boredom. As such, there was no definitive way to test whether the engaging room in which participants were prohibited from acting was more boring than the empty room. However, following removal of non-compliers, a marginal effect emerged, which was significant with a one-tailed test. Despite this positive finding this study has some limitations. First, a large portion of the sample was lost due to removal of non-compliers, possibly due to the fact that participants were not explicitly told to refrain from engaging, but were only told to “stay seated, remain awake, and entertain themselves with their own thoughts”. Second, determination of non-compliance relied on participant self-reports which may have underestimated the full extent of rule non-compliance. The next study aimed to address these shortcomings in order to maximize the key effect of interest.

2.6 Study 2.2: Introduction

Study 2.2 parallels that of Study 2.1 with a more direct focus on only the key contrast between the empty room and the engaging room in which participants were prevented from acting (affordances –ve). In addition, this study attempted to strengthen the magnitude of the effect observed in Study 2.1 by increasing the duration of the experiment. Participants who were less prone to boredom were also preselected in order to avoid potential ceiling effects in boredom scores, that is, people in both conditions attaining maximum levels of state boredom (thus reducing the magnitude of the effect). Furthermore, to ensure the study had sufficient power, a larger sample size was used and rule compliance was ensured by making explicit the instruction not to engage. Finally, participants were surreptitiously video recorded, in order to definitively determine the extent of rule compliance.

2.7 Study 2.2: Methods ²

Sample Size. In Study 2.1 the primary effect size (the effect of condition on reported boredom) had a moderate effect size (*Cohen's d* = 0.42). Given that measures were taken to maximize the effect in the study reported here (i.e., longer duration, pre-selection of low boredom prone participants, etc.), it was assumed that the true effect size would be at least $d = 0.42$. Thus, to attain 80% power it was determined that $n = 90$ would be needed per condition. Although it is possible that the true effect size is smaller, 90 participants per condition was selected as the target N for feasibility concerns. Ninety participants per condition was the maximum number of participants that was deemed practical given that data needed to be collected from one person at a time and a large portion of participants failed to comply with the study rules and thus needed to be excluded from analyses.

Participants

Two hundred and twenty-nine undergraduates (185 females, mean age = 20.34 (3.22) years) participated in exchange for partial course credit. In terms of self-reported ethnicity, 42.1% identified as White/Caucasian, 21.0% as East Asian, 14.5% as South Asian, 5.7% as Middle Eastern, 4.8% as Southeast Asian, 3.1% as Black/African, 3.1% as West Indian/Caribbean, 2.6% as Hispanic, with 3.0% of the sample responding 'other' or declining to indicate the ethnicity they identified with. In accordance with pre-registration, in order to

² This study was preregistered on AsPredicted under the title of "The Role of Action Space on the Experience of Boredom under Constraints" (#2577) on January 16, 2017. <http://aspredicted.org/blind.php?x=gh2jr7>

avoid potential ceiling effects in boredom scores, participants were preselected based on boredom proneness levels. The short Boredom Proneness Scale (SBPS; Appendix A; Struk, Carriere, Cheyne & Danckert, 2015) was used to measure boredom proneness and was administered at the beginning of each academic term as part of a larger survey used for pre-screening purposes. Participants qualified to participate in this study if their SBPS score was within 0th to 75th percentile (i.e., no more than one quartile above the median). Participants were randomly assigned to one of two experimental conditions. Data were collected throughout the 2017 academic year and into the winter term of 2018. It was decided, a priori, to gather the data from as many participants as needed to attain 90 rule-complying participants per condition (see below for compliance rules). This study received ethics clearance from University of Waterloo Office of Research Ethics.

Procedure and experimental setup

The procedure was identical to Study 2.1 with the following exceptions. All conditions now employed a hidden camera (encased within a coffee mug; Lawmate Thermos Hidden DVR Spy Camera with 740p High Resolution) that was placed on top of a filing cabinet in the corner of the room facing the participant's seating position. Participants in both conditions were instructed to refrain from engaging with their environment and to instead stay seated, remain awake, and entertain themselves with their thoughts for a 15-minute period. After the 15-minute period, the researcher returned to administer a brief questionnaire on a tablet. Prior to departure, participants were informed of the purpose of the experiment, and the use of video recording was disclosed and consent to review the video recording was

obtained. Following the participant's departure, the video recording was reviewed by the researcher and the participant was deemed a rule-breaker if they did any of the following: did not remain seated, fell asleep, or interacted with their environment (these exclusion criteria can be found in the preregistration). The exclusion criterion were determined, a priori, based on participant feedback from Study 2.1.

2.8 Study 2.2: Results

Normality

All data analyses were conducted in R (R Core Team, 2015). Shapiro-Wilks tests of normality (Shapiro & Wilk, 1965) indicated that none of the study variables were normally distributed (all $ps < 0.05$). As such, non-parametric comparisons were conducted throughout. Independent-samples non-parametric comparisons were conducted using Wilcoxon's rank-sum test (Wilcoxon, 1945)³. For all comparisons, medians, first and third quartiles, Mann-Whitney-Wilcoxon U statistics were employed and non-parametric effect sizes were reported as a point-biserial correlation r (Cohen, 1988; Fritz, Morris, & Richler, 2012).

³In pre-registration it was indicated that a two-sample permutation (exact significance) t-test would be conducted if assumptions of normality were violated. However, it is acknowledged that the Wilcoxon test is more appropriate and is thus conducted instead. The results from both analyses are reported, and it is noted here that results do not differ substantially and thus don't change any interpretations.

Rule Breakers

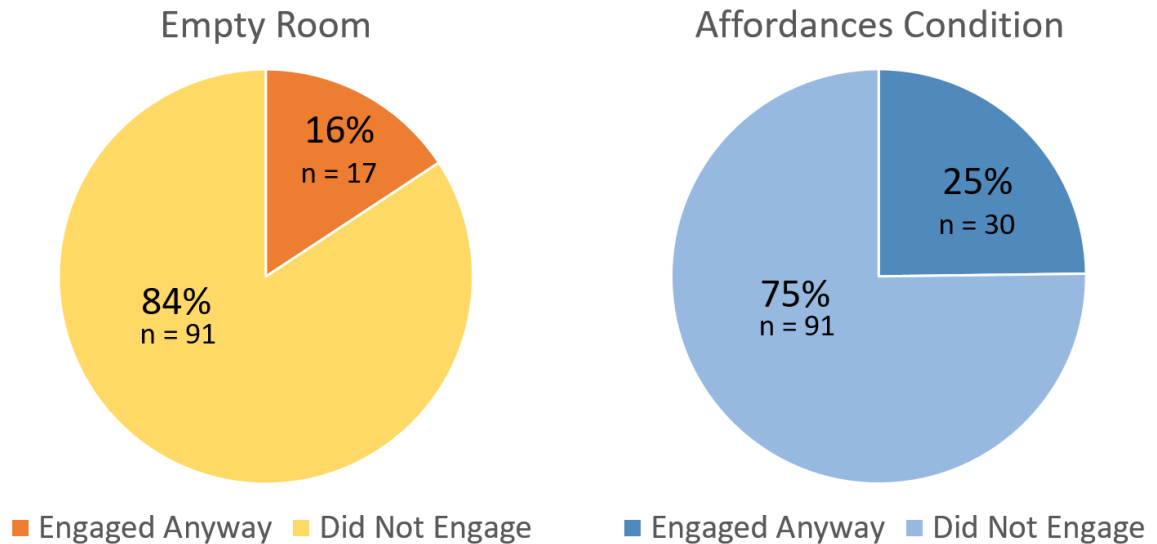


Figure 2.7 Proportion of rule breakers (engaged anyway) versus rule compliers (did not engage).

Of the 108 participants in the empty room, 17 (16%) broke the rules, while for the 121 participants in the affordances –ve condition, 30 (25%) broke the rules (Figure 2.7). There was a trend towards higher rates of rule breaking in the affordances –ve condition compared with the empty room, although this did not reach significance ($\chi^2(1) = 2.34, p = 0.126$). Given that participants could not be randomly assigned to break rules, the number of rule breakers versus non-rule breakers is highly uneven, and none of the study variables are normally distributed, an appropriate factorial analysis could not be conducted. Instead, a number of point-biserial correlations between rule breaking and the study variables was conducted for each condition (*Family-wise* $\alpha = 0.05/6 = 0.008$). In the empty room, rule

breakers (as opposed to rule followers) tended to report higher levels of wanting ($r = 0.27$, $p = 0.004$), but not boredom ($r = 0.24$, $p = 0.011$) or frustration ($r = 0.17$, $p = 0.072$). In the affordances –ve condition, none of the variables differed among rule breakers versus rule followers (all $ps > 0.052$). Finally, rule breakers, did not differ in their reports of boredom, wanting, or frustration across the two conditions (all $ps > 0.205$).

Condition Differences

Table 2.1 Descriptive statistics and condition differences for rule-compliers and full sample.⁴

	Empty Room <i>n</i> = 91 (108)			Affordances Condition <i>n</i> = 91 (121)			<i>U</i>	<i>p</i>	<i>r</i>
	<i>M</i>	<i>Q1</i>	<i>Q3</i>	<i>M</i>	<i>Q1</i>	<i>Q3</i>			
Boredom	3	2	5	4	3	6	2932	0.00058	0.26
	3	2	5.25	4	3	6	5137	0.00478	0.19
Wanting	4	2	6	5	3	7.5	3297	0.01686	0.18
	4	2	7	5	3	7	5720	0.1015	0.11
Frustration	1	1	2	2	1	3	3239	0.00570	0.21
	1	1	2	2	1	3	5201	0.00411	0.19

Note. Statistics for full sample is presented in bold, rule-followers are non-bolded. *M* = median, *Q1* = first quartile, *Q3* = third quartile, *U* = Mann–Whitney–Wilcoxon *U* statistic, *p* = significance value, *r* = effect size (point-biserial correlation).

Because a valid test of the study hypothesis requires that participants follow instructions, the following analyses were done on rule-followers only (see Table 2.1 for full

⁴ In pre-registration it was indicated that a two-sample permutation (exact significance) *t*-test would be conducted. Although instead Wilcoxon Ranked-Sum test was conducted, significance values from the originally planned analyses are reported here: $p = 0.00069$ (0.00676) for boredom; $p = 0.01378$ (0.08522) for wanting; $p = 0.02166$ (0.00952) for frustration.

sample analyses). As predicted, participants reported greater levels of boredom in the affordances –ve condition ($Mdn = 4$) than in the empty room ($Mdn = 3$; $U = 2932$, $p = 0.00058$, $r = 0.26$). Likewise, participants reported greater levels of wanting in the affordances –ve condition ($Mdn = 5$) than in the empty room ($Mdn = 4$; $U = 3297$, $p = 0.01686$, $r = 0.18$). However, contrary to study prediction, frustration levels were also significantly greater in the engaging room ($Mdn = 2$) than in the empty room ($Mdn = 1$; $U = 3239$, $p = 0.00570$, $r = 0.21$).

Exploratory analyses

Gender differences

Gender proportions did not significantly differ across conditions ($\chi^2(1) < 0.01, p = 1.00$). Females ($Mdn = 4$) reported marginally higher levels of boredom than males ($Mdn = 3; U = 3311, p = 0.05224, r = 0.13$). Females ($Mdn = 5$) also reported marginally higher levels of wanting than males ($Mdn = 4; U = 3372, p = 0.07510, r = 0.12$). There were no differences in reported frustration levels between females ($Mdn = 2$) and males ($Mdn = 1; U = 3633, p = 0.2336, r = 0.08$).

Mediation analysis.

Wanting. As part of post-hoc analyses, the hypothesis that the effect of the experimental manipulation on wanting was mediated by boredom was tested. The following analyses were performed on the rule-following subsample only. Prior to testing this mediation, it was first tested whether boredom was a significant predictor of wanting, which it was ($\beta = 0.77, p < 0.001$). The standardized effect of the experimental manipulation (i.e., empty room vs. affordances –ve condition) on wanting prior to the inclusion of boredom in the regression model was $\beta = 0.18, p = 0.013$. Following the inclusion of boredom, the effect of the manipulation on wanting was no longer significant, $\beta = -0.01, p = 0.821$, suggesting full mediation. To test the magnitude and significance of the indirect effect, a bootstrapping approach described by Preacher & Hayes (2004) with the aid of the mediation package in R was utilized (Tingley, Yamamoto, Hirose, Keele & Imai, 2014). After 10,000 Monte Carlo

simulations, a significant average causal mediation effect of 0.19, $p = 0.006$, was observed, reflecting a proportion mediated of 1.053, $p = 0.0100$. An alternative model in which wanting was the mediator of the effect of the manipulation on boredom was tested. Although the model produced a significant average causal mediation effect of 0.1377, $p = 0.0112$, this represents a proportion of the total effect mediated of 0.54, $p = 0.0108$, and the effect of the manipulation on boredom remained significant ($\beta = 0.18$, $p = 0.013$). This suggests that in the alternative model, wanting only serves as a partial mediator of the effect of the manipulation on boredom (Figure 2.8).

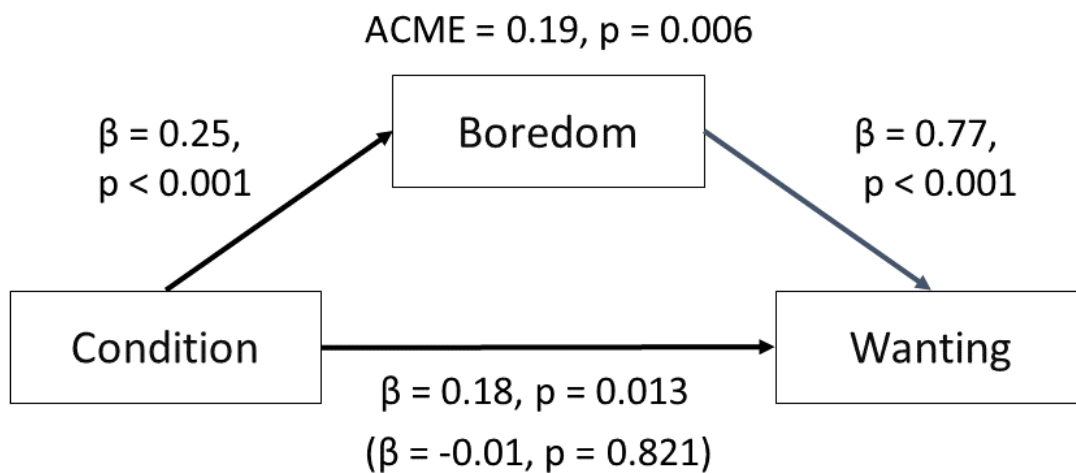


Figure 2.8 Mediation model. Boredom as a mediator fully explains the relationship between the study manipulation and wanting. ACME = average causal mediation effect (indirect effect).

Frustration. Since differences in frustration across conditions were unanticipated, a test was conducted to determine whether the effect of the manipulation on frustration was

mediated by boredom. Prior to testing this mediation, it was first tested whether boredom was a significant predictor of frustration, which it was ($\beta = 0.50, p < 0.001$). The standardized effect of the manipulation on frustration prior to the inclusion of boredom in the regression model was $\beta = 0.17, p = 0.021$. Following the inclusion of boredom, the effect of the manipulation on frustration was no longer significant, $\beta = 0.05, p = 0.476$, suggesting full mediation. After 10,000 Monte Carlo simulations, a significant average causal mediation effect of 0.12, $p < 0.001$, was observed, reflecting a proportion mediated of 0.73, $p = 0.018$. An alternative model in which frustration was the mediator of the effect of the manipulation on boredom was tested. Although the model produced a significant average causal mediation effect of 0.08, $p = 0.02$, this represents a proportion of the total effect mediated of 0.31, $p = 0.022$, and the effect of the manipulation on boredom remained significant ($\beta = 0.17, p = 0.009$). This suggests that in the alternative model, frustration only serves as a partial mediator of the effect of the manipulation on boredom. In other words, the manipulation primarily affected boredom, which in turn increased frustration.

2.9 Discussion

Consistent with the opportunity-cost model of boredom (Kurzban et al., 2013), when participants were asked to refrain from engaging with the environment and instead entertain themselves with their own thoughts, those placed in a room with many options for engagement (affordances –ve condition) reported higher levels of boredom than those placed in an empty room. This suggests that having a dearth of options for engagement (i.e., being in an empty room, with only your thoughts for entertainment) is in fact *less* boring than being exposed to (but unable to interact with) numerous options for engagement. Presumably, this occurs because the task of entertaining oneself with one’s own thoughts is associated with greater opportunity costs in an environment that is rich in potentially valuable or engaging alternatives.

If boredom motivates an individual to re-establish satisfying engagement, then we should expect that conditions that elicit boredom ought to also promote the desire to engage with one’s environment. Consistent with this view, it was found that participants in the affordances –ve condition reported higher levels of wanting to engage with their environment than did those in the empty room. Furthermore, preliminary evidence suggested that exposure to alternative activities (i.e., increased opportunity costs) primarily affects boredom, which precedes the desire to engage with the environment.

Since frustration was regarded as a state that arises when obstacles are encountered *during goal pursuit* –a condition that both study rooms lacked since goals were explicitly not pursued– it was predicted that frustration would be unaffected by the manipulation. Instead,

it was found that participants in the affordances –ve condition reported significantly greater levels of frustration than those in the empty room. However, unlike boredom, most people reported relatively little to no frustration in both conditions (i.e., all scores were on the low end of the scale; Table 2.1). This suggests that any differences in frustration may be an artifact of demand characteristics: that is, participants may have simply assumed that being unable to engage in a room full of alternative activities ought to be frustrating.

My results dovetail well with functional theories of boredom that suggest that boredom signals dissatisfaction with the current situation and a desire to engage in a more satisfying activity. These results are consistent with how trait-boredom proneness is viewed—a tendency to experience boredom more frequently and intensely (Farmer & Sundberg, 1986). Boredom-prone individuals may see options for engagement, but fail to effectively launch into them (Mugon et al., 2018). I also speculate that the mechanism by which the state of boredom is elevated when options for engagement are present but restricted (as in the affordances –ve condition), is via the representation of increased opportunity costs. This notion is consistent with prior research showing that high-boredom-prone individuals are more likely to be assessment oriented – placing an emphasis on evaluating and comparing alternatives for action (Higgins, Kruglanski, & Pierro, 2003; Kruglanski et al., 2000; Struk, Scholer, & Danckert, 2016; Mugon et al., 2018). Presumably, this kind of fruitless rumination over potential options for engagement makes the opportunity costs associated with many (typically not boring) situations salient, and when coupled with

an inability to engage in alternative activities, the state of boredom can become particularly intense.

On a practical level, results suggest, somewhat counterintuitively, that being exposed to many outlets for engagement may have its downsides. That is, in the presence of opportunity costs (in this case, alternative activities) our current activity may become boring, and hence, sustaining attention on the activity will likely prove difficult. This is particularly problematic when attainment of an adequate outcome is highly dependent on maintenance of engagement, and disengagement is not a viable option. For example, a student with a cell phone in his pocket may become more bored with a lecture relative to his peers who do not have access to a cell phone⁵. This is because the opportunity costs associated with the lecture are more salient when one is equipped with a device that affords many alternative, satisfying activities. Despite the apparent opportunity cost, commitment to attending to the lecture material does not avail oneself of engaging in the satisfying alternative, and thus prevents the alleviation of boredom.⁶

In conclusion, the present studies found that the inability to engage with an environment that afforded many alternative activities promoted feelings of boredom and a desire to engage with the environment. These results corroborate the notion that activities characterized by high opportunity costs (i.e., the presence of alternative activities with the

⁵ Consistent with this example, prior research suggests that problematic smartphone use is driven by boredom (Elhai, Vasquez, Lustgarten, Levine, & Hall, 2018).

⁶ It is, however, important to note that access to alternative satisfying activities could help alleviate boredom in some contexts, such as those in which engagement is not necessary for task completion. The most common example of this would be waiting: waiting does not require sustained engagement and permits engagement in other satisfying alternatives, such as conversing with someone.

potential to be more engaging than the primary task) contribute to the experience of boredom, which signals dissatisfaction with the current activity and a desire to engage in some alternative. These findings suggest that in the presence of satisfying alternatives an activity may become boring, and hence, that boredom could be alleviated by eliminating exposure to activities that are irrelevant to the primary task. What remains unclear is what kinds of opportunities are individuals sensitive to, and whether different contexts under which boredom occurs bias us to engage in specific activities.

Chapter 3: Exploring the Consequences of Boredom on Subsequent Task Engagement

3.1 Introduction

The studies just discussed demonstrated that opportunity costs are associated with the experience of boredom, which in turn promoted the desire to engage with the environment. These results support prior work that suggests that boredom motivates task or goal switching (Bench and Lench, 2013; van Tilburg & Igou, 2011; 2013;), as well as reframing or altering a current activity to make it less boring (Nett, Goetz & Daniels, 2010; Sansone, Weir, Harpster, & Morgan, 1992; Smith, Wagaman, & Handley, 2009). However, the specific activity that we end up choosing or the steps that we take to make an activity less boring remain poorly understood. This notion has been explored by Westage and Wilson (2018), who proposed that there are different conditions that lead to boredom and thus different responses are required to remediate the state. The goal of this study was to investigate whether different conditions that lead to boredom in turn make us sensitive to distinct opportunities for action thereby motivating different behaviours.

Desire for Optimal Challenge

Fenichel (1945) argued that an organism, although generally motivated to increase mastery, may revert to enjoying one's existing ability level as a way of coping with anxiety that arises from failure. However, White (1959) highlights that there is an enjoyment that comes from novelty and complexity, and that although we may seek low levels of stimulation and rest at the end of the day, that is not what we seek when we have energy. Perhaps then,

we are always motivated to seek stimulating activity. However, there is an optimal amount of stimulation that we need which changes depending on our circumstances. Hebb (1955) suggested that if arousal is low, individuals will find ways to challenge themselves. Likewise, if arousal levels are high, individuals will seek activities that reduce arousal ultimately bringing themselves closer to an optimal level. This notion of a “Goldilocks” zone of stimulation parallels theories of achievement motivation, which suggest people engage in activities that have a high likelihood of success, but not so high that they does not pose any challenge (Atkinson, 1957; McClelland, 1951).

In order to attain a specific level of stimulation (optimal skill-challenge match), an individual needs to be sensitive to deviations away from a desired level of stimulation (over or under-stimulation) and generate *compensatory* actions aimed at reducing such deviations (Carver and Sheier, 1998). Regulation of this fine balance of stimulation is evident during animal foraging. An animal must balance the need for exploration with that of exploitation, in order to attain an optimal rate of uncertainty reduction and/or resource acquisition (Charnov, 1976; Cohen et al., 2007). Exploration is the act of searching for information or resources (e.g., watching an avant-garde film or trying a different spot on the lake to catch a fish), for the purpose of improving your mental models of the world and discovering new sources of nourishment. Exploratory behaviour, although potentially highly rewarding, can be challenging, and has associated risks. In addition, learning is energetically costly to the organism (Cohen et al., 2007). Exploitation, on the other hand, is the act of securing or enjoying known quantities (e.g., re-watching a favourite movie or returning to your favourite,

reliable fishing spot). Exploitation behaviours, are less challenging because they are less risky and rely on expertise and already learned skills (Cohen et al., 2007). The fact that foraging permits self-regulation of optimal challenge levels makes it an ideal behaviour to study how different circumstances bias future behaviours.

Boredom as a Self-Regulatory Signal

In Csikszentmihalyi's (1975) model of flow, boredom has been more directly implicated with a mismatch between one's skill and the challenge posed by an activity. Specifically, boredom is thought to arise when skill levels far exceed the challenge imposed by the task. Furthermore, the model suggests that a state of anxiety arises when challenge exceeds one's capabilities. More recently, the value-control theory of achievement emotions suggests that within achievement settings, situations characterized by low value, or either low or high perceived control, promote boredom (Pekrun, 2006). The perception of control depends on the skill of an agent and the demands of the current task (Skinner, 1996, Pekrun, 2006). However, perception of control is the belief that an agent is able to produce a desired outcome, and thus perceptions of control may also be illusory (Higgins, 2014; Taylor & Brown, 1988). Consistently, my prior work demonstrated that participants who played a game of rock paper scissors against a computer that was rigged to make the participant win or lose 100% of the time led to varied reports of perceived control (Struk, 2015). Importantly, boredom had a curvilinear relationship with control, such that both low and high levels of perceived control were associated with higher levels of boredom. This curvilinear relationship was also observed in self-reported task difficulty and boredom following

engagement in varied difficulties of an air traffic control task in which participants had to determine whether the trajectories of two planes overlap and would thus “collide” (Westgate & Wilson, 2018). Overall, this body of work suggests the experience of boredom is linked to the perception that we are not optimally challenged.

Pekrun’s (2006) value-control theory of achievement emotion was the first to describe how different situational characteristics promote boredom. However, this theory makes no prediction that these different antecedents will be associated with distinct consequences for future behaviours or any compensatory actions. The model only suggests that boredom leads to a loss of motivation to engage in a given activity. The Meaning and Attention Components (MAC) model of boredom, on the other hand, is the first to formally propose that we may engage in compensatory mechanisms that remediate the source of boredom (Table 3.1; Westgate and Wilson, 2018). This model states that boredom has two components (meaning and attention) which are defined by their causes which in turn dictate what behaviours they motivate. The meaning component indicates that boredom arises when there is a mismatch between the current activity and the valued goal. This motivates individuals to reconstrue the current activity or seek an alternative activity that is more in line with their goals. The attentional component indicates that boredom may arise when there are mismatches between cognitive demands and available resources. These mismatches are thought to give rise to “attentional boredom”. One such mismatch can occur when the cognitive demand required by the task is far below the available resources (understimulation). Boredom in this case would motivate an individual to increase demand

(e.g., making a task more complex) or decrease resources (e.g., switching to non-dominant hand in a game of tennis). Another mismatch can occur when demands exceed the available resources (overstimulation). Boredom in this case would motivate an individual to reduce demand (e.g., simplify the task) or increase resources (e.g., increase arousal).

Current Study

The goal of the current experiment was to investigate directly whether deviations from optimal stimulation tip the balance between exploration and exploitation. Specifically, if we are overstimulated (too challenged) do we favour exploitation behaviours, while if we are understimulated (underchallenged) do we instead favour exploration behaviours (Table 3.1)?

Table 3.1 Simplified MAC model with study goals bolded. Adapted and modified from Westgate & Wilson (2018). Table depicts four conditions that promote boredom and compensatory response associated with each one. The goal of present study is to create conditions of high meaning, and of under and overstimulation.

	Meaning component	
	Low Meaning	High Meaning
Attention component	Task is INCONGRUENT with valued goals	Task is CONGRUENT with valued goals
Understimulation: Demand < Resources	Seek a demanding alternative task	Increase demand of current task (Exploration)
Overstimulation: Demand > Resources	Seek an undemanding alternative task	Reduce demand of current task (Exploitation)

In the experiment all participants engaged in two tasks. For the primary task, two conditions were designed to induce boredom driven by distinct causes; in the “hard” condition participants engaged in an activity that exceeded their skill level. This was intended to induce boredom borne of overstimulation. In the “easy” condition participants engaged in an activity that was well below their skill level, intended to induce boredom driven by understimulation. A third condition, referred to as the “medium” condition, was intended to function as a control, such that participants engaged in an activity in which challenge levels were matched to their skill level – that is, the task was not too easy, or too hard. A further manipulation was used in all conditions intended to ensure that participants experienced high meaning in the task. That is, as evident in Table 3.1 meaning also has a prominent influence on boredom. Given the goal here was to examine the consequences of boredom arising from distinct levels of challenge (i.e., over- vs understimulation), it was important to make an attempt at controlling meaning. Following the primary task, participants answered self-report measures concerning perceived task difficulty, boredom and meaning to ensure that the manipulation was effective.

Following the primary task participants engaged in a foraging (Berry Picking) task, in which they had to explore the environment (which cost some amount of energy represented as “juice” in the task) in order to find patches of berries, and collect as much “juice” as possible by collecting the largest “berries”. The primary hypothesis was that those in the “hard” condition would become more sensitive to opportunities to exploit, while those in the “easy” condition would be sensitive to opportunities to explore. To assess this, following the

Berry Picking task participants were asked a number of questions probing the extent to which they wanted to explore or exploit. Furthermore, a number of objective indices of exploration and exploitation were derived from the observed behaviour within the foraging task.

3.2 Methods

Participants

Two samples of participants were tested in this experiment, one from the University of Virginia and the other from the University of Waterloo. The Virginia sample consisted of one hundred and sixty-nine undergraduates (107 females, mean age = 18.96 (0.96) years) who participated in exchange for partial course credit. In terms of self-reported ethnicity, 52.7% identified as White, 23.7% as Asian, 16.6% as multi-ethnic, 7.7% as Black, 3.6% as Other. The Waterloo sample consisted of one hundred and twelve undergraduates (79 females, mean age = 20.07 (1.81) years) who participated in exchange for a bonus course credit. 32.4% identified as White/Caucasian, 26.9% as East Asian, 18.5% as South Asian, 7.4% as Southeast Asian, 3.7% as Black/African, 2.8% as Middle Eastern, 2.8% as West Indian/Caribbean, 0.9% as Hispanic, with 4.6% of the sample responding ‘other’ or declined to indicate their ethnicity. Participants were randomly assigned to one of three experimental conditions. Data was collected throughout the Winter 2018 term. Both studies gained full ethics approval from the respective universities. It was decided a priori that data collection would start at the beginning of Winter 2018 term and end at the end of that term.

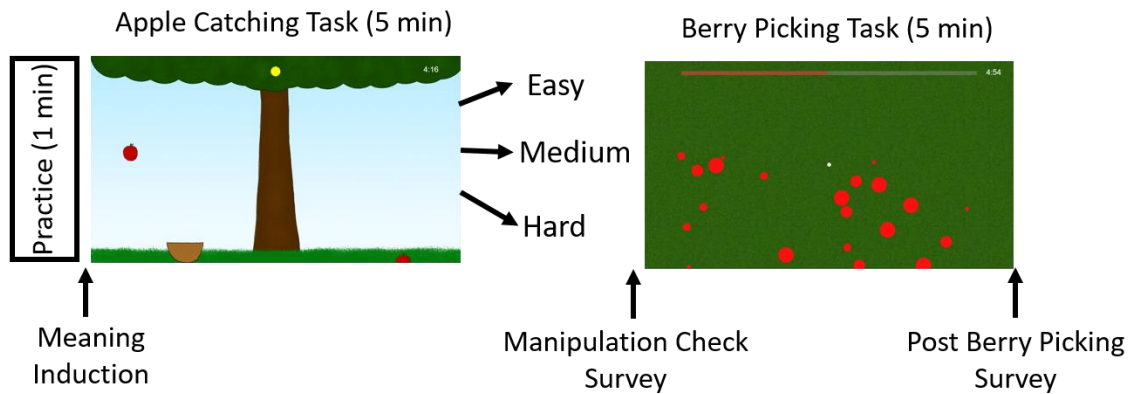


Figure 3.1 Experimental procedure. Following 1 minute of Apple Catching Task practice, participants underwent a meaning induction. Next, participants engaged in one of 3 versions of the apple catching task (easy, medium or hard difficulty) for 5 minutes. Next, participants completed a manipulation check (post apple catching task). Next, all participants completed a berry picking task for 5 minutes. Finally, participants completed the post berry picking survey.

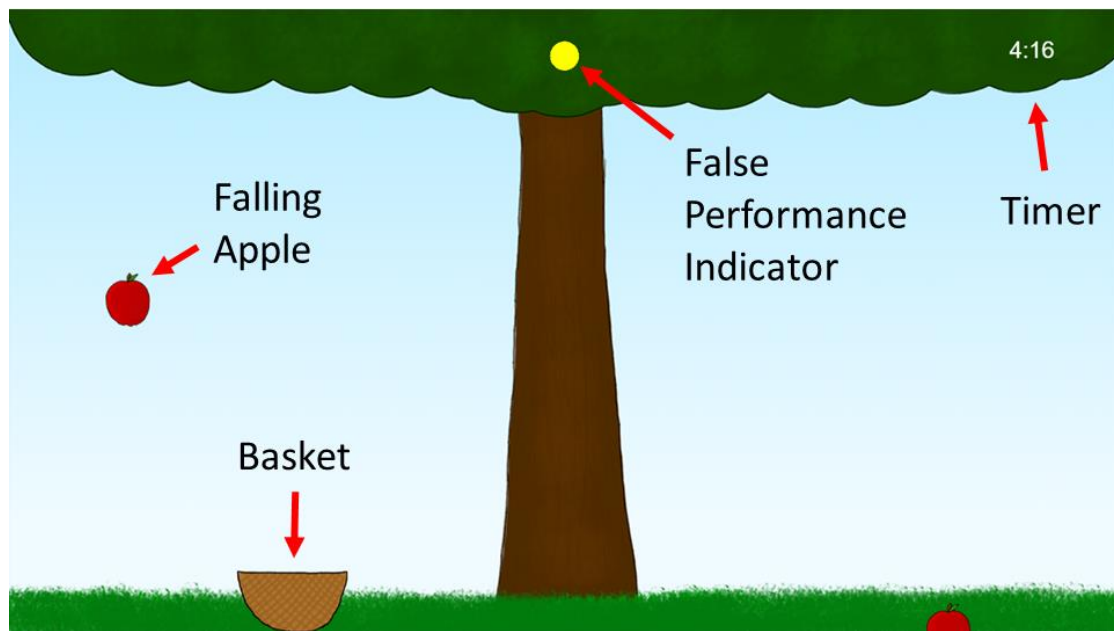


Figure 3.2 Diagram of the Apple Catching Task.

Procedure and experimental setup

Figure 3.1 depicts the experimental procedure. To manipulate the skill-demand match/mismatch participants were asked to do an “Apple Catcher” task for 5 minutes (Figure 3.2). In this task, participants have to catch falling apples by correctly positioning a basket using arrow keys. Since participants completed this task on their own laptop, with varying screen aspect ratios and resolutions, the task window was adjusted to display a 16:9 aspect ratio which means that some participants had blank spaces to the left and right of the task window. Despite this adjustment all participants could see the same amount of virtual space (1,920 x 1,080 pixels) and were able to move the basket at the same rate (30 pixels of virtual space per frame). To ensure that all participants moved the basket and saw the apples falling at a consistent rate, the movement speed was adjusted to match the frame rate (e.g., 60 pixels of virtual space per frame if the frame rate was 30 frames per second). Participants completed a one-minute practice period in which they were able to adjust the difficulty level of the task. Following the practice phase, in order to increase the sense of meaning for all participants, they were told that their performance on the experimental portion of the Apple Catcher task would determine whether \$1 would be donated to a charity of their choosing (Westgate & Wilson, 2018). Participants were asked to select a charity they wished to donate to and write one to two sentences describing why this charity was important to them (see Appendix B for possible charities participants could choose from). In order to increase effectiveness of the meaning induction, a circle was placed at the top of the screen of the Apple Catching task that was pre-programmed to change colours (from red to yellow to green). Participants were

told that the circle was an indicator of their performance, if the circle was red they were performing too poorly, yellow indicated that they were close to acceptable performance, and green meant that they performed adequately for donation. Participants were then assigned to one of 3 conditions based on challenge level; the ‘hard’ condition – in which participants arbitrarily missed 50% of all apples, the ‘medium’ condition – in which participants caught around 75% of all apples, and the ‘easy’ condition – in which apples fell rarely (every 3 seconds) and slowly (3 seconds to fall), easily permitting a 100% catch rate. The apple catching rate was established in a pilot study (Appendix C). The difficulty level was adjusted every 10 seconds to match the desired catching rate, with the exception of the ‘easy’ condition in which the difficulty level was fixed. Participants completed a questionnaire following the Apple catcher task that pertained to their experience during the Apple catcher task (Table 3.2). Responses to this questionnaire were recorded on a 9-point Likert scale ranging from “Not At All” to “Extremely”.

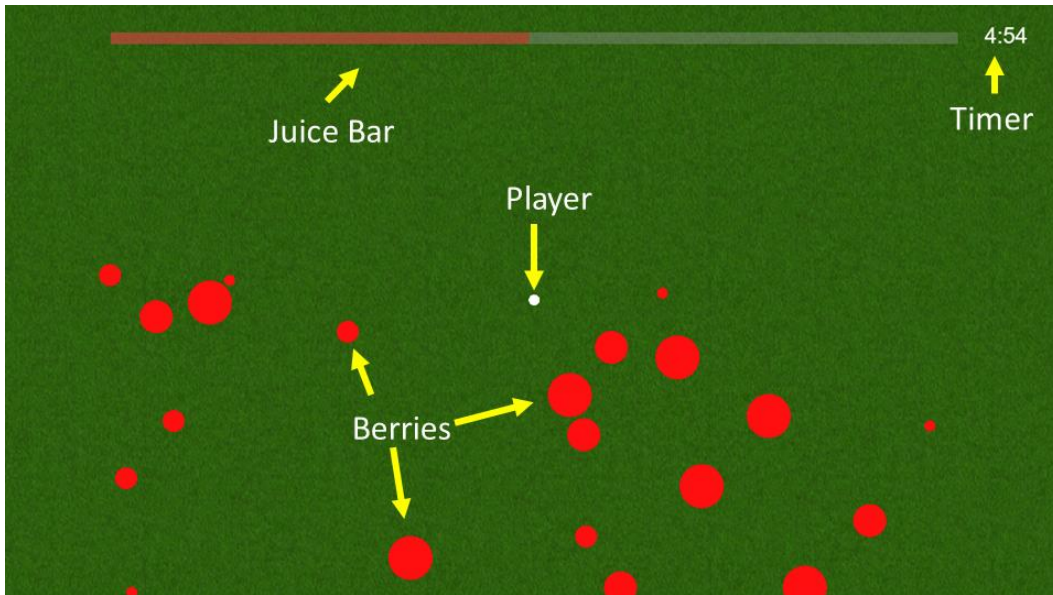


Figure 3.3 Diagram of the Berry Picking task. The juice bar is visible at the top of the screen. A timer (counting down from 5 minutes) was present in the top right corner. Berries were depicted as red circles of varying sizes. The player is demarcated as a white circle which was always present in the centre of the screen.

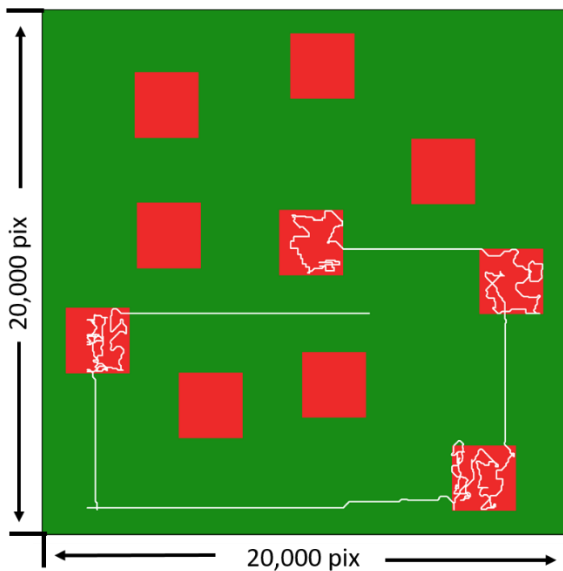


Figure 3.4 Diagram of the Berry Picking task environment, and a sample path. Grass texture without any berries is depicted in green. Berry patches are depicted in red. White line depicts an example of a foraging path (participants start at the centre of the environment).

Following the Apple Catcher task, participants completed the “Berry Picking” task for 5 minutes (Figure 3.3). This was used to measure the degree to which participants engaged in foraging strategies representative of exploration vs. exploitation. In this task, participants explored a vast virtual “grassy” field (20,000 x 20,000 pixels) and maximized their “juice” by collecting red “berries” that were distributed in patches (10 patches; Figure 3.4). Each patch was defined as a square (2,600 x 2,600 pixels) positioned randomly and at least 5,000 pixels away from the centroid of a neighbouring patch. There were four sizes of berries, 4, 8, 12, and 16 pixels in radius. Each patch had an equal number of berries (80), with equal numbers of each berry size. All participants could see the same amount of virtual space (1,920 x 1,080 pixels of the virtual environment). To ensure that all participants explored the virtual environment at the same rate the movement speed was adjusted to match the frame rate supported by their browser (e.g., 16 pixels of virtual space per frame if the frame rate was 30 frames per second). Participants were told that their goal was to collect as much “juice” as possible within a 5 minute period, and that there was a cost associated with movement – the juice bar decreased with movement. The foraging game allowed participants to control the extent to which they explored the environment and exploited the resources they encountered. Following the Berry Picking task participants were asked to fill out a survey asking questions pertaining to their experience (Table 3.3). All responses were recorded on a 9-point Likert scale ranging from “Not At All” to “Extremely”.

Measures

Post Apple Catcher Survey

Table 3.2 List of questions presented following the Apple Catcher game.

Variable	Question
Boredom	“How boring was the Apple Catcher game?”
Meaning	“How personally meaningful was the Apple Catcher game?”
Difficulty	“How difficult was the Apple Catcher game?”

Table 3.2 describes the survey questions asked for each of the measured constructs. In order to assess whether the experimental manipulation was effective I measured participants' self-reported sense of meaning, task difficulty, and boredom. Several other exploratory variables were included (see Appendix D for a complete list of items). An indication that the manipulation was effective involved observing: 1) an equivalently high sense of meaning across all conditions, 2) high task difficulty and high boredom in the “hard” condition, 3) medium task difficulty and low boredom in the “medium” condition, and 4) low task difficulty and high boredom in the “easy” condition.

Post Berry Picking Survey

Table 3.3 Self-report measures following the Berry Picking game.

Variable	Question	Latent Variable
Patches	“Some people stay in just one place the whole time; other people move around a lot to find all the different berry patches. How important was it to you to find all the berry patches in the game?”	Exploration
Explore	“How much did you care about exploring all the space in the game?”	Exploration
Picking	“Some people pick all the berries they see before moving on; other people pick a few and then move on to look for more berry patches. How important was it to you to pick all the berries before moving on and looking for more?”	Exploitation

Table 3.3 describes the survey questions asked following the Berry Picking game.

Note that several other measures were added for exploratory purposes (for a complete list of all questions see Appendix E). The aim of these items was to assess participants’ self-reported exploration and exploitation tendencies.

Behavioural Metrics

A number of metrics were derived from the foraging task as a measure of exploration and exploitation behaviour (Table 3.4).

Table 3.4 List of behavioural measures derived from the Berry Picking game.

Variable	Description	Latent Variable
Berries	# of berries collected	Exploitation
Length	total path length taken	Exploration
Patches Discovered	# of patches found	Exploration
Area	Prop. of areas discovered (out of 100 equally partitioned areas)	Exploration
Search Time	Prop. of time spent moving between patches	Exploration
Patch Time	Prop. of time spent within patches	Exploitation

3.3 Results

Normality

All data analyses were conducted in R (R Core Team, 2015). Shapiro-Wilks tests of normality (Shapiro & Wilk, 1965) indicated that study variables were not normally distributed across all conditions (all $ps < 0.05$) with the exception of: Berries, Juice Bar, Area and Search Time variables (Table 3.3). For consistency, non-parametric comparisons were conducted throughout. Independent-samples non-parametric comparisons were conducted using Wilcoxon's rank-sum test (Wilcoxon, 1945). When more than two groups were present non-parametric comparisons were conducted using Kruskal-Wallis rank-sum test (Hollander & Wolfe, 1999). A Bonferroni correction was applied to pairwise comparisons without a priori predictions.

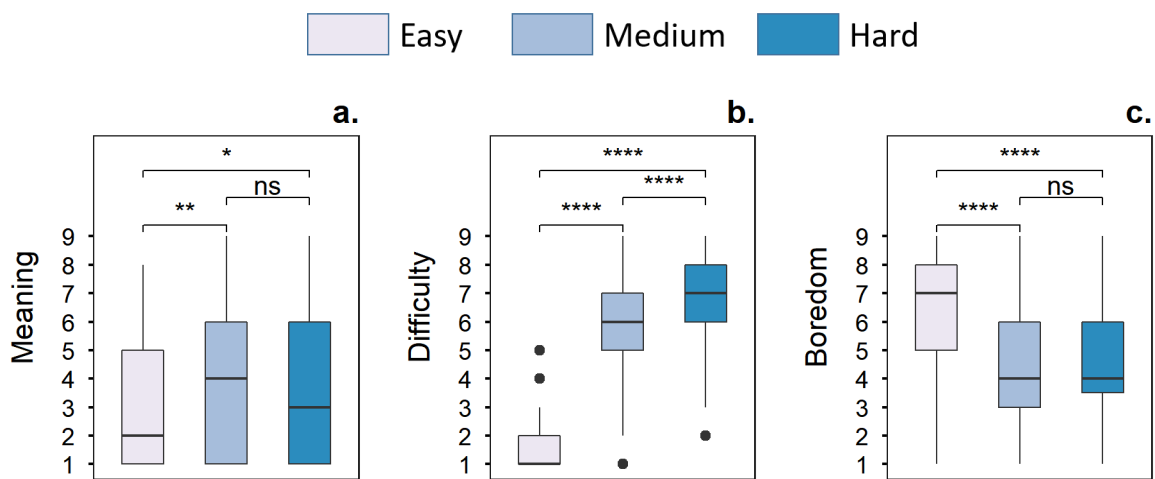


Figure 3.5 Boxplots for post Apple Catcher survey variables for each condition. For comparisons unadjusted Wilcoxon ranked-sum significance values are used: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, **** = $p < 0.0001$

Manipulation Check

As a manipulation check, comparisons across all post Apple Catcher survey variables were conducted (Figure 3.5). Contrary to what was expected the meaning manipulation failed to attain equal meaning across conditions. That is, meaning significantly differed across conditions ($\chi^2(2) = 8.01, p = 0.0182$). Specifically, the easy condition was less meaningful than the medium condition ($p = 0.04$) and marginally less meaningful than hard condition ($p = 0.113$; Figure 3.5a). As expected, the difficulty manipulation successfully affected difficulty across conditions ($\chi^2(2) = 197.22, p < 0.001$) with the medium condition being more difficult than the easy condition ($p < 0.001$) and the hard condition being more difficult than the medium condition ($p < 0.001$; Figure 3.5b). As expected, reported boredom differed across conditions ($\chi^2(2) = 44.26, p < 0.001$). However, only the easy condition was considered more boring than the medium and hard conditions ($p < 0.001$). Contrary to expectations, the hard condition did not differ from the medium condition ($p = 0.260$; Figure 3.5c).

Berry Picking Task

Consistent with study predictions, a significant difference in the area explored was found across conditions ($\chi^2(2) = 8.92, p = 0.012$) such that participants in the hard condition explored significantly less than those in the medium condition ($p = 0.006$). Unexpectedly, participants in the easy condition also explored a smaller area of the environment than those in the medium condition ($p = 0.015$). Furthermore, a significant difference in search time was found across conditions ($\chi^2(2) = 6.18, p = 0.046$) such that participants in the hard condition

spent significantly less time searching than those in the medium condition ($p = 0.022$). However, contrary to predictions, participants in the easy condition spent marginally less time searching than those in the medium condition ($p = 0.052$). No other variables reached statistical significance (all $ps > 0.140$).

Moderation Analysis

This study hypothesized that boredom would have different consequences depending on the eliciting conditions. To test this, high levels of boredom are needed in both the “easy” and “hard” conditions, a situation not obtained given the equivalent levels of boredom in the medium and hard conditions. Thus, in order to proceed with a sufficiently powered test of the hypothesis, a moderation analysis was conducted. Specifically, it is expected that the relationship between reported boredom levels from the Apple Catcher task and a given measure of exploration or exploitation will be different across conditions. Initially, the “medium” condition was meant to serve as a control condition since it was anticipated to be the condition inducing the lowest levels of boredom. However, since the source of boredom is ambiguous in the medium condition, keeping this condition would preclude any interpretable results. Furthermore, since boredom served as a regressor in the moderation analysis, there was no longer a need for a (low boredom) control condition. More specifically, low boredom levels found within both the easy and hard Apple Catcher conditions will instead serve as their own controls within their respective conditions (boredom scores had a substantial amount of variability in both the easy condition ($SD =$

1.95) and the hard condition (SD = 2.05)). This analysis would also allow for control of uneven levels of meaning between the hard and easy conditions.

To conduct this analysis two regression models were constructed for each dependent variable. In the first model, boredom, meaning and condition were entered as regressors⁷. The second model was identical to the first, except that it contained an interaction term between boredom and condition. Next, an analysis of variance analysis (ANOVA) was conducted to determine whether the model fit significantly improved following the addition of the interaction term. Note that evidence for my hypothesis is highlighted by a significant interaction term between boredom and condition.

Post Berry Picking Survey

As predicted, the relationship between boredom and the desire to explore the entire environment was significantly moderated by condition ($F(1,189) = 4.00, p = 0.047$; Figure 3.6b), such that there was a negative relationship between boredom and the desire to explore for the hard condition but not the easy condition. As predicted, the relationship between boredom and the desire to pick all the berries before moving on from a patch was significantly moderated by condition ($F(1,189) = 5.29, p = 0.023$; Figure 3.6c), such that there was positive relationship between boredom and the desire to pick all berries for the hard condition but not the easy condition. No other interactions reached significance (all $ps > 0.402$; Figure 3.6).

⁷ Note that moderation analyses without meaning as a covariate does not alter the interaction term substantially for all dependent variables.

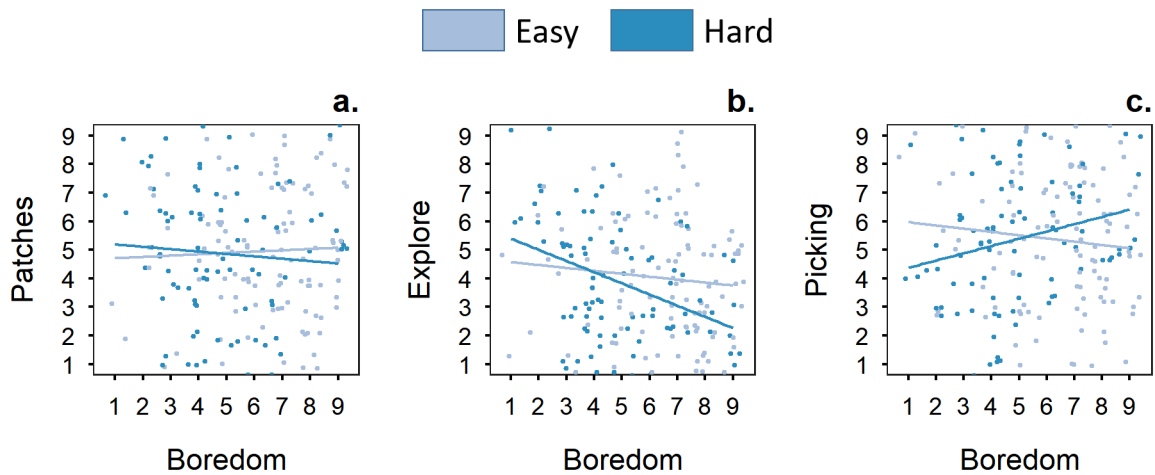


Figure 3.6 Scatter plot for each self-report variable in the Berry Picking survey. A line of best fit is present for Easy (Green) and Hard (Orange) conditions.

Behavioural Measures

As predicted, the relationship between boredom and search time was significantly moderated by condition ($F(1,190) = 5.35, p = 0.022$; Figure 3.7e), such that there was a positive relationship with search time for the easy condition and a negative relationship in the hard condition. Furthermore, the relationship between boredom and area explored was marginally significantly moderated by condition ($F(1,190) = 3.8, p = 0.053$; Figure 3.7d), such that there was a positive relationship with area explored for the easy condition and negative relationship in the hard condition. No other interactions reached significance (all $ps > 0.372$).

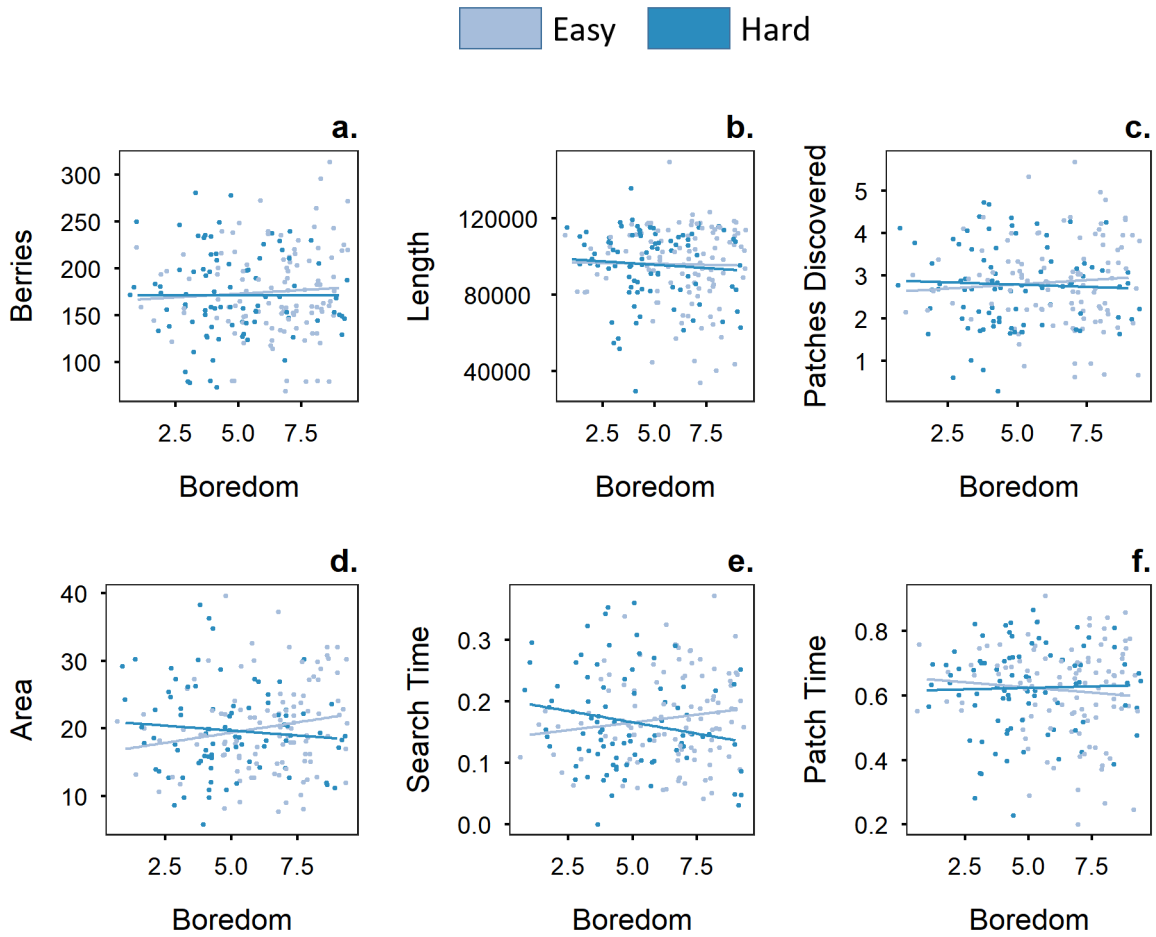


Figure 3.7 Scatter plot for each dependent variable derived from the berry picking task. A line of best fit is present for Easy (Green) and Hard (Orange) conditions.

3.4 Discussion

The primary goal of this study was to test the hypothesis that boredom resulting from either over or understimulation would alter an individual's sensitivity to opportunities for exploitation or exploration respectively. To do so, participants engaged in a task with varying degrees of difficulty (e.g., hard, easy or medium) after which they were asked a number of questions meant to determine which opportunities to act they were sensitive to in the Berry Picking task. Furthermore, actual exploration and exploitation tendencies during the Berry Picking task were assessed.

Despite efforts to pre-calibrate difficulty, meaning, and boredom before the experiment, the manipulation only fully succeeded in manipulating difficulty in the desired manner (i.e., boredom and meaning were still manipulated, but not in the manner intended). It is known that low meaning increases boredom and is thought to promote disengagement (and motivate seeking of different activities; Westgate & Wilson 2018). Since I wanted to investigate effects of skill-challenge mismatch, the goal of the meaning manipulation was to keep meaning equivalent and high across all experimental conditions. However, the easy condition was rated as less meaningful than the optimal and hard conditions, and meaning levels were generally low across all conditions. This may be because the effect of choosing a charity on participants sense of meaning at the beginning of the experiment decays with time and is overshadowed by the effects of the task, especially in the easy condition. This is not surprising at face value, as catching one apple falling every 3 seconds, falling at a rate of only 3 seconds is hardly a meaningful even when participant's efforts result in a donation to a

charity. Other researchers also suggest that skill-challenge mismatches are fundamentally less valued or meaningful (Pekrun, 2006; Struk, 2015). Indeed, it has been suggested that lack of meaning may be the defining characteristic of boredom (van Tilburg & Igou, 2012). Although the meaning manipulation used here had proven successful in others' research (Westgate & Wilson, 2018), and possibly could be improved by increasing the amount donated to charity, ultimately more work needs to be done to determine whether skill-challenge mismatches can truly be dissociated from meaninglessness.

With regard to boredom, the manipulation failed to attain high levels of boredom in the hard condition with boredom levels roughly equivalent to those reported in the medium condition. High levels of frustration may provide a clue as to why participants did not report high levels of boredom in the hard condition (Appendix F; Figure F.1). In this case, frustration may be regarded as a proxy for engagement as participants in this condition were actually *more* engaged as they attempted to establish control (and were frustrated by their attempts). Indeed, participants in the hard condition experienced less perceived control than those in the medium condition (Appendix F; Figure F.1). It is likely that after a longer period of time (i.e., playing the Apple Catcher game for more than 5 minutes) and/or after many failed attempts to establish control, participants would disengage and become bored. This is consistent with prior research that demonstrates that boredom arises in low perceived control circumstances after longer timespans (Dicintio & Gee, 1999; Pekrun et al., 2010; Struk, 2015). In order to make the hard condition more boring, the apple catching task may still be adequate, but may require even lower catch rates (less than 50%) and a longer play duration.

As predicted, experience in the hard condition led to reduced exploration of the environment in the foraging task. However, a similar pattern of behaviour was also observed for the easy condition. That is, in both the easy and hard conditions, participants spent less time exploring and explored a smaller area of the environment than those who were in the medium challenge condition. This pattern of results suggests that any type of skill-demand mismatch (over or understimulation) may promote a reduction in exploratory behaviour. However, a reduction in exploratory behaviour may also indicate disengagement more generally, although the antecedents for disengagement may differ across conditions. High demand in the hard condition may reduce subsequent exploratory behaviours in order to attain a more optimal challenge level. In contrast, low meaning (and challenge) in the easy condition may lead to reduced exploratory behaviours simply because participants disengage from the task altogether. Ultimately, the failure to attain equivalent levels of meaning and high levels of boredom in both the easy and hard conditions precludes an accurate test of the study hypothesis via a simple between groups comparison.

To investigate the study hypothesis that boredom arising from overstimulation promotes exploitation behaviours, whereas boredom arising from understimulation promotes exploration behaviours, the shortcomings of the manipulation were addressed by conducting a set of exploratory moderation analyses. This was done by assessing whether the impact of boredom on various measures of exploration and exploitation varied depending on the hard or easy condition. This analysis yielded some evidence in favour of the hypothesis. Specifically, it was observed that the reported desire to explore the environment, as well as

the actual area explored, and time spent searching, all had a negative relationship with boredom in the hard condition. These same factors exhibited either a positive or no relationship with boredom in the easy condition. This is generally consistent with the hypothesis that those who become bored because the demands exceed their resources would be less inclined to explore and would instead exploit local resources. Likewise, those who became bored because the demands did not exhaust their available resources would try to engage in exploratory behaviours.

An alternative explanation can be derived from the observation that boredom primarily had an effect in the hard condition. Specifically, bored participants in the hard condition expressed less desire to explore their environment and were more concerned about picking all the berries within the patch, while the opposite was not true for the easy condition. This asymmetry suggests that unlike boredom in the easy condition, boredom in the hard condition may promote disengagement. These results, although unexpected, are consistent with predictions of the opportunity cost model (Kurzban et al., 2013). According to Kurzban and colleagues (2013) the primary and subsequent tasks are inherently linked together such that their combined value is not only dictated by the external incentives (i.e., participants complete both tasks in order to receive course credit) but also a social obligation to the researcher. Thus, unless the primary activity has an intrinsic value, the value of the entire experiment (primary and subsequent activity) diminishes over time, as participants progressively feel like they have fulfilled more and more of the obligation to apply effort in a

given activity. Given that only the hard condition truly required substantial amount of effort to engage in, only this condition showed a signature of disengagement.

Overall, the current study highlights that not all states of boredom are created equal. When we become bored because we are understimulated we are inclined to seek more challenging activities, while if we become bored because we are overstimulated we are more inclined to seek less challenging activities, results which are consistent with the MAC model (Westgate & Wilson, 2018). These results however are in contrast to the notion that boredom is purely a signal to explore (Cohen et al., 2007; Gomez-Ramirez and Costa, 2017; Yu, Chang & Kanai, 2018). In fact, in the current study, the more bored participants were following the hard condition the less they explored and the less they reported *wanting* to explore. Instead, what the results of this study suggest is that boredom signals a deviation from optimality and motivates us to remediate this deviation via an appropriate action, demand reduction if demand is too high, and demand increase if demand is too low. In the context of foraging this means that boredom can promote both exploratory or exploitative behaviours. This study examined how different situational factors that increase boredom make us sensitive to different opportunities for action; however, it remains unclear what makes an individual inherently predisposed to specific actions.

Chapter 4: Genes and Sensitivity for Action⁸

4.1 Introduction

In the previous chapter I observed how situational factors make individuals sensitive to different opportunities for actions. However, animals display a variety of actions even though they are in the same situation. Indeed, during foraging, species as diverse as the fruit fly (*Drosophila melanogaster*), honey bees, and nematodes appear to be predisposed to either exploration or exploitation behaviours (Anreiter, Kramer & Sokolowski, 2017).

Manipulations of a single gene, the *foraging gene* (*for*) levels are sufficient to affect such predispositions in foraging behaviour of multiple species despite the many genes involved in generating the behaviour (Anreiter et al., 2017; Ben-Shahar, Robichon, Sokolowski, & Robinson, 2002; Licas & Sokolowski, 2009). Searching for and securing food – foraging – is a fundamental and ubiquitous goal in the animal kingdom, observed across many species (Anreiter et al., 2017; Carter & Redish, 2016; Janson, 2016). In terms of goal pursuit in general, it is known that humans too display individual differences in how they pursue goals (Kruglanski et al., 2000). However, it is unknown whether the human version of the foraging gene plays a similar role in regulating how we pursue goals. The goal of this chapter was to investigate the influence of the human foraging gene on foraging behaviour and self-regulation more broadly.

⁸ A version of this chapter is published as: Struk, A. A., Mugon, J., Huston, A., Scholer, A. A., Stadler, G., Higgins, E. T., Sokolowski, M. B. & Danckert, J. (2019). Self-regulation and the foraging gene (PRKG1) in humans. *Proceedings of the National Academy of Sciences*, 116(10), 4434-4439.

Proclivities for Action

In the previous chapter I discussed how animals satisfy their need to be effective by seeking an optimal level of stimulation. That is, animals pursue demanding activities that slightly exceed their current skill level which allows for optimal stimulation. This optimal level of stimulation forms a homeostatic goal which is regulated through compensatory actions. However, not all animals desire to attain the same level of homeostasis and may differ in their propensity to successfully achieve homeostasis. Indeed, it is likely that both of these parameters vary within species. Not only is the optimum of one animal different from the optimum of another, but *how* and how well they attain and maintain this homeostasis likely varies.

Regulatory Mode Theory delineates two self-regulatory modes or means of goal pursuit in humans. Locomotion emphasises execution of actions, a ‘just do it’ approach, and assessment emphasises evaluation of alternatives—a ‘do the right thing’ approach (Kruglanski et al., 2000). Individuals not only vary in the degree to which each mode is dominant in a given circumstance but also seem to exhibit a particular chronic disposition in the extent to which each mode is utilized. Each regulatory mode may have implications for how well an individual is capable satisfying effectance motivation. Indeed, high (versus low) locomotion individuals are more likely to be intrinsically motivated as they see inherent value in action and thus see action as an end in itself (Kruglanski et al., 2000). Thus, locomotion ensures that we are engaged with our environment at a level at or beyond what is necessary to satisfy our need to be effective. The evaluative concerns of a high (versus low) assessment individual,

on the other hand, makes them place an emphasis on extrinsic rewards. Assessment may thus motivate behaviours that are incongruent with satisfaction of effectance motivation, such as doing an undemanding activity that has the highest utility (e.g., staying in a high paying but monotonous job instead of finding something new; Kruglanski et al., 2000). Consistent with this notion, prior research suggests that each of these regulatory modes may influence how well we can satisfy our need for effectance. Not only does locomotion buffer us from the tendency to experience boredom (what I and others previously argued is a hallmark of effectance regulation failure), but also that assessment seems to predispose us to the experience of boredom (Struk et al., 2016; Isacescu et al., 2017; Mugon et al., 2018).

In terms of individual differences in behaviour, it is known that within a number of different species, members display a variety of foraging behaviours (Anreiter et al., 2017). *Drosophila melanogaster*, the best studied of these species, exhibits phenotypes labelled ‘rovers’ and ‘sitters’ that differ in foraging behaviour (Allen, Anreiter, Neville, & Sokolowski, 2017; Anreiter et al., 2017; de Belle, Hilliker, & Sokolowski, 1989; Osborne et al., 1997; Sokolowski, 1980). Adult rovers explore their environment widely with longer search paths than do adult sitters. In contrast, adult sitters ‘hug’ the boundary of a foraging environment, even after 24-hours of food deprivation that would normally prompt wider exploration (Anreiter et al., 2017; Hughson et al., 2017). These patterns of behaviour reflect differences in the extent to which animals favour exploring vs. exploiting their environs (Charnov, 1976). The search behaviours of adult rovers and sitters may be related, in part, to differing levels of risk aversion (Anreiter et al., 2017; Burns et al., 2012; Hughson et al.,

2017). That is, exploration carries with it some level of risk (de la Flor et al., 2017). In an empty arena, akin to rodent open field tests (Bailey & Crawley, 2009), sitter flies move along the periphery hugging the edges, whereas rovers explore the centre of the arena using what is known as darting exploration (Burns et al., 2012). These environs present the animal with a choice between sheltered and exposed regions (Mohammad et al., 2016). Thus, rovers could be said to show higher risk tolerance given their propensity to more fully explore their environs than sitters (Anreiter et al., 2017; Burns et al., 2012; Hughson et al., 2017; see also Moore, Cooper, Biewener, & Vasudevan, (2017) for a similar characterisation in rodents). In contrast, sitters manage risk by preferentially exploiting proximal resources (Hughson et al., 2017).

Rovers and sitters are somewhat akin to the locomotion and assessment distinctions of goal-pursuit in humans. Those for whom assessment is the dominant regulatory mode may behave in a conceptually similar manner to sitters. This is because assessors are sensitive to the value of action outcomes (i.e., they value the reward of exploitation and are sensitive to the risks associated with exploration; Panno, Pierro, & Lauriola, 2014). In contrast, those for whom locomotion is the dominant regulatory mode may behave in a conceptually similar manner to rovers. This is because locomotors are sensitive to the value of being in action (i.e., they value movement and are less sensitive to the risks associated with exploration).

The Foraging Gene

In terms of foraging, a variation in a single gene named “the *foraging gene (for)*” seems to have a large effect on foraging behaviour across species (Anreiter et al., 2017; Ben-

Shahar et al., 2002; Licas & Sokolowski, 2009). The sitter and rover foraging strategies observed in *Drosophila melanogaster* can be attributed primarily to variation in the *for* gene (de Belle et al., 1989; Osborne et al., 1997; Allen et al., 2017). The human orthologue of *for*, known as *PRKG1*, also encodes a cGMP-dependent protein kinase (Reaume & Sokolowski, 2009). *PRKG1* proteins are found across the nervous system and are thought to underpin neuroplasticity and learning (Feil, Hofmann, & Kleppisch, 2005), and likely influence behaviour in myriad ways. Variation in *PRKG1* was recently associated with interactions between maternal sensitivity and early life adversity (Sokolowski et al., 2017), and alcoholism and trauma (Polimanti et al., 2017).

Prior research demonstrated that genotypes of rs13499, a single nucleotide polymorphism (SNP) in the 3' untranslated region (3'UTR) of *PRKG1*, are associated with differences in the adoption of distinct regulatory modes (Struk et al., 2019⁹). Specifically the A allele of rs13499 was associated with assessment predominance. Interestingly, the A allele of rs13499 was associated with lower expression of *PRKG1* in the Dorsolateral Prefrontal Cortex (DLPFC; CMC; <https://www.synapse.org/#!/Synapse:syn2759792/wiki/69613>), analogous to the lower expression of *for* in sitter flies (Kaun, Hendel, Gerber, & Sokolowski, 2007; Osborne et al., 1997). The DLPFC is critical for goal-directed behaviour, executive control, and self-regulation (Pessoa, 2009; Wagner, Maril, Bjork, & Schacter, 2001).

⁹ Sample 1 from the Struk et al., 2019 article includes an undergraduate sample from Columbia University, which demonstrates this finding. Sample 2 from the article is presented here. See Appendix G for results from sample 1.

Although research shows that the *for* gene's contributions to foraging varies within and between species (Ben-Shahar et al., 2002; Ingram, Oefner, & Gordon, 2005; Lucas & Sokolowski, 2009; Sokolowski, 2010), this balance between exploration and exploitation has not been investigated in humans. The goal of this study was two-fold; to replicate the finding that rs13499 is associated with adoption of distinct regulatory modes, and to extend the understanding of the role of PRKG1 on foraging behaviour. To do this, the current study also explored whether variations in rs13499 would be associated with characteristic goal pursuit patterns, as well as metrics obtained from two virtual foraging tasks.

4.2 Methods

Participants

A total of 450 undergraduates from the University of Waterloo participated in this study¹⁰. Data was collected during Fall 2015, Winter 2016 and Winter 2017 academic terms. Of the 450 participants, data for 13 was incomplete and excluded from further analysis (final sample = 437; 215 females; mean age = 19.99 (2.62) years; one participant did not disclose their sex). 43% identified as White/Caucasian, 25% as East Asian, 14% as South Asian, 3.9% as Southeast Asian, 3.7% as Middle Eastern, 3.4% as Black/African, and 9.5% identified with other ethnic groups. 2% declined to indicate their ethnicity. Written informed consent was obtained from each participant prior to commencing the study which was approved by the Office of Research Ethics at the University of Waterloo in February 2015.

Procedure

All participants completed a package of questionnaires at the beginning of the term as part of the institutional mass testing. In the lab, after reading the information sheet and consenting to participate in this study, participants took part in three computer tasks. Participants did the scrabble task and connect the dots task, for 10 minutes each (see Appendix H for description of these tasks). All participants also did two versions of the foraging task for a total of 10 minutes (see the next section: “4.2 Methods: Foraging Task” for description of this task). All tasks were presented in a counterbalanced order. After

¹⁰ Sample 2 from Struk et al., 2019 article. See Appendix G for results from sample 1.

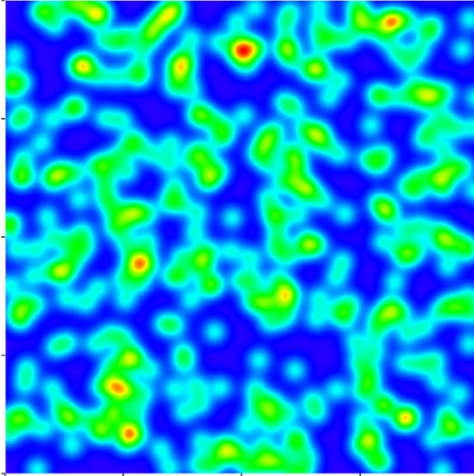
completion of all the tasks, participants provided a saliva sample using the oragene-DNA collection kit from DNAgenotek (<http://www.dnagenotek.com/ROW/index.html>; see section “4.2 Methods: DNA collection, extraction, polymorphism determination, and gene expression” for more information). Prior to departure, participants were informed of the purpose of this study and were thanked for their participation. Note that this study only analysed results from the Foraging Task as it is the closest analogue to foraging environments in which *Drosophila* behaviour was studied in.

Foraging Task¹¹

An assay of human foraging was programmed using python 2.7 with the aid of pygame (Shinners, 2011). The task was shown on a touch screen placed flat on the table and inclined by ~25 degrees for ease of use (i.e., a vertical monitor would place undue strain on the shoulder). The foraging task consisted of a virtual 2D environment populated by red ‘berries’. The background was a grass-like texture (512 x 512 pixels) tessellated within a 20,000 x 20,000 pixel environment. The screen displayed only a portion of the environment at a time, encompassing 1,920 x 1,080 pixels. Participants navigated using their index finger to swipe the screen. ‘Berries’ were red circles varying in size from a radius of 4 to 16 pixels. 384 berries were present in the environment.

¹¹ The foraging task was designed for the experiment outlined in this chapter first. It was then modified for online/laptop use as shown in the previous chapter.

Uniform Environment



Patchy Environment

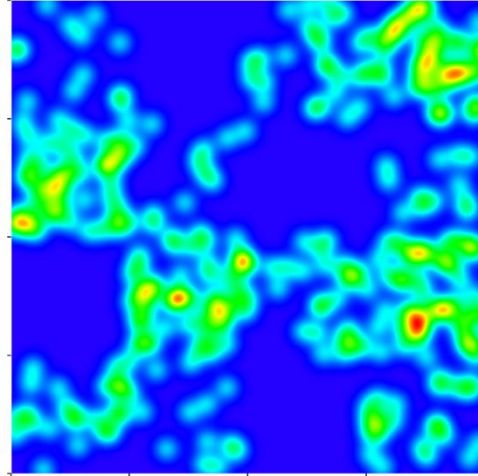


Figure 4.1 Density plot of berries in the uniform and patchy environments.

Two distributions of berries were used, labelled uniform and patchy (Figure 4.1). The uniform environment was segmented into 16 equal zones (5,000 x 5,000 pixels each), with each zone containing 24 berries (2 of each size) pseudo randomly distributed such that no two berries could be 100 pixels from the centre of another berry. The patchy environment consisted of 4 distinct zones (high, medium, and low density zones, and an empty zone). There were 4 zones of each type. High density zones had 48 berries (4 of each size), medium density zones had 24 berries (2 of each size), and low density zones had 12 berries (1 of each size). Zones were distributed such that no two zones of the same type were adjacent to each other (Figure 4.1 gives a density plot of berry distribution).

In both environs participants had to collect as many berries as possible within 5 minutes. The two environs were presented in counterbalanced order. A counter showing how many berries had been collected and a clock counting down the remaining time were displayed in the upper right corner.

DNA collection, extraction, polymorphism determination, and gene expression

The Oragene OG-500 DNA kit (DNA Genotek, Ottawa, ON) was used for DNA collection from saliva samples (~2 mL). DNA extraction was done according to manufacturer's instructions. The Clinical Genomics Centre (CGC) in Toronto performed the DNA isolation, quantitation, normalization and SNP genotyping on the saliva samples.

The *PRKG1* gene is located on Chromosome 10, cytological location 10q11.23-21.1 with a molecular location between 50,991,358–52,298,350 base pairs. Selected SNPs within the *PRKG1* gene occurred in protein coding regions (exons) or the 3' untranslated region (UTR) and were predicted to either affect protein function or influence the regulation of *PRKG1* mRNA transcripts. The SNPs in the exonic regions of *PRKG1* were monomorphic in the current sample and are not discussed further. The rs13499 SNP lies in the 3' untranslated region (3' UTR) of *PRKG1* that is adjacent to the kinase domain, common to all transcripts. The variant rs13499 is located at chr10:52297965 (GRCh38.p7), mapping to the 3'UTR of *PRKG1* and the intronic region of *PRKG1-AS1*, a long non-coding RNA that is likely coexpressed with *PRKG1*. The genomic location of rs13499 resides in 4 different *PRKG1* mRNA transcripts suggesting a gene regulatory role for this SNP.

SNP genotyping was done as part of a larger study. Details of identical methods used can be found in Sokolowski et al. (2017). Briefly, samples were genotyped using Maldi-Tof Mass Spectrometry via The MassARRAY® System by Agena Bioscience. This approach uses multiplexing to assay multiple SNPs for each sample simultaneously and entails the single base extension (SBE) of an oligo probe designed to anneal directly adjacent to a SNP of interest. Data was analysed using MassArray Typer software (v 3.4). Each multiplex reaction was assessed using standard quality control parameters and poorly performing SNPs and/or samples were disqualified. SNPs included in this assay were: rs13499, rs1406473, rs2043556, rs2339686, rs10995225, rs7070276, rs6265, rs5993883, rs4680, rs1076560, rs1800497, rs27072, rs2242447, rs3785143, rs2066713. This study only analysed rs13499 as there was prior evidence that this SNP was linked to current study variables of interest, furthermore it is known to be expressed in brain regions that are implicated in self-regulation (Struk et al, 2019).

Regulatory Mode Questionnaire

The Regulatory Mode Questionnaire (RMQ) measures individual differences in locomotion and assessment regulatory modes (Kruglanski et al., 2000; Appendix I). Each regulatory mode orientation is assessed by a 12 item subscale (e.g., “By the time I accomplish a task, I already have the next one in mind”—endorsing this item indicates a locomotion preference) rated on a 6-point Likert scale ranging from “Strongly Disagree” to “Strongly Agree.” High scores reflect greater emphasis of either the locomotion or assessment modes. Kruglanski et al. (2000) reported an internal consistency of 0.82 for the

locomotion and 0.78 for the assessment scales, and test-retest reliability of 0.77 for the locomotion and 0.73 for the assessment scales.

The regulatory mode predominance (RMP) score was calculated by subtracting assessment from locomotion scores, and scaling the difference score such that positive scores indicate a locomotion predominance and negative scores indicate an assessment predominance—a common approach to capturing the regulatory mode predominance within individuals (Zee, Cavallo, Flores, Bolger, & Higgins, 2018).

Foraging Classification Method

Ultimately I used classification analyses to comprehensively characterise search behaviour. To do this, individual search paths were first subjected to an analysis of recurrent movement patterns using recurrence-quantification analysis (RQA; Solman & Kingstone, 2015; Figure 4.3). Results from the RQA analysis were further classified individual search paths into distinct categories using three separate classification methods: Expectation-Maximization (EM), K-means, and hierarchical clustering (using the centroid agglomeration method). Each of these methods made use of the proportion of recurrent movement patterns (as determined by RQA) as the basis for clustering. Three distinct methods were chosen in order to determine which would best classify the majority of study participants. It turned out that no single method outperformed another. In addition, concordance between the three methods was high (76.5%). For the 76.5% of participants consistently classified by all three methods, a label was designated for them based on visual inspection of the individual search paths. This led to two groups labelled Boundary Biased (participants spent the majority of

their search path hugging the boundary of the virtual environment) or Systematic (participants systematically went left-to-right or up-to-down across the environment;). The remaining 23.5% of the individual search paths could not be confidently categorized as either Boundary Biased or Systematic. This group was labelled as ‘Mixed’ (Figure 4.2).

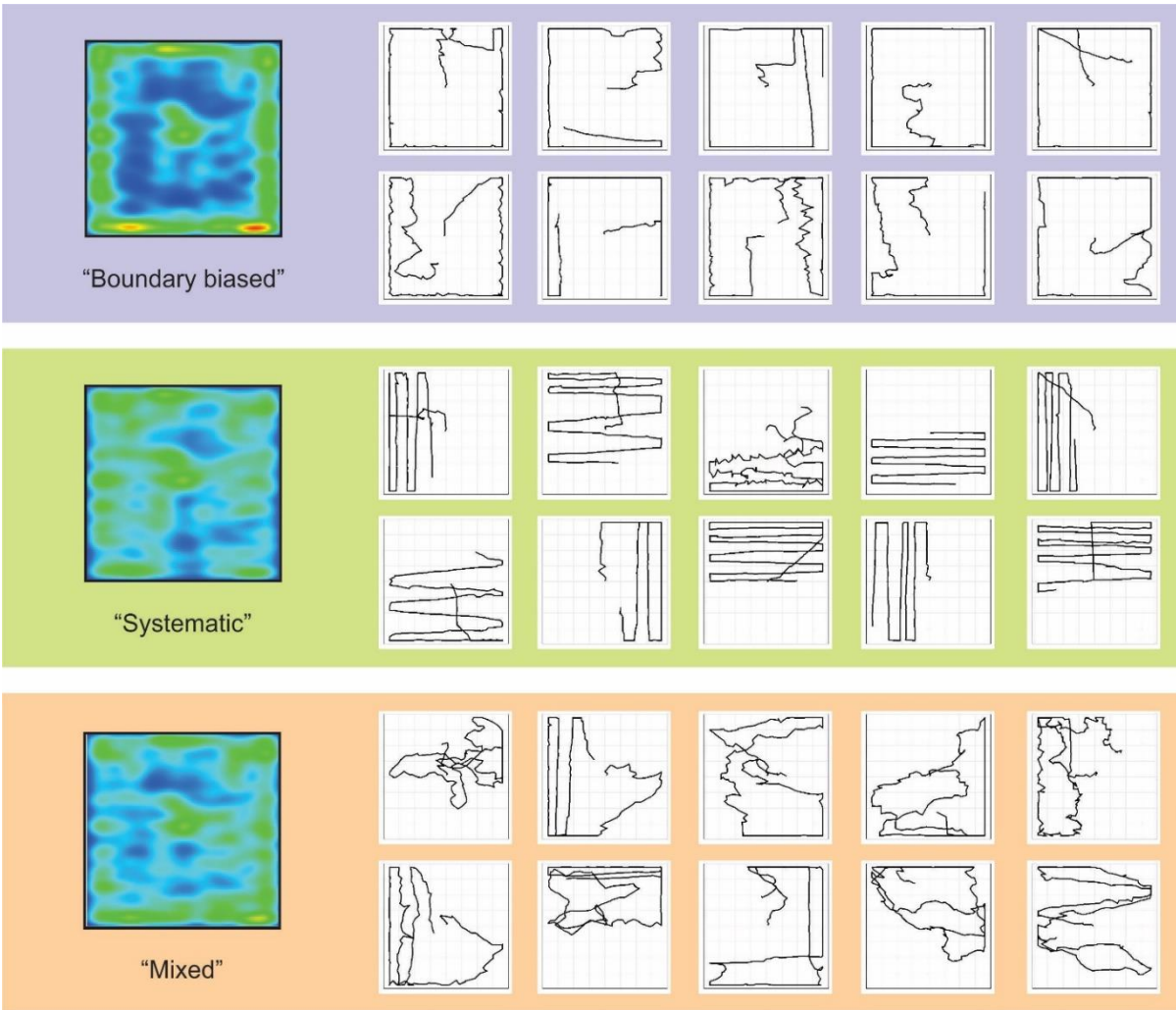


Figure 4.2 Example foraging paths in the uniform environment. Purple = Boundary Biased; Green = Systematic; Orange = Mixed.

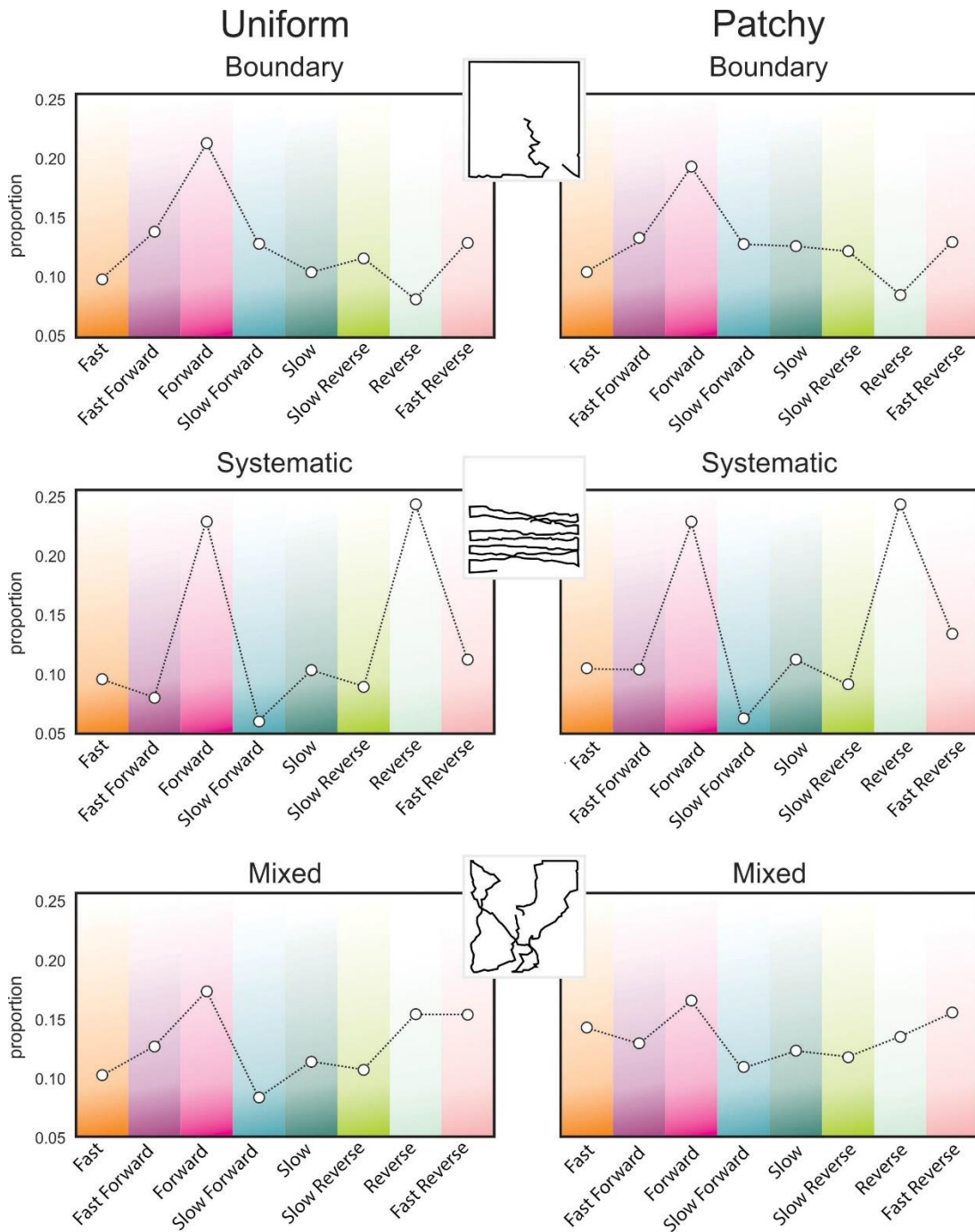


Figure 4.3 Recurrent movement patterns for the uniform and patchy environments. Boundary Biased (upper), Systematic (middle) and Mixed (lower panels) groups are shown for the uniform (left) and patchy (right) environments. The 8 movement characteristics based on direction and speed of movement are labelled along the x-axis.

Next, in an attempt to get a higher level of consistent classification, human observers were used to classify individual search paths (JD, AS and JM did the classifications). Each was given an exemplar of Boundary Biased or Systematic (Mixed was not considered a category for this approach) and asked to classify the whole sample. Human observer classification led to a similar level of concordance achieved by the three algorithmic approaches (75% concordance). Thus, while some search paths in the 'Mixed' group appear similar to the Systematic group, three distinct groups were retained. Furthermore, the initial technique used to determine recurrent movement patterns (i.e., RQA), clearly demonstrated differences in movement patterns among the three groups (Figure 4.3). Figure 4.3 shows distinct patterns of recurrent movements for each group. While the clearest difference is between the Boundary Biased and Systematic groups, the Mixed group nevertheless shows a distinct pattern of recurrent moves. See Figure 4.2 for examples of foraging paths as well as the combined heat map of each characterized foraging strategy. Note that calculation of movement types within this algorithm is based on angle of deviation relative to the prior movement and time (Solman & Kingstone, 2015).

4.3 Results

Genotype, ethnicity and sex

rs13499 showed significant variation across individuals. This SNP had a minor allele frequency (MAF) of C = 0.335 which is similar to the global MAF of C = 0.3111/1558 (1000 genomes). The rs13499 polymorphism generates three genotypes AA, CA and CC. The frequencies were 45% ($n = 198$), 44% ($n = 192$), and 11% ($n = 47$) for the AA, CA, and CC genotypes respectively. The rs13499 genotypes, were in Hardy Weinberg Equilibrium ($\chi^2(1) = 0.01, p = 0.99$). Genotype distribution was independent of sex ($\chi^2(2) = 1.47, p = 0.481$; for males AA = 0.45; CA = 0.42; CC = 0.13: for females AA = 0.46; CA = 0.45; CC = 0.09). The distribution of genotypes was in HW equilibrium for both sexes (males $\chi^2(1) = 0.456, p = 0.499$; females $\chi^2(1) = 0.607, p = 0.436$).

With respect to self-reported ethnicity, differences in Caucasian (the largest ethnic group) and Non-Caucasians (a combination of ethnicities) were examined. The distribution of genotypes did not differ by ethnicity (Caucasian AA = 0.44; CA = 0.44; CC = 0.12; for Non-Caucasian AA = 0.46; CA = 0.45; CC = 0.09; $\chi^2(2) = 0.48, p = 0.785$) and no significant interactions were found between ethnic group and rs13499 genotypes on all study variables.

Regulatory Mode Preference

Individuals with the homozygous AA genotype were associated with significantly higher assessment predominance (RMP) than those with the CA or CC genotypes ($p = 0.007$, additive model). The difference was highly significant with assessment predominance

highest in the AA genotype ($M = -0.14$, $SD = 1.0$), lowest in the CC genotype ($M = 0.2$, $SD = 0.86$) and intermediate in the CA genotype ($M = 0.1$, $SD = 1.02$; note that smaller, negative numbers indicate an assessment predominance; Figure 4.4).

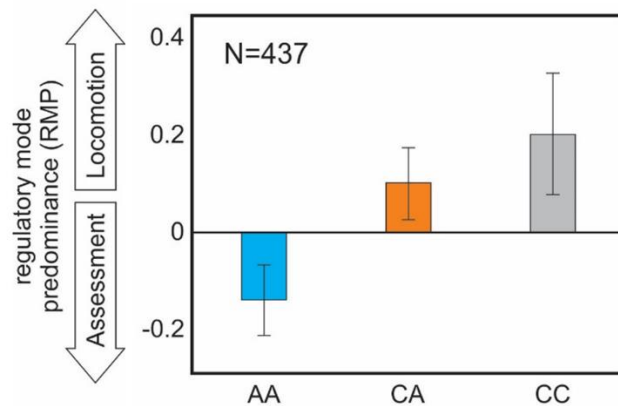


Figure 4.4 Regulatory mode preference (RMP) by genotype. rs13499 polymorphism generates three genotypes (AA, CA, CC). Frequencies were 45% ($n = 198$), 44% ($n = 192$), and 11% ($n = 47$) for AA, CA, and CC genotypes respectively. These results are similar to Sample 1 from the Struk et al., 2019. See Appendix G for comparison.

There were trends towards differences across males and females, although none reached significance. Nevertheless, males of the AA genotype had marginally greater assessment predominance (RMP; $p = 0.054$), reduced locomotion score ($p = 0.061$) when compared to the CC genotype, with those of the CA genotype having intermediate scores. There was no significant association for assessment ($p = 0.704$). For females, those with the AA genotype had marginally greater assessment predominance when compared to the CC

genotype, with the CA genotype showing intermediate scores (RMD; $p = 0.069$). There was no significant association for locomotion ($p = 0.245$) or assessment scores ($p = 0.282$, all statistics represent an additive regression model).

There were some minor differences evident for individual metrics based on ethnicity. In contrast to Non-Caucasians, Caucasians had higher locomotion scores ($p = 0.0215$, t-test).

Foraging Task

Table 4.1 Metrics from the foraging task for uniform and patchy berry distributions.

Variable	AA		CA		CC		F	p
	Mean	SD	Mean	SD	Mean	SD		
	n = 198 (51% male)		n = 192 (52% male)		n = 47 (43% male)			
	Uniform Foraging Environment							
path length (pixels)	139267	24836	139547	22178	139213	24207	0.00	0.963
# of moves	249	49	249	55	248	47	0.03	0.885
# berries picked	152	20	154	21	150	23	0.00	0.959
turning angle	33.56	10.53	35.31	11.1	32.99	10.45	0.29	0.591
berry size (pixels)	6.62	0.22	6.62	0.21	6.61	0.28	0.02	0.881
berries visible	1.84	0.18	1.86	0.19	1.89	0.18	3.65	0.057
	Patchy Foraging Environment							
path length (pixels)	143769	25967	147084	25593	142259	27362	0.14	0.707
# of moves	263	55	257	56	254	57	1.65	0.199
# berries picked	147	25	153	22	149	27	2.65	0.105
turning angle	34.19	10.24	34.44	10.31	33.37	9.75	0.42	0.838
berry size (pixels)	6.64	0.19	6.68	0.19	6.73	0.17	10.1	0.002
berries visible	2.06	0.25	2.12	0.26	2.16	0.23	8.63	0.003

Uniform Foraging Environment

Next foraging performance as a function of genotype was examined (Table 4.1). While there were trends evident across genotypes when examining individual metrics (Table

4.1), ultimately classification analyses to comprehensively characterise search behavior was used. 76.2% of participants were characterized as either Boundary Biased (59.4%), or Systematic (16.7%) by all 3 clustering methods . The third group was classified as “Mixed” (23.9%). Search paths within this group tended to meander or showed a combination of Boundary Bias and Systematic strategies.

The three foraging strategies differed significantly in terms of path length ($p < 0.0001$, ANOVA). In contrast to the Boundary Biased group, the Systematic and Mixed strategy groups had longer path lengths ($p \text{ adjusted} < 0.001$, Tukey’s HSD). The Systematic and Mixed groups did not differ on path length ($p \text{ adjusted} = 0.95$, Tukey’s HSD). The three groups differed in terms of average turning angle ($p < 0.001$, ANOVA), with the Systematic group having smaller average turning angles than either the Boundary Biased or Mixed groups ($p \text{ adjusted} < 0.001$ and 0.003 respectively, Tukey’s HSD). The Mixed strategy group had a smaller average turning angle than did the Boundary group ($p \text{ adjusted} = 0.023$, Tukey’s HSD). There were no differences across groups in the number of berries picked ($p = 0.203$, ANOVA; Table 4.1).

This novel assay of human foraging behaviour suggests that humans cluster into three distinct search strategies, one of which—the Boundary Biased group—resembles behaviour observed in adult sitter *Drosophila melanogaster*. The other two groups, although distinct from one another, tended to cover more of the search environment, much like the rover fly.

Those with the AA genotype were more likely to adopt a Boundary Biased search strategy (compared to either Systematic or Mixed groups) than the CC genotype, with the CA

genotype showing an intermediate preference for this strategy ($p = 0.02$, additive model).

Thus, variation in rs13499 is associated with foraging strategy choice in a manner consistent with the adult sitter phenotype in the fly. That is, those with the AA genotype of rs13499 demonstrate a stronger Assessment orientation and tend to hug the boundary of the search environment in much the same manner observed in the *Drosophila* ‘sitter’ phenotype.

Within the uniform environment, Caucasians more often adopted a systematic strategy ($p = 0.043$, t-test), were less likely to adopt a boundary bias ($p = 0.056$, t-test), made fewer movements ($p = 0.03$, t-test), and picked more berries ($p = 0.04$, t-test). There were no significant interactions between sex and rs13499 genotype on all foraging metrics.

Patchy Foraging Environment

The foraging task first used here had berries spread uniformly throughout. This does not represent typical environments faced by animals or humans in which resources are sparsely distributed, forcing exploration decisions. Therefore, the same participants also foraged in an environment in which berries were sparsely distributed (labelled ‘patchy’; Methods). In this instance, task metrics did differentiate between genotypes (Table 4.1 and Figure 4.5). With respect to berry size, individuals with the AA genotype picked smaller berries than those with the CA genotype, which in turn picked smaller berries than those with the CC genotype ($p = 0.002$). Similarly, those with the AA genotype stopped to pick berries in patches with fewer berries visible. For this metric, those with the CC genotype had the highest scores, with the CA genotype intermediate (Table 4.1; $p = 0.003$; Figure 4.5). This latter effect was marginally significant in the uniform environment (Table 4.1). There was no

influence on the total number of berries picked ($p = 0.959$) or path length ($p = 0.707$, all statistics represent an additive regression model; Table 4.1).

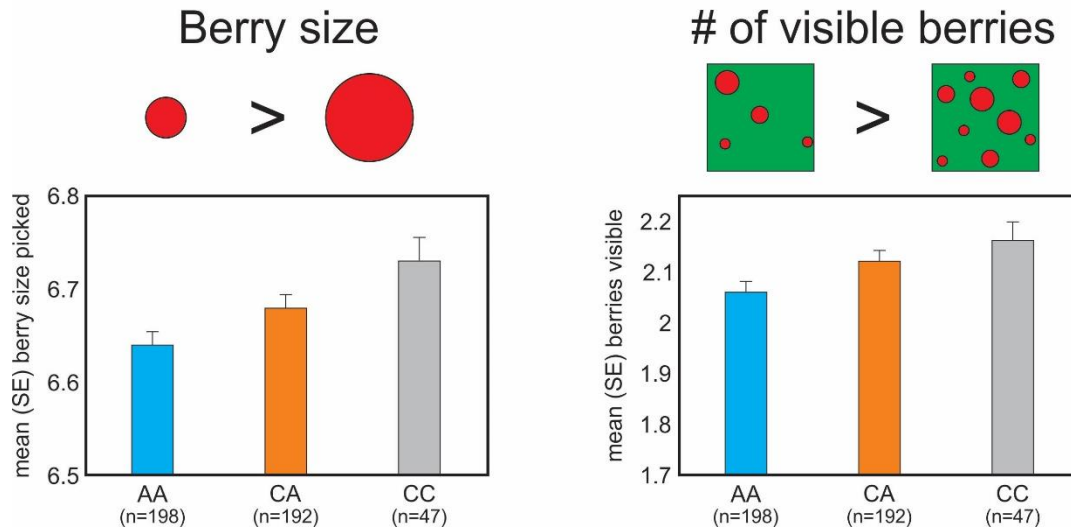


Figure 4.5 Differences in mean (\pm SE) size of berry picked (left) and number of berries visible when stopping to pick (right) by genotype (below; AA = blue, CA = orange, CC = grey).

These results show that the AA genotype is associated with exploiting the local environment more extensively, picking berries as they encounter them (as opposed to stopping to pick berries only when many are visible) and picking all available berries (even smaller, more difficult to pick berries). There was no relationship with the number of berries picked ($p = 0.105$) indicating that the AA genotype is associated with adopting of a more risk averse strategy akin to ‘sitters’.

Within the patchy environment, Caucasians exhibited smaller turning angles ($p = 0.008$, t-test). There were no significant interactions between sex and rs13499 genotype on all foraging metrics.

4.4 Discussion

Results of the current study show that genetic variation in *PRKGI* is associated with distinct regulatory mode preferences and characteristic search patterns on the foraging task. That is, in this study's assay of human foraging three distinct search strategies were observed—Boundary Biased, Systematic and Mixed. The first of these—Boundary Biased—was prominently associated with the AA genotype at the rs13499 SNP, a genotype that also tended to adopt an Assessment regulatory mode. The opposite claim—that those with the C allele resemble rovers—is more difficult to substantiate but warrants further research. Certainly, those with a C allele were less likely to hug the boundary of the environment than were the AA genotypes. At the very least, the similarities observed here between sitters and assessors and their association with *PRKGI/for* across such phylogenetically distant species as humans and fruit flies, implies an adaptive component to this profile.

The distinct profiles of the rover/sitter and locomotor/assessor have been portrayed in terms of risk tolerance. The more extensive foraging paths seen in rovers reflect a higher level of risk tolerance. Although not as relevant for humans, any exploratory behaviour in animals carries some level of risk, including greater exposure to predators. The more extensive search paths of the rover indicate the animal is willing to accept those risks in the pursuit of resources. Similarly, the human locomotor can be thought of as showing higher risk tolerance, preferring to 'get on' with things. The contrasting claims can be made for sitters/assessors. In the fruit fly, the sitter tends to explore their environs more cautiously, hugging the boundary of the environment, rather than risking forays further afield to more

exposed regions (Hughson et al., 2017; Sokolowski, 2010). The strongest association here is with human assessors who show behaviours that bear a remarkable resemblance to this phenotype in the fruit fly. They are more likely to adopt a boundary bias, to begin picking berries even when the visible cache of berries is small (or smaller relative to the stopping rule chosen by those with the C allele; Table 4.1; Figure 4.5), and pick even the hard to get, smaller berries – perhaps not wanting to waste any available resources. Although these differences are being portrayed in terms of risk tolerance, it is worth noting risk tolerance or aversion were not directly tested here. Future work could explicitly manipulate levels of risk (e.g., using tasks such as the Iowa Gambling Task; Bechara, Damasio, Tranel, & Damasio, 1997), to more directly examine the relation between risk aversion and self-regulatory profiles. Any variation in adopted regulatory mode in humans likely depends on many genes and their interactions, with one’s preference for assessment or locomotion not solely driven by variation in *PRKGI*. Genes known to regulate Dopamine, a neurotransmitter involved in calculating value and reward signals in the brain, represent another likely target, among many, for exploring the genetic contributions to self-regulation (Cohen, Young, Baek, Kessler, & Ranganath, 2005).

A composite measure of regulatory mode preference was used, one commonly used in the literature (Zee et al., 2018), to explore differences in behaviour and genotype. It remains the case that one can adopt either regulatory mode as circumstances dictate (Kurganski et al., 2000). So how robust are such preferences across time? The original work on assessment and locomotion (Kurganski et al., 2000) showed cross-temporal stability

responses were quite high (locomotion $r = 0.77$; assessment $r = 0.74$). In addition, across multiple large samples, previous work has shown associations between regulatory mode and other individual difference metrics (notably, boredom proneness which is robustly negatively correlated with Locomotion and positively correlated with assessment; Mugon, et al., 2018). With respect to foraging performance, more direct data is required. Comparing performance across the two environs, although problematic given each environment is explicitly expected to engender different behaviours, showed that 75.3% of participants who adopted a Boundary Bias strategy in the uniform environment also did so in the patchy environment. Clearly, more research is needed to explore the consistency of behaviours across time in the same environments and across different tasks that rely on efficient self-regulatory control.

This study suggests an association between human regulatory mode preferences and foraging behaviour akin to that observed in the adult fruit fly ‘sitter’. Using an assay of human foraging this study demonstrated –perhaps unsurprisingly, that human foraging is more complex than the rover and sitter phenotypes well characterised in *Drosophila melanogaster* (Sokolowski, 1980; Osborne et al., 1997; Allen et al., 2017). Humans show at least three distinct foraging strategies. How these strategies, along with variation in *PRKG1*, relate to other aspects of goal pursuit requires further work. In humans, genetic variation in *PRKG1* is related to maternal sensitivity to adverse events early in life (Sokolowski et al., 2017), and is implicated in the relation between alcoholism and trauma (Polimanti et al., 2017). In addition, there are a multitude of associations between the *for* gene and behaviour in the fruit fly that warrant investigation in the human, from stress responses to learning and

memory (Sokolowski, 2010). The suggestion here is that the human orthologue of the *for* gene plays a key role in the regulation of behaviour across many domains.

Chapter 5: General Discussion

The work presented in this thesis spans two major but related themes; namely, what mechanisms underlie our desire for actions and what factors influence what we choose to do? Chapter 2 demonstrated that people are sensitive to opportunity costs signalled by the state of boredom, which in turn increases the desire to engage in alternative activities. Chapter 3 provided evidence that our sensitivities to different opportunities for action depend on situational factors such as perceived difficulty of a prior activity. Finally, Chapter 4 provided evidence that genetic factors such as variations on the *PRKGI* gene may alter our sensitivity to different opportunities for action, potentially because of differential risk sensitivity. This chapter summarizes the current findings and situates them within a broad self-regulatory framework.

In addition to our tendency to pursue goals for the purpose of satisfying basic biological needs and maximizing pleasure, individuals are also motivated to act for the sake of acting (Keynes, 1936; Woodworth, 1918; White, 1959). This drive to act is thought to be a critical component in how an animal learns to be effective in influencing the world around it (White, 1959). However, we do not just choose any action. Instead, an animal will ideally engage in an action that has the greatest utility for mastering its environment (White, 1959). Indeed, a number of researchers have suggested that there exists an optimal set of activities that provide sufficient novelty and challenge for an animal and that animals are sensitive to deviations from this optimality (Csikszentmihalyi, 1975; Hebb, 1955; Pekrun, 2006; Westgate & Wilson, 2018). Minimization of opportunity costs (i.e., the value of engaging in

alternative activities) appears to explain much of the preferences that underlie choices (Charnov, 1976; Friedrich von Wieser, 1911/1927; Kurzban et al, 2013; Ramirez and Costa, 2017). Although it has been suggested that failure to satisfy the drive to act (and thus deviate from optimality) is linked to the state of boredom (Fenichel, 1951, White, 1959), it has only recently been suggested that boredom may signal opportunity costs (Kurzban et al, 2013; Ramirez and Costa, 2017). Research presented in Chapter 2 is the first to empirically test this notion and demonstrated that boredom is especially likely to arise when opportunity costs are high. Results from this study also suggest that boredom makes us want to engage in alternative activities, which is consistent with the notion that we want to minimize opportunity costs. Furthermore, this finding is consistent with the notion that “boredom is a state of wanting” (Eastwood et al., 2012; Elpidorou, 2014, 2018).

Optimal Stimulation Model of Boredom

It has been proposed that boredom is involved in ensuring that we do not fall into the habit of seeking and staying in a state of certainty and/or idleness, by impelling us to explore novel and challenging circumstances (Csikszentmihalyi’s, 1975; Cohen et al., 2007; Gomez-Ramirez & Costa, 2017; Yu et al., 2018). Most recent instantiations of such models of boredom rely on theories of intrinsic motivation that posit that the inherent satisfaction that comes from action (and not its outcome) is derived from the capacity of such actions to facilitate learning (i.e., knowledge based theories of intrinsic motivation; for review see Gomez-Ramirez & Costa, 2017; Oudeyer, & Kaplan, 2009; Yu et al., 2018). Predictive processing is a mechanism thought to underlie learning (i.e., mastery), whereby predictions

about the world are made using existing models, and prediction errors (PE; mismatches between predictions and current sensory inputs) are used to refine and inform future models (Clark, 1998). However, predictive processing is silent on the matter of why we build models of the world. To explain why we are engaged in predictive processing, we must contextualize this process within the cybernetic theory – the study of functions and processes of systems that have goals (Ashby, 1961; Seth, 2015). Indeed, the “free energy principle” links predictive coding with cybernetics, as it suggests that construction of mental models happens because of a system’s imperative toward homeostasis (Friston, 2010). In this formulation, the organism has a goal of minimizing the long-run average surprise (PE) of sensory states, and this goal impels us to act and construct better models of the world.

According to the free energy principle, PE reduction can be regarded as a homeostatic goal. That is, individuals want to be in a state of certainty and when they are in a state of uncertainty (PE) they update their mental representations of the world such that their new models better predict sensory experience (Friston, 2010; Oudeyer, & Kaplan, 2009; Seth, 2015; Yu et al., 2018). However, a system with the goal of minimizing prediction error inevitably encounters the so-called “dark room problem” – that is, the best solution to minimizing PE is to crawl into a corner of a dark room and do nothing. In such a world, every possible sensory experience is maximally predictable (Friston, Thornton, & Clark, 2012). Clearly, this is not something that animals typically do and it would be regarded as maladaptive if they did (Friston et al., 2012). Indeed, to construct an accurate model of the world an organism must not only have a homeostatic goal of minimizing prediction error but

must also have a “heterostatic goal” – a goal to bring a system away from its current state (low accuracy models; Oudeyer, & Kaplan, 2009; Seth, 2016). Actions motivated by such a goal are exemplified by exploration, which permits the disambiguation of uncertainties and disruption of existing models of the world (Bongard, Zykov & Lipson, 2006; Gregory, 1980; Seth, 2014). Indeed, existing models implicate boredom in such a heterostatic goal, ensuring that we do not succumb to “the dark room problem” (Gomez-Ramirez & Costa, 2017; Yu et al., 2018).

Findings from Chapter 3 are somewhat contradictory to the above notion as boredom was demonstrated to not only promote exploration but also to potentially promote or instigate exploitation behaviours. Indeed, the above accounts of boredom appear to be incomplete as they suggest that boredom only arises when novelty or challenge of the situation is low and only promotes us to seek situations which offer increased challenge and novelty. This is inconsistent with what we know about boredom in humans. Indeed, the tendency to experience boredom is not only linked to sensation seeking (Kass & Vodanovich, 1990), but also apathy (Goldberg, Eastwood, LaGuardia, & Danckert, 2011). Furthermore, the state of boredom has not only been linked to high arousal, but also to low arousal (for review see Danckert, Hammerschmidt, Marty-Dugas, Smilek, 2018; Eastwood et al., 2012; Yu et al., 2018). Finally, the state of boredom has been shown to arise not only from situations that foster high perceived control and low challenge but also low perceived control and high challenge (for review see Struk, 2015; Westgate & Wilson, 2018). This body of research

suggests that boredom arises for multiple reasons and may push us towards engaging in a wide variety of behaviours beyond exploration.

The notion that boredom may motivate a variety of behaviours was originally expressed by Westgate and Wilson (2018), who proposed that boredom originating from overstimulation (task demands that exceed one's skill) would motivate actions that aim to reduce demands, while boredom originating from understimulation (when skills exceed task demands) motivates actions that increase demands. Indeed, in the study presented in Chapter 3, participants who became bored because of either over or understimulation displayed an alteration in subsequent foraging behaviour in a manner consistent with Westgate and Wilson's (2018) hypotheses. Specifically, participants who became bored following overstimulation tended to exhibit more exploitation behaviour, which is arguably less demanding than exploration since it relies on known and easily accessible resources. Participants who became bored following understimulation on the other hand, tended to exhibit more exploratory behaviour, which can be regarded as more demanding than exploitation since it requires risk taking to discover new resources.

It is difficult to argue against the notion that boredom arises when we face unchallenging and mundane situations and is involved in motivating us to explore challenging and novel activities. However, a more nuanced model of boredom is necessary to reconcile such notions of boredom with the results of Chapter 3, as well as prior findings and theories that suggest that boredom can arise in situations other than those of low challenge or high certainty (Struk, 2015; Westgate & Wilson, 2018). One reason these "exploration

focused” models of boredom are incomplete as they are fundamentally biologically implausible. They assume that 1) animals are always capable of minimizing PE (if PE is non-zero) and 2) organisms’ motivation to increase PE is unconstrained (i.e., the degree to which PE may increase has no upper limit; Gomez-Ramirez & Costa, 2017; Yu et al., 2018). In natural settings, animals that follow such principles would have a tendency to expose themselves to highly complex sensory experiences that they cannot learn to comprehend or to great challenges that they cannot master. It is known that unregulated heterostatic systems would simply strive to maximize the difference between the current state and some reference state indefinitely (e.g., the system will try to maximize PE; Ashby, 1961; Carver & Scheier, 1998; Oudeyer, & Kaplan, 2009). To resolve this issue, a heterostatic goal can be converted to a homeostatic goal by placing constraints on it (Oudeyer, & Kaplan, 2009). That is, in the case of a system that is impelled to increase PE, a threshold of ideal PE can be set so the system does not pursue states where PE is above or below the threshold level. Importantly, this is done allostatically – that is, the system acts on the environment to attain homeostasis (e.g., place itself in situations that result in an ideal level of PE). Indeed, a similar formulation titled “Intermediate level of novelty motivation (ILNM)” has been described by Oudeyer & Kaplan (2009) to help account for intrinsically motivated behaviour seen in humans. ILNM accounts for intrinsically motivated behaviours such as seeking intermediate levels of novelty (Berlyne, 1960), optimal arousal (Hebb, 1955), optimal challenge (Csikszentmihalyi, 1991), and optimal incongruity between expectations and stimulus properties (Hunt, 1965; Dember and Earl, 1957).

It is possible that humans follow a model like ILNM and that boredom signals deviations from the desired threshold level of stimulation (PE) and motivates us to bring ourselves back to this optimal state. Nonetheless, it is important to note that this model has several shortcomings. First, it is unclear how an animal would choose the optimal threshold for PE. Second, this model makes an assumption that animals are always capable of reducing PE. This means that an animal that behaves according to ILNM will fall into a habit of finding an optimal PE, but once it encounters a situation where it cannot reduce PE it would be stuck. These issues may be resolved if we consider a system that is capable of monitoring its ability to reduce PE in a given instance, one that is sensitive to any failure to reduce PE at a desired rate. Regardless, a model of boredom that is based on a cybernetic system that has an allostatic goal of attaining an optimal level of stimulation (activities that offer greatest utility for mastering its environment, whether it is a specific degree of non-zero PE level or rate of PE minimization) appears to be necessary to explain much of the findings in this dissertation. Furthermore, such an optimal stimulation model of boredom (OSMB) makes a number of novel hypotheses.

Self-Regulation of Stimulation

First, the OSMB is consistent with findings of Chapter 2 which demonstrate that the presence of opportunities for engagement coupled with the inability to act on those opportunities promotes boredom. Here, the presence of opportunities to act functions as a reference value for the degree of stimulation one could attain (the optimal level of stimulation possible in a given context). A discrepancy from this optimum occurs if the

current activity does not offer as much stimulation (as it did in study of Chapter 2 as participants only had their thoughts as a source of stimulation). This discrepancy promotes a state of boredom which cannot be remediated, since participants were constrained from acting.

So far, I discussed how OSMB may explain why boredom arises when we fall below the optimum level of stimulation (e.g., we are unchallenged) motivating exploratory behaviour. However, like the Westgate and Wilson (2018) model of boredom, OSMB predicts that boredom will arise when we are above the optimal level of stimulation (e.g., we are too challenged) and may motivate behaviours that reduce the demands of the task. Chapter 3 provides evidence that boredom motivates both of these compensatory actions. Participants who were overstimulated (experienced high PE) tended to exhibit exploitation behaviours (which require little demand and reduce PE), while those who were understimulated (experienced low PE) tended to exhibit exploration behaviours (which are more demanding and increase PE). These compensatory reactions are consistent with predictions made by the OSMB. That is, individuals want to be at some optimal level of stimulation, with a range of different compensatory actions representing valid avenues to brings us closer to the optimum.

OSMB would make another interesting prediction. That is, although an individual desires to attain an optimal level of stimulation, following detection of a discrepancy (originating from over or under-stimulation), there is likely a delay between any compensatory action aimed at resolving the discrepancy and registration of the impact of

one's action. This lag can lead to over compensatory responses, and presumably in some individuals, difficulty in attaining the optimal level of stimulation, since constant overcompensation will force an oscillation between extremes. Indeed, individuals who are prone to boredom also tend to have poor self-regulatory abilities (Struk, Scholer, & Danckert, 2015). Whether these individuals are prone to boredom because they are unable to attain or maintain a desired level of stimulation (i.e., constant over compensation leading to oscillation between extremes of very low and very high PE) deserves further exploration.

Individual Differences in Desired Level of Stimulation

It is possible that what is regarded as optimal depends heavily on the context and prior experiences. That is, an individual can still experience boredom in an environment with many affordances because none of the activities offer as much stimulation as the individual desires (e.g., they may be accustomed to a specific level of stimulation). This is similar to an animal's decision to leave a patch of resources knowing that it is likely (based on prior experience) that it will encounter a new, more rewarding patch (Charnov. 1976). Put simply, prior experiences will vary individual desired levels of stimulation and the capacity to achieve that desired level. This may help explain variance in boredom levels across both conditions of the study presented in Chapter 2. Future studies should attempt to quantify individuals' desired level of stimulation and investigate the hypothesis that one's tendency to experience boredom may depend on their desired level of stimulation.

Chapter 4 demonstrated how individuals are genetically predisposed to prefer one way of regulating goals over another and are biased to act in a specific way while foraging. These results can be recast in terms of OSMB, whereby individuals are genetically predisposed to desire different levels of stimulation (e.g., what is stimulating for one person, may be overstimulating for another). Each level of optimal stimulation can present its own costs and benefits. Given that OSMB underlies explorative behaviours, desire for high stimulation may promote more exploratory behaviours which can be rewarding but are energetically costly and risky. Low desired levels of stimulation, on the other hand, may reduce exploratory behaviours, which has the benefit of ensuring access to existing resources at the expense of potentially more rewarding, but unknown resources. It is likely ideal for the fitness of the group to have varying levels of the propensity to explore. Thus, not all members of the group are at risk of failing to find adequate resources and not all members of the group are at the mercy of local environments which inevitably change and fail to provide necessary resources for survival. Previous research suggests a 70/30 split in favour of rovers in the natural *Drosophila* population (Sokolowski, 1980). However, for the current human sample, a 54/46 split in favour of locomotors (who are phenotypically similar to rovers) was observed. The more even split in this sample of humans may be due to different distribution of resources and costs of exploration. For *Drosophila*, their environment demands greater exploration as their food sources are more widely distributed, which creates greater selection pressure in favour of rovers.

Although an individual difference in our propensity to explore likely exists, the pattern of results observed in Chapter 4 has an alternative explanation with far reaching consequences. That is, despite having a desired level of stimulation, some individuals may fail to attain the desired level because they are genetically predisposed to be averse to risk. In a sense, aversion to risk can be regarded as a separate motivational force that may interfere with effective regulation of stimulation (risk is often involved in attaining the optimal level of stimulation). Indeed, it has been suggested that we possess a meta-level regulatory system that is discrepancy-enlarging, and thus mediates avoidance, aversive or prevention motives (Carver & Scheier, 1998; Gray, 1970; Higgins, 1997; Roseman, 1984). It is possible that the function of this regulatory system may be in direct conflict with the regulatory system described by OSMB. For example, even though exploration may satisfy our desire for stimulation, it may be imperative for survival to exploit local resources despite the mundane (low stimulation) nature of the activity. This interpretation is consistent with prior findings that demonstrate that those who emphasize an assessment regulatory mode – which aims to minimize risk through evaluation and comparison of alternatives – show a positive correlation with boredom proneness (Struk et al., 2015). Indeed, it has been suggested that such a predisposition may even contribute to a failure to launch into action (Mugon, Struk, & Danckert, 2018). This interpretation of Chapter 4's results suggests that some genetic predispositions are important for survival of the species, but they may have detrimental implications for an individual's well-being. Indeed, failure to act in accordance with our intrinsic motives is known to be highly detrimental to physical, social and emotional health

(for review see Deci, & Ryan 2008; Miquelon & Vallerand, 2008). Future research should investigate the associations between variations of PRKG1, and other genes known to be involved in self-regulation, on markers of mental health. Such an investigation may yield important insights into mental health and yield novel intervention strategies.

The question of how and why we choose to act in specific ways has puzzled thinkers for centuries. Despite great advances in our understanding of the human mind and animal behaviour in general, much remains to be understood in this regard. The work I present here augments our knowledge of what makes us act, and why we act in the ways that we do. However, as with any scholarly enterprise, we are left with more questions than we started with. It is my hope that my work will serve as a launch pad for furthering this line of inquiry.

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Appendix A

Short Boredom Proneness Scale

SBPS (Struk, Carriere, Cheyne, & Danckert, 2015)

Instructions:

The following are some statements that may or may not describe you, in general, on a typical day. Please rate each statement using the 7-point scale above by circling the number that corresponds to how much you do or do not feel like the sentence describes you. Remember to rate each statement based on how much it describes you in general.

1	2	3	4	5	6	7
strongly disagree	disagree	somewhat disagree	neutral	agree	somewhat agree	strongly agree

1. I often find myself at "loose ends", not knowing what to do. 1 2 3 4 5 6 7
2. I find it hard to entertain myself. 1 2 3 4 5 6 7
3. Many things I have to do are repetitive and monotonous. 1 2 3 4 5 6 7
4. It takes more stimulation to get me going than most people. 1 2 3 4 5 6 7
5. I don't feel motivated by most things that I do. 1 2 3 4 5 6 7
6. In most situations, it is hard for me to find something
to do or see to keep me interested. 1 2 3 4 5 6 7
7. Much of the time I just sit around doing nothing. 1 2 3 4 5 6 7
8. Unless I am doing something exciting, even dangerous,
I feel half-dead and dull. 1 2 3 4 5 6 7

Appendix B

List of Charities Available to University of Waterloo Students:

Acronym	Name	Slogan
HSF	Heart and Stroke Foundation	Heart disease prevention and research,
WWF	World Wildlife Fund	Protecting the future of nature,
CRC	Canadian Red Cross	Helping prevent and alleviate human suffering in the face of emergencies.
UNICEF	United Nations Children's Emergency Fund (UNICEF)	Children first.
DWB	Doctors Without Borders	Providing emergency medical care where it is needed the most,
WCSWR	Women's Crisis Services of Waterloo Region	Providing safe shelter, education and outreach services,
WRFB	Waterloo Region Food Bank	Providing better health by curing hunger

List of Charities Available for University of Virginia Students:

Acronym	Name	Slogan
ACS	American Cancer Society	Dedicated to eliminating cancer,
WWF	World Wildlife Fund	Protecting the future of nature,
ARC	American Red Cross	Helping prevent and alleviate human suffering in the face of emergencies.
UNICEF	United Nations Children's Emergency Fund (UNICEF)	Children first.
DWB	Doctors Without Borders	Providing emergency medical care where it is needed the most,
MH	Madison House	Organizing service programs to address the needs of the community,
BRAFB	Blue Ridge Area Food Bank	Providing better health by curing hunger

Appendix C

Pilot Study for Chapter 3

Participants

One hundred and fourteen University of Virginia undergraduates (56 females, mean age = 18.33 years) participated in exchange for partial course credit. In terms of self-reported ethnicity, 62.1% identified as White/Caucasian, 17.5% as Asian, 13.6% as multi-ethnic, 4.9% as Black, 2% Other. Participants were randomly assigned to one of three experimental conditions. Data were collected throughout the Fall 2018. It was decided, a priori, to gather as much data as possible in a single day. Following data analysis an additional sample was collected within a single day.

Procedure and Results

Procedures were identical to those detailed in section 3.2, with the exception of differences in the apple catch rate. In the initial sample, the “too easy” condition was characterized by a 100% catch rate, “just right” by an 85% catch rate and “too hard” by a 60% catch rate. The goal was to attain an adequate separation between groups, with emphasis on the “just right” condition obtaining a reported difficulty score of about 5 (i.e., the middle of the scale). The descriptive statistics associated with difficulty ratings were as follows; “too easy” ($n = 31$, $M = 1.61$, $SD = 1.56$), “just right” ($n = 20$, $M = 3.96$, $SD = 1.51$), “too hard” ($n = 26$, $M = 6.45$, $SD = 1.67$). The “just right” and “too hard” conditions were deemed not sufficiently difficult. In the second sample, the “too easy” condition was characterized by a

Appendix D

Post Apple Catching task survey

Variable	Question
Boredom	“How boring was the Apple Catcher game?”
Interest	“How interesting was the Apple Catcher game?”
Enjoyment	“How enjoyable was the Apple Catcher game?”
Entertainment	“How entertaining was the Apple Catcher game?”
Frustration	“How frustrating was the Apple Catcher game?”
Meaning	“How personally meaningful was the Apple Catcher game?”
Inattention	“How difficult was it to concentrate on the Apple Catcher game?”
Difficulty	“How difficult was the Apple Catcher game?”
Control	“How in control did you feel during the Apple Catcher game?”

Appendix E

Post Berry Picking task survey

Variable	Question
Boredom	“How boring was the Berry Picking game?”
Interest	“How interesting was the Berry Picking game?”
Enjoyment	“How enjoyable was the Berry Picking game?”
Entertainment	“How entertaining was the Berry Picking game?”
Frustration	“How frustrating was the Berry Picking game?”
Meaning	“How personally meaningful was the Berry Picking game?”
Inattention	“How difficult was it to concentrate on the Berry Picking game?”
Control	“How in control did you feel during the Berry Picking game?”
Random	“How randomly distributed were berries?”
Picking	“Some people pick all the berries they see before moving on; other people pick a few and then move on to look for more berry patches. How important was it to you to pick all the berries before moving on and looking for more?”
Patches	“Some people stay in just one place the whole time; other people move around a lot to find all the different berry patches. How important was it to you to find all the berry patches in the game?”
Juice	“How important was it to you to collect as much juice as possible?”
Worry	“How worried were you about running out of juice?”,
Strategy	“How much did you care about developing an effective strategy for gathering berries?”
Explore	“How much did you care about exploring all the space in the game?”

Appendix F

Chapter 3: Exploratory Variables and Analyses

Several additional exploratory variables were included in the post Apple Catcher survey (see Appendix D for the full description of these items). For transparency, between group differences for these variables are displayed in Figure F.1.

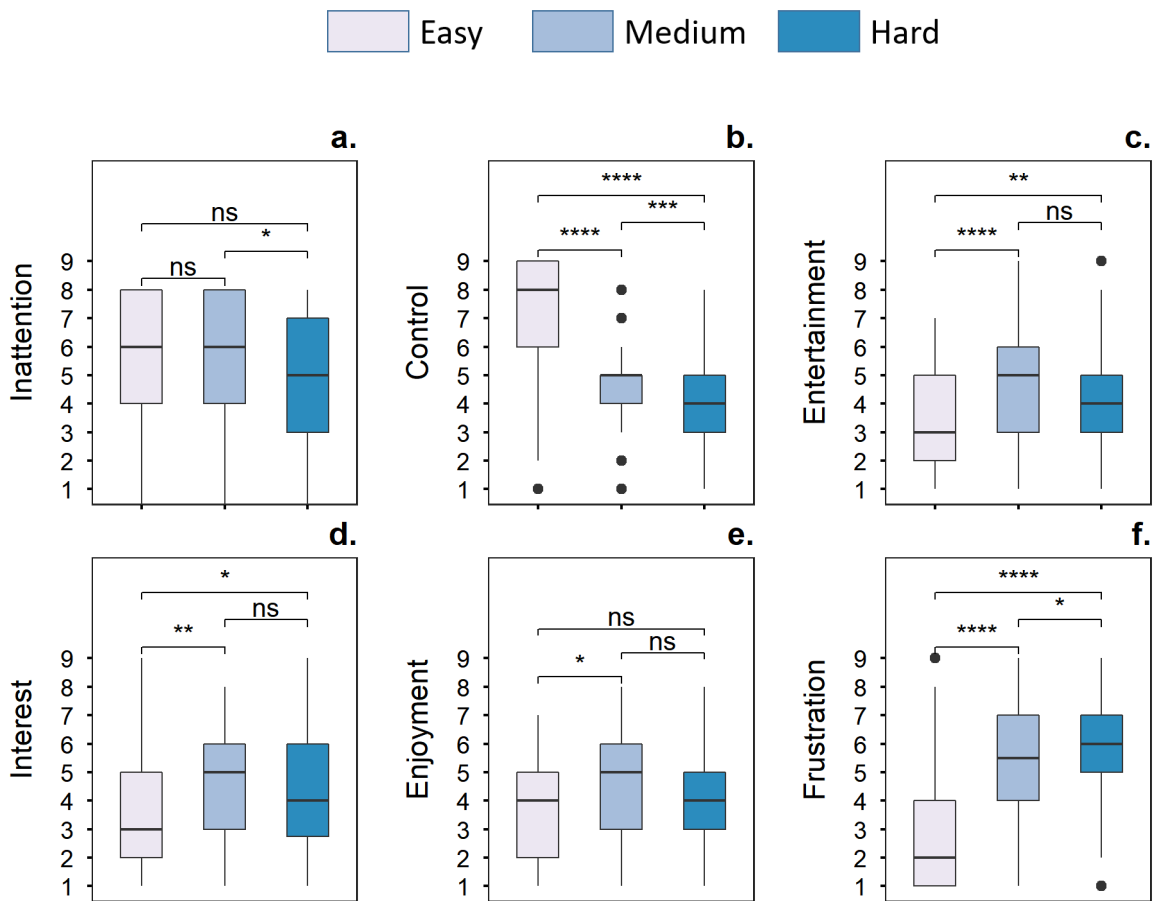


Figure F.1 Boxplots for post Apple Catcher survey variables for each condition. For comparisons unadjusted Wilcoxon ranked-sum significance values are used: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, **** = $p < 0.0001$

Several additional items were also included in the post Berry Picking survey that did not assess exploration or exploitation (see Appendix E for full description of these items). For transparency, moderation analyses testing the interaction between condition and boredom on these variables are reported here (Figure F.2).

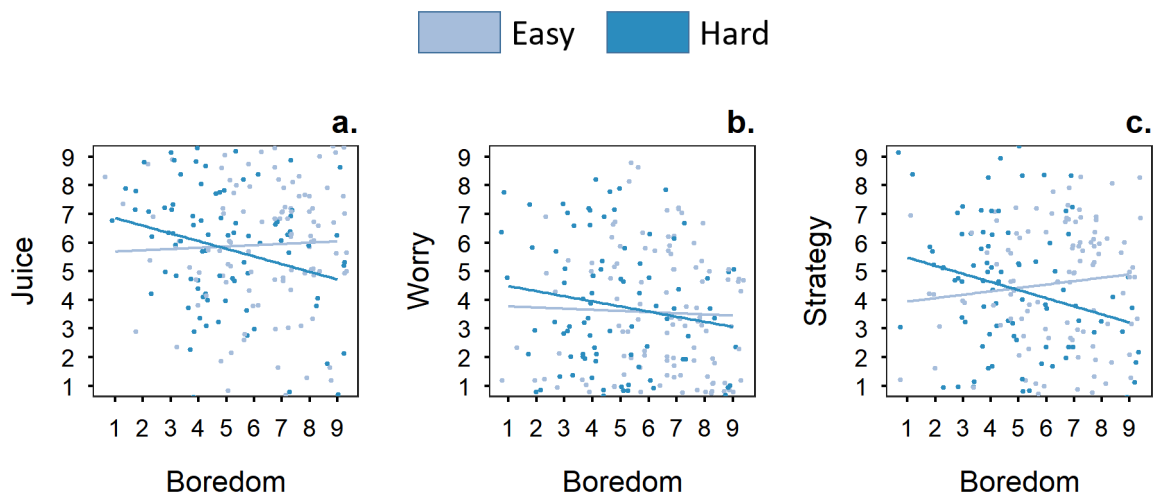


Figure F.2 Scatter plot for each unique (Berry Picking specific) self-report variable in the Berry Picking survey. A line of best fit is present for Easy (Green) and Hard (Orange) conditions. There was a significant boredom by condition interaction for juice ($F(1,186) = 4.17, p = 0.043$), and strategy ($F(1,187) = 7.06, p = 0.009$).

Self-report measures following the Apple Catching task were also included in the post Berry Picking survey (Appendix E). For transparency, moderation analyses testing the interaction between condition and boredom (following the Apple Catching task) on these variables are reported here (Figure F.3)

Easy Hard

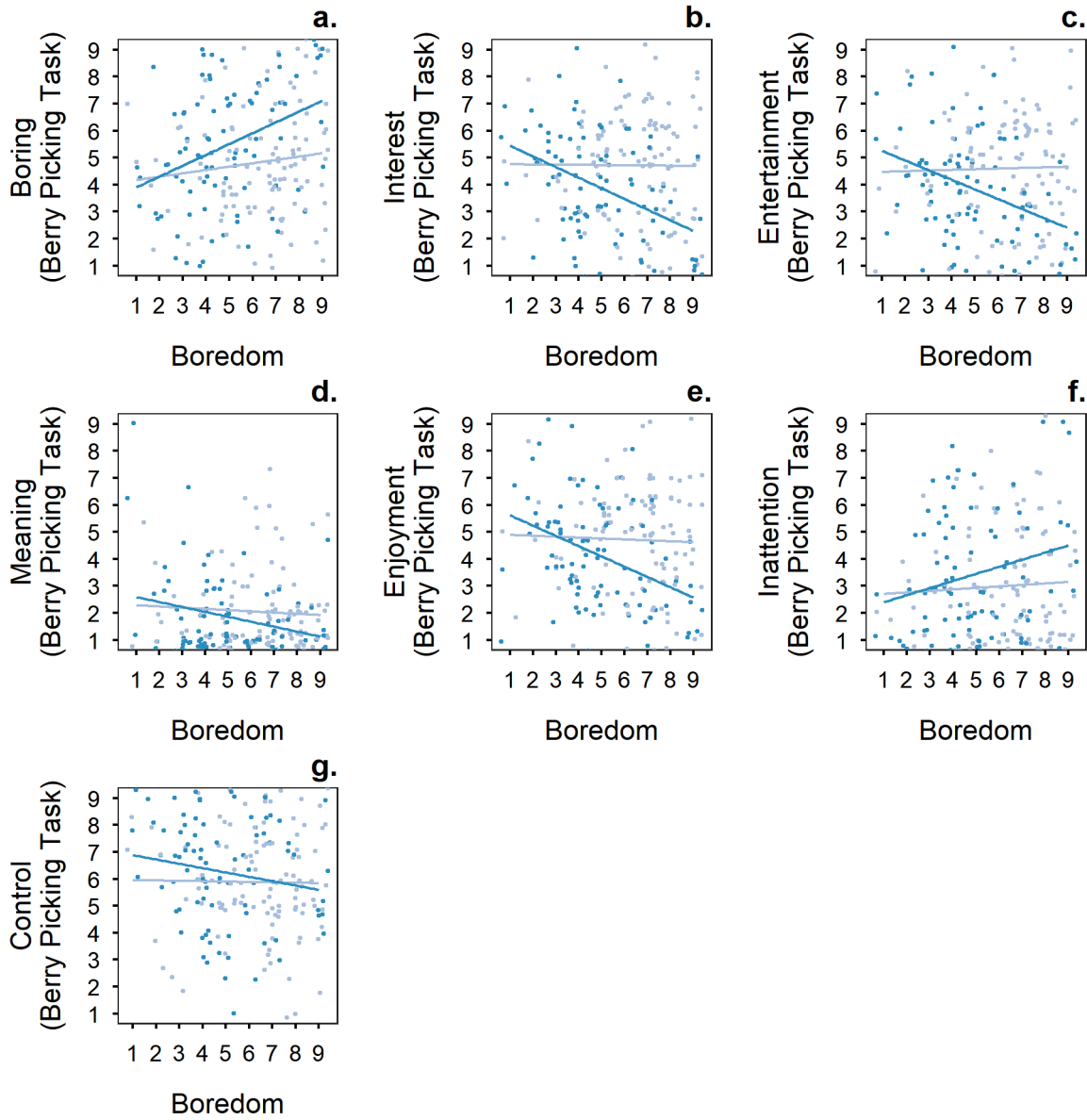


Figure F.3. Scatter plot for each non-unique (from post Apple Catching) self-report variable in the Berry Picking survey. A line of best fit is present for Easy (Green) and Hard (Orange) conditions. There was a significant boredom (post Apple Catching) by condition interaction on interest (post Berry Picking; $F(1,190) = 7.94, p = 0.005$), entertainment (post Berry Picking; $F(1,190) = 7.46, p = 0.007$), enjoyment (post Berry Picking; $F(1,190) = 6, p = 0.015$), marginally on boredom (post Berry Picking; $F(1,190) = 3.31, p = 0.07$). No other interaction reached significance (all $ps > 0.152$).

Appendix G

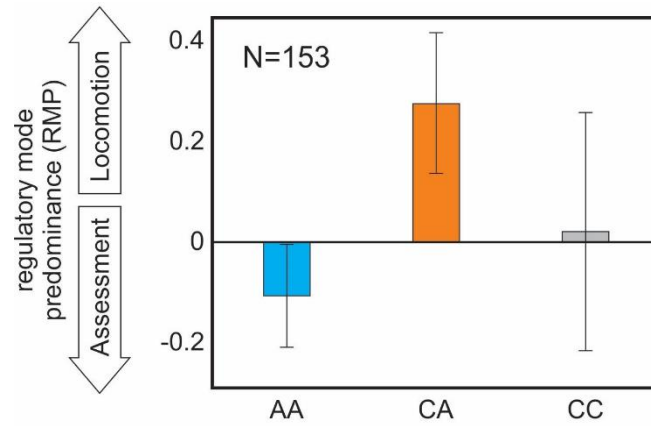


Figure G.1 Regulatory mode preference (RMP) by genotype for Sample 1 (Struk et al., 2019). rs13499 polymorphism generates three genotypes (AA, CA, CC). Frequencies were 53% ($n = 81$), 34.4% ($n = 53$), and 12.6% ($n = 19$) for AA, CA, and CC genotypes respectively.

Appendix H

Scrabble Task

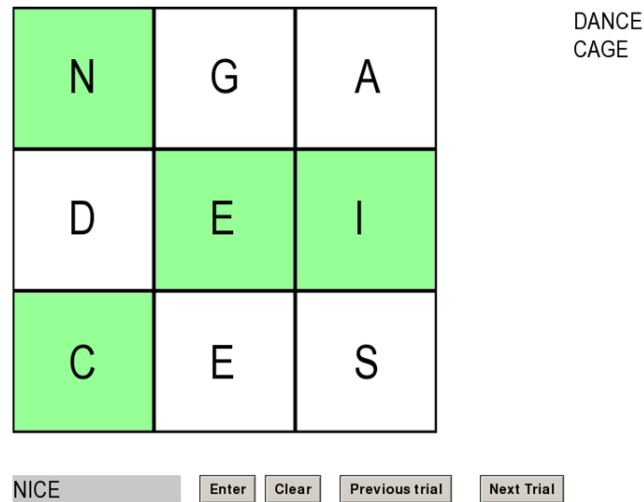


Figure H.1 Screenshot of the scrabble task.

In the scrabble task participants were asked to form as many words as they could from a set of given letters (Figure H.1). Letters were presented within a 3 x 3 grid with random letters in each grid. The main constraint in this task is that every word made had to include the letter in the centre of the grid which was highlighted. Participants were told that plurals and proper names would not be accepted. Once participants had written as many words as they could from the given set, they were able to click 'next' to move on to the next problem set. They could also click back to return to a previous problem set. Finally, they were told that each set contained one 9-letter word. The task took approximately 10 minutes

to complete and the goal was to come up with as many words as possible. Participants entered their responses via a standard keyboard.

Connect the Dots

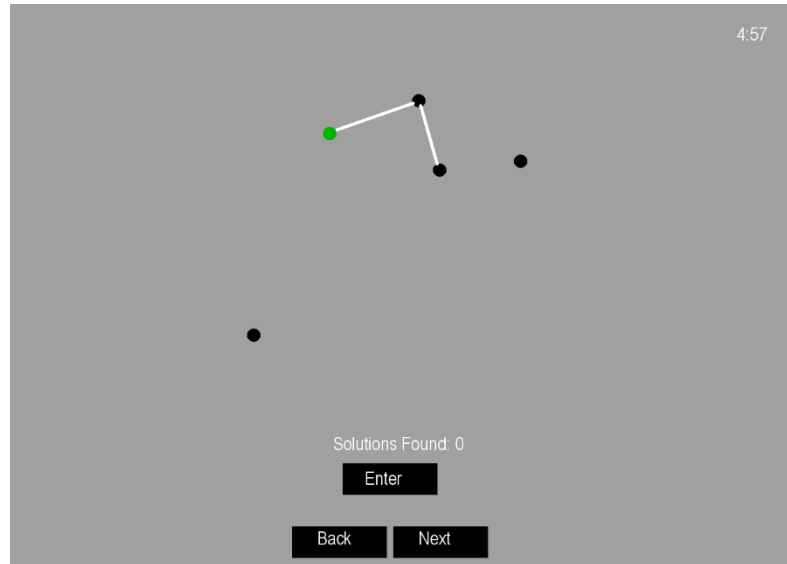


Figure H.2 Screenshot of the connect the dots task.

In the connect the dots task participants were presented with one green dot and 4-6 black dots randomly positioned on the screen (Figure H.2). Participants were asked to connect all dots, starting from the green dot, and to find as many ways of connecting the dots as possible. As dots were connected, a white line appeared between them, once the connection was made it could not be undone, and no connection could cross with another connection. Once participants connected all dots they could, they could press the “reset” button to reset the problem to try again or they could press a “submit” button which indicated that they

found a complete solution (this also resets all connections). Finally, participants could press the “next” button which produces a new problem to solve (i.e., a different array of dots), or they could press the “back” button to revisit previous problems. Participants used a touch screen to connect the dots and press the buttons.

Appendix I

Regulatory Mode Questionnaire

RMQ (Higgins, Kruglanski, & Pierro, 2003)

Instructions:

Read each of the following statements and decide how much you agree with each according to your beliefs and experiences. Please respond according to the following scale:

1	2	3	4	5	6
strongly disagree	moderately disagree	slightly disagree	slightly agree	moderately agree	strongly agree

1. I don't mind doing things even if they involve extra effort. 1 2 3 4 5 6
2. I never evaluate my social interactions with others after they occur. 1 2 3 4 5 6
3. I am a "workaholic." 1 2 3 4 5 6
4. I feel excited just before I am about to reach a goal. 1 2 3 4 5 6
5. I enjoy actively doing things, more than just watching and observing. 1 2 3 4 5 6
6. I spend a great deal of time taking inventory of my positive and negative characteristics. 1 2 3 4 5 6
7. I like evaluating other people's plans. 1 2 3 4 5 6
8. I am a "doer." 1 2 3 4 5 6
9. I often compare myself with other people. 1 2 3 4 5 6
10. I don't spend much time thinking about ways others could improve themselves. 1 2 3 4 5 6
11. I often critique work done by myself and others. 1 2 3 4 5 6
12. When I finish one project, I often wait awhile before getting started on a new one. 1 2 3 4 5 6
13. I often feel that I am being evaluated by others. 1 2 3 4 5 6
14. When I decide to do something, I can't wait to get started. 1 2 3 4 5 6
15. I am a critical person. 1 2 3 4 5 6
16. I am very self-critical and self-conscious about what I am saying. 1 2 3 4 5 6
17. By the time I accomplish a task, I already have the next one in mind. 1 2 3 4 5 6
18. I often think that other people's choices and decisions are wrong. 1 2 3 4 5 6
19. I am a "low energy" person. 1 2 3 4 5 6

- | | | | | | | |
|--|---|---|---|---|---|---|
| 20. Most of the time my thoughts are occupied with the task that I wish to accomplish. | 1 | 2 | 3 | 4 | 5 | 6 |
| 21. I <u>rarely</u> analyze the conversations I have had with others after they occur. | 1 | 2 | 3 | 4 | 5 | 6 |
| 22. When I get started on something, I usually persevere until I finish it. | 1 | 2 | 3 | 4 | 5 | 6 |
| 23. I am a "go-getter." | 1 | 2 | 3 | 4 | 5 | 6 |
| 24. When I meet a new person I usually evaluate how well he or she is doing on various dimensions (e.g., looks, achievements, social status, clothes). | 1 | 2 | 3 | 4 | 5 | 6 |