THE ROLE OF EMOTIONS AND PHYSIOLOGICAL AROUSAL IN MODULATING IMPULSIVE BEHAVIOUR

Aleksandra Maria Herman

PhD in Neuroscience

University of Sussex

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DECLARATION

I hereby declare that this thesis has not been and will not be, submitted in whole or in part to another University for the award of any other degree.

Signature:……

PREFACE

The thesis incorporates material already published or submitted in the journals listed below:

Chapter 1

Herman, A. M., Critchley, H. D., & Duka, T. (2018). The role of emotions and physiological arousal in modulating impulsive behaviour. *Biological Psychology*, *133*, 30–43. http://doi.org/10.1016/j.biopsycho.2018.01.014

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University of Sussex

Aleksandra M. Herman

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The role of emotions and physiological arousal in modulating impulsive behaviour

SUMMARY

Impulsivity refers to both a stable personality trait and a set of behaviours which undergo momentary changes depending on the current circumstances. Impulsivity plays a vital role in daily life as well as clinical practice as it is associated with drug misuse and certain neuropsychiatric conditions. Because of its great health and well-being importance, it is crucial to understand factors which modulate impulsive behaviours. The current studies investigated the role of emotions and physiological arousal as modulators of impulsive actions and decisions in healthy individuals.

A set of experiments was conducted using a variety of methods including behavioural testing, physiological recordings, psychopharmacology and neuroimaging. Studies 1 and 2 clarified the influence of emotional states on distinct dimensions of impulsive behaviours. Study 3 investigated the neural correlates behind the impact of emotions on impulsive actions. Finally, studies 4 and 5 focused on the relationship between physiological arousal and behavioural and trait impulsivity.

Our findings demonstrate that a degree to which one's internal (emotional or physiological) state changes, is associated with behavioural impulsivity level. Importantly, distinct dimensions of impulsivity are differentially sensitive to those changes. Namely, increased state level of physiological arousal is associated with decreased motor 'stopping' impulsivity, enhanced subjective ratings and objective measurements of arousal are also related to decreased temporal impulsivity. Increased ratings of stress and increased physiological arousal, however, are associated with higher reflection impulsivity. At the neural level, successful response inhibition requires enhanced activation of prefrontal and parietal areas in impulsive individuals, particularly in negative emotional context, suggesting that behavioural control might be more effortful for highly impulsive individuals.

In conclusion, changes in internal bodily state are related to behavioural impulsivity level. Staying more attuned to those changes and finding adaptive ways to adjust behaviour according to bodily needs might be vital to reducing impulsivity levels.

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CHAPTER 1.

GENERAL INTRODUCTION

This chapter has been published with minor modifications in Biological Psychology:

Herman, A. M., Critchley, H. D., & Duka, T. (2018). The role of emotions and physiological arousal in modulating impulsive behaviour. *Biological Psychology*, 133, 30–43. http://doi.org/10.1016/j.biopsycho.2018.01.014

Contribution

I gathered the literature and prepared the initial manuscript.

1.1 Abstract

Impulsivity received considerable attention in the context of drug misuse and certain neuropsychiatric conditions. Because of its great health and well-being importance, it is crucial to understand factors which modulate impulsive behaviour. As a growing body of literature indicates the role of emotional and physiological states in guiding our actions and decisions, we argue that current affective state and physiological arousal exert a significant influence on behavioural impulsivity. As ‘impulsivity' is a heterogeneous concept, in this paper, we review key theories of the topic and summarise information about distinct impulsivity subtypes and their methods of assessment, pointing out to the differences between the various components of the construct. Moreover, we review existing literature on the relationship between emotional states, arousal and impulsive behaviour and suggest directions for future research.

Keywords: Impulsivity; Emotions; Mood; Physiological Arousal; Stress; Stop Signal Task; Delay Discounting; Risk-Taking

1.2 Introduction

The importance of impulsivity has long been recognised, both in everyday life, as it plays a vital role in the decision-making process, and in many neuropsychiatric conditions. Impulsive behaviour is a diagnostic criterion of several neuropsychiatric conditions including personality disorders (borderline and antisocial personality disorders), substance use disorders, or attention deficit and hyperactivity disorder (ADHD; American Psychiatric Association, 2013). High levels of trait impulsivity are also associated with risk-taking and increased alcohol use in social drinkers (Granö, Virtanen, Vahtera, Elovainio, & Kivimäki, 2004; Grau & Ortet, 1999), and predict increased food intake in normal-weight healthy women (Guerrieri, Nederkoorn, Stankiewicz, et al., 2007; Guerrieri, Nederkoorn, & Jansen, 2007).

Therefore, impulsivity has a great clinical as well as general-health importance. A better understanding of modulators of impulsive behaviour could help identify risky states and support impulsive individuals in a clinical and general population. One of the factors which may exert an impact on our impulsive state is emotions. A growing body of evidence shows that emotions influence our cognition and behaviour, including memory and learning, attention, or perception (Asutay & Västfjäll, 2012; Dolan, 2002; Sharot, Delgado, & Phelps, 2004; Talarico & Rubin, 2007; Zadra & Clore, 2011). It seems that impulsivity is not independent of emotional influences either. The tendency to act impulsively while experiencing distress (negative urgency, Whiteside & Lynam 2001) is a well-established personality trait. Cyders & Smith (2007; 2009) also proposed another facet of mood-based rash action, which is driven by strong positive emotions (positive urgency). Moreover, research suggests that engaging in impulsive actions, which may result in negative consequences in the future, such as emotional eating, heavy drinking or smoking, while experiencing negative affect might serve as a means of alleviating one's mood state (Cooper et al., 1995; Bekker et al., 2004; Smyth et al., 2007; Abrantes et al., 2008; Magid et al., 2009). Indeed, impulsive behaviour, such as episodes of binge eating and purging in bulimia nervosa, are thought of as maladaptive attempts to alleviate one's mood (Smyth et al., 2007).

This review aims to indicate the role of emotional and physiological states as important modulators of impulsive actions and decisions. When a growing body of literature shows the detrimental effects of inability to regulate one's emotions (Cisler, Olatunji, Feldner, & Forsyth, 2010; Wilcox, Pommy, & Adinoff, 2016) and a high prevalence of mood disorders in society (Kessler, Chiu, Demler, & Walters, 2005), it seems particularly important to understand how affective states modulate behaviour and decision-making. While there are other relevant factors such as gender, age or genetic polymorphisms, these are beyond the scope of this review. A better understanding of the relationship between emotion, physiological states, and impulsivity, as well as the neural circuitry underlying these relationships, could facilitate treatment of

impulse-related disorders and promote methods to improve decision-making of those suffering from mood disorders. However, in this review, we focus on healthy volunteers as most of the work looking at the role of emotional and physiological states on impulsivity has been conducted in healthy individuals. Since the term ‘impulsivity’ incorporates a wide range of behaviours, it is important to describe the complex construct of impulsivity before discussing the role of emotional and physiological states in shaping impulsive action. Therefore, the first sections will deal with research trying to define and systematise the construct of impulsivity.

1.3 Defining Impulsivity

Although impulsivity is considered a symptom of many psychiatric and neurological conditions (American Psychiatric Association, 2013), it is also an element of a personality of healthy individuals (Evenden, 1999a, 1999b). There are, however, many definitions of this construct (Evenden, 1999a, 1999b; Moeller, Barratt, Dougherty, Schmitz, & Swann, 2001).

According to Daruna and Barnes (1993), impulsivity is reflected in a variety of maladaptive behaviours, unplanned or prematurely expressed, inappropriate to situations, risky or resulting in undesirable consequences. Other authors define impulsivity as an inability to delay gratification and as the opposite of self-control (J. Monterosso & Ainslie, 1999). American Psychiatric Association (2013) describe impulsivity as a failure to control impulses or temptations to perform actions which are detrimental to the individual or other people.

According to Moeller (Moeller et al., 2001), impulsivity should be defined as a predisposition for rapid, unplanned actions in response to external and internal stimuli without considering potential negative consequences of these actions. Importantly, impulsivity, in this definition, is associated with automaticity: quick decision-making, lack of planning and foresight, which prevents an appropriate assessment of the consequences. Likewise, Eysenck (S. Eysenck & Eysenck, 1978) discriminates between *impulsiveness* and *venturesomeness*, the latter being related to conscious risk-taking.

The above definitions consider impulsivity as a maladaptive and pathological feature; yet, it is widely accepted that impulsivity is a part of normal behaviour, and every person can be characterised by their impulsive tendencies. Therefore, impulsivity may be perceived as a personality trait. For instance, in his original theory, Hans Eysenck proposed that personality consists of two dimensions of higher-order traits, i.e. extraversion vs introversion and emotional stability vs neuroticism. In this primary construct, impulsivity was considered to be a part of extraversion; however, in the revised model, impulsivity is regarded as a part of the third dimension — psychoticism vs impulse control (H. J. Eysenck & Eysenck, 1985). In Eysenck’s notion, impulsivity is related to risk-taking, lack of planning, and making up one's mind quickly. A similar concept was proposed by Martin Zuckerman under the name “sensation seeking”.

According to Zuckerman, high sensation seekers are people who show a constant need for stimulation and novel experiences, despite the risks (Zuckerman, 1984).

Gray (1972;1981), on the other hand, argued that impulsivity and anxiety are the major factors of personality with which other features should be described. In this model, extraversion is characterised by low anxiety and high impulsivity levels, while neuroticism is associated with high anxiety and high impulsivity levels. Grey proposed an existence of two behavioural systems which underlie these personality traits. The behavioural activation system is related to impulsivity and is associated with sensitivity to reward and approach behaviours, while the behavioural inhibition system underlies anxiety and is activated in response to punishment signals and novelty. Noteworthy, the Barratt Impulsiveness Scale (BIS; Barratt, 1959; Patton, Stanford, & Barratt, 1995), a questionnaire commonly used both in clinical setting and research to assess impulsivity levels, was primarily developed to separate the personality trait of impulsiveness from the personality trait of anxiety.

1.4 Subtypes of Impulsivity

Difficulties in unequivocally defining impulsivity and placing it within personality models prove that impulsivity is a multidimensional construct, where components are independent of one another and reflect different aspects of behaviour (Congdon & Canli, 2008; Evenden, 1999a; Moeller et al., 2001). Various approaches to the complex construct of impulsivity led to distinguishing different subtypes of this feature.

For instance, two commonly used impulsivity scales, identify various components of impulsivity construct. In BIS (version BIS-11) three dimensions of impulsivity are defined: inattention (a difficulty in focusing on the task at hand), motor (acting on the spur of the moment or inability to withhold the response), and non-planning (which refers to the lack of consideration or not planning tasks carefully) (Patton et al., 1995). Whiteside and Lynam (2001), on the other hand, performed a comprehensive factor analysis of various impulsivity scales to separate distinct subtypes of impulsivity which were previously grouped together. Their analysis led to distinguishing four personality facets related to impulsive behaviour: urgency (a tendency to act under the influence of strong impulses, often associated with negative affect), lack of premeditation (a tendency to take actions without careful planning or thinking of consequences), lack of perseverance (an inability to fulfil the task despite boredom or tiredness), and sensation seeking (a tendency to seek novelty and excitement). Measures of each personality dimension together form the UPPS (Urgency, Premeditation, Perseverance, Sensation seeking) Impulsive Behaviour scale. Subsequently, Cyders and Smith (2007, 2008), proposed an additional component called Positive Urgency, which refers to a tendency to act impulsively while experiencing strong positive emotions.

Opposite to the generally held view, Dickman (1990) argued that impulsivity is not solely a maladaptive feature. He pointed out that making snap decisions about matters of little importance (‘what am I having for dinner tonight?’) is beneficial. Moreover, spontaneous behaviours enable us to seize opportunities, gain new experiences, which enrich our lives. Additionally, impulsive individuals outperform less impulsive subjects in tasks in which a little time is available to reach a decision (Dickman & Meyer, 1988). Therefore, Dickman distinguished ‘functional impulsivity’, which reflects the advantageous aspects of spontaneous behaviour, from ‘dysfunctional impulsivity’, which is a maladaptive feature associated with negative consequences. Similarly, others argued that when it comes to everyday situations, fast and frugal decisions may be beneficial and better than in-depth considerations as they lead to optimising strategies in the face of limited time and resources (Gigerenzer, Todd, & ABC Research Group, 1999). One showed that the consequences of impulsive traits depend on the nature of the task: When delayed rewards are favoured over immediate rewards, low-impulsive individuals outperform highly impulsive ones; however, when immediate gratification is preferred, highly impulsive individuals perform better (Otto, Markman, & Love, 2012). Taken to extreme, the urge to override immediate gratification in favour of the long-term goals may be maladaptive and even life-threatening, which is best exemplified with patients suffering from anorexia nervosa, who suppress their urge to eat and show decreased preference towards immediate rewards compared to healthy controls, a feature reversed with treatment (Decker, Figner, & Steinglass, 2015).

In behavioural approaches, the impulsivity construct is often divided into at least two major dimensions. The first reflects disinhibition, and is often referred to as motor impulsivity or impulsive action, while the second dimension reflects impulsive decision-making (also referred to as impulsive choice or cognitive impulsivity; Bechara, Damasio, & Damasio, 2000; Broos et al., 2012; Brunner & Hen, 1997; Reynolds, Ortengren, Richards, & de Wit, 2006). Impulsive action can be further divided into action cancellation and action restraint, while impulsive choice can be separated into risk or uncertainty-based choice and delay-based choice (Winstanley, Olausson, Taylor, & Jentsch, 2010). de Wit (2009) proposed a third dimension of impulsivity i.e. lapses of attention, arguing that sustained attention is necessary to suppress drug-seeking behaviours in addicts.

Evenden (1999a), on the other hand, claimed that impulsivity can affect an action at different stages of the process: during the preparation stage, the action execution stage, and the outcome phase. Therefore, he proposed a model of impulsivity which reflects the role of impulsivity at each of those stages, i.e. (1) impulsive preparation, which involves responding before all necessary information is obtained, (2) impulsive execution, which is related to a failure in following instructions and difficulty awaiting turn, and (3) impulsivity at the outcome stage, which results in an inability to delay gratification. Evenden’s model is in agreement with

a recent factor analysis of behavioural impulsivity measurements (Caswell, Bond, Duka, & Morgan, 2015), which distinguished three independent subtypes. 'Reflection'-impulsivity refers to the preparatory stage of an action and is defined as a tendency to make decisions in situations of uncertainty (Kagan, 1965a). 'Motor'-impulsivity refers to the action execution stage and reflects an inability to inhibit a motor response when it is no longer suitable. Finally, 'temporal'-impulsivity, which is related to the outcome stage of the behaviour, reflects a difficulty in delaying gratification (Ainslie, 1975).

In conclusion, impulsivity proves to be a concept difficult to define and no commonly agreed way of separating it into components exists. Selected views on impulsivity are summarised in Figures 1.1 and 1.2. It is worth noting, however, that many of the views share some similarities. The concept of motor impulsivity (or impulsive action) is well-established both in personality-based and behavioural approaches. Nevertheless, as discussed in more detail in the following section, motor impulsivity subtype is not uniform and can be further separated into components. In contrast, a tendency to take risk is usually included as a part of the definition of impulsivity, but not all behavioural models take account of this component.

1.5 Ways of assessing impulsivity in humans

A variety of methods is being used to study impulsivity. There are two major approaches: behavioural one, which uses laboratory measurements, and self-assessment questionnaires. Low correlations between scores on those questionnaires and behavioural tasks suggest that they provide information about different aspects of impulsivity, i.e. trait and behavioural impulsivity, respectively (Broos et al., 2012; Clark, Robbins, Ersche, & Sahakian, 2006; Reynolds et al., 2006; Wingrove & Bond, 1997). The abundance of methods used to assess impulsivity might be confusing; therefore, here we offer a summary of means of measuring impulsivity. Specifically, we focus on differentiating between distinct impulsivity subtypes.

1.5.1 Trait impulsivity

Self-report questionnaires are a common method of assessing trait impulsivity in clinical practice and research setting. The popular questionnaires include aforementioned Barratt Impulsiveness Scale-11 (BIS-11; Patton et al., 1995) which consists of 30 items organised into three subscales (inattention, motor and non-planning) and the UPPS scale (Whiteside & Lynam, 2001), which consists of 45 items organised into four subscales (Urgency, Premeditation, Perseverance, and Sensation-seeking). Zuckerman's Sensation Seeking Scale (SSS, Zuckerman et al., 1978) is an older questionnaire but still used in research. It consists of four factors: thrill and adventure seeking (sensation seeking through engagement in exciting sports or risky activities involving speed and danger), disinhibition (a desire for social stimulation and

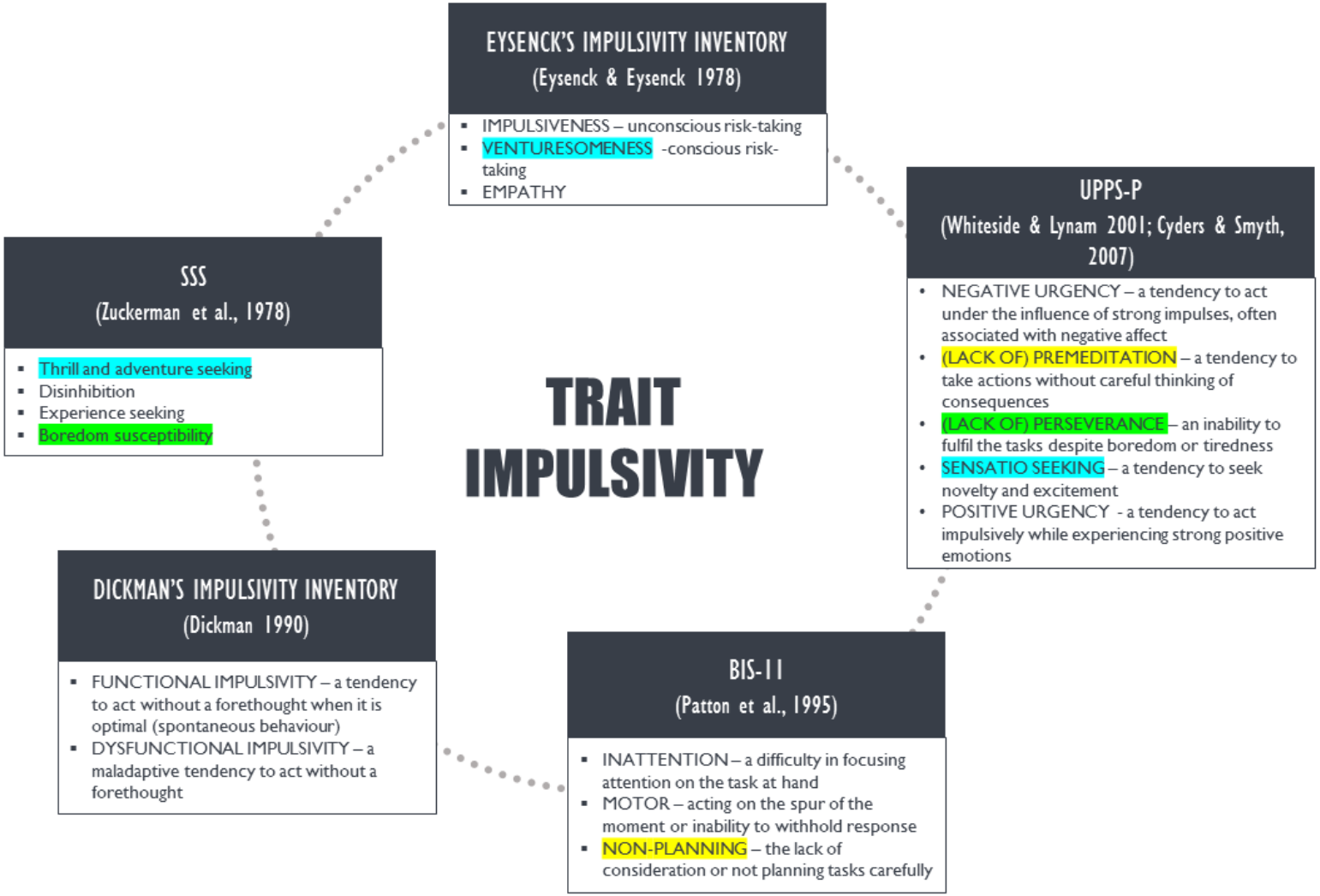

Figure 1.1 Selected views on impulsivity as a personality trait proposed by several researchers. Similar concepts are depicted in the same colour.

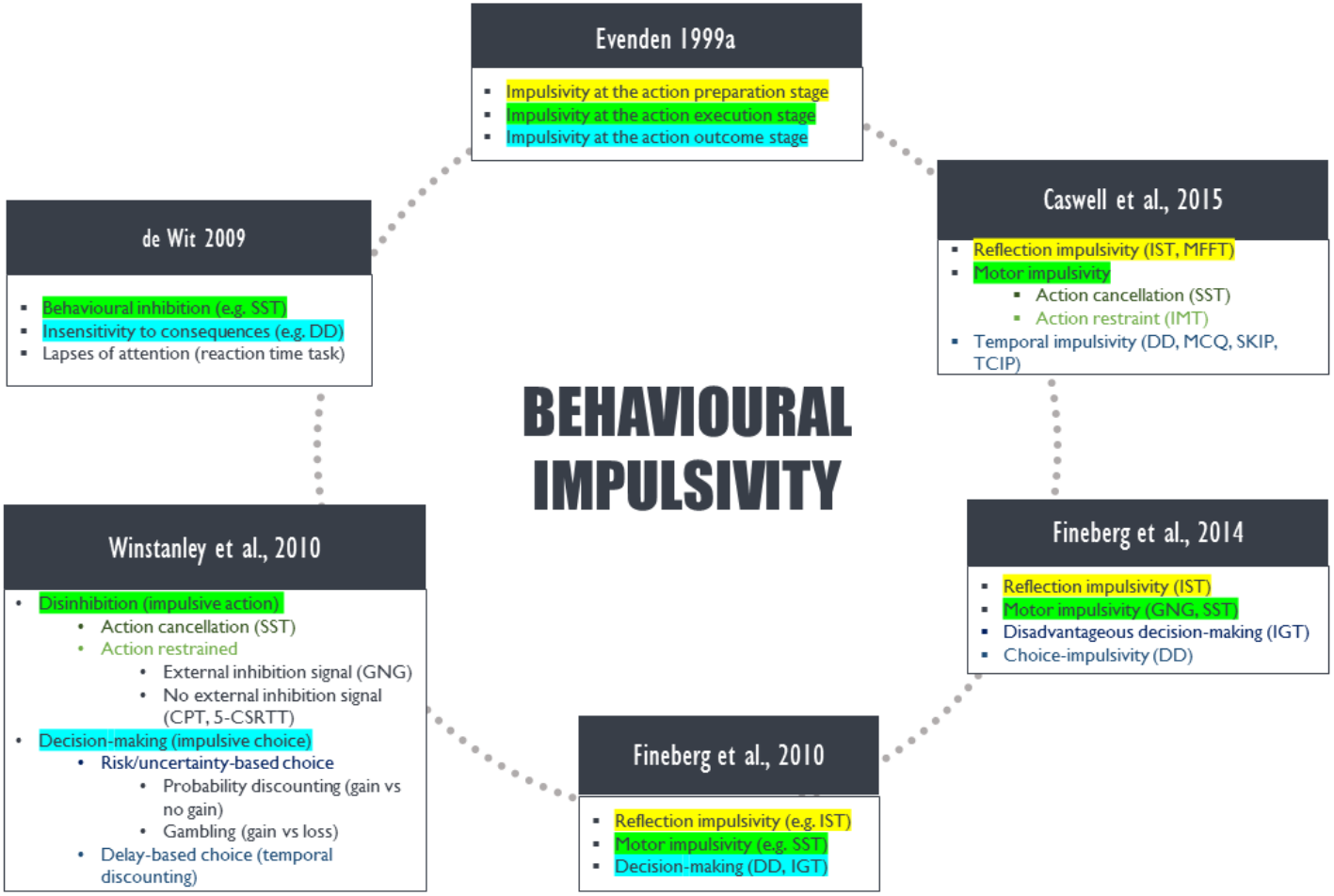

Figure 1.2 Selected views on behavioural impulsivity with examples of tasks used to assess particular impulsivity subtypes. Similar concepts are represented in the same colours. This figure was partly adapted from Winstanley et al., 2010.

disinhibited behaviour via alcohol, partying or sex), experience seeking (a desire for experience a non-conforming lifestyle through unplanned activities or drugs), and boredom susceptibility (an aversion to repetition and routine).

1.5.2 Behavioural impulsivity

Questionnaires are a simple and easily applicable form of assessing general impulsivity levels; however, these are subjective measures limited by individual's insight into their own behaviour and participants' honesty in answering the questions (Evenden, 1999b; Moeller et al., 2001). As they are designed to assess the tendency of a subject to act impulsively, i.e. stable over time personality trait, these measures are not appropriate to measure impulsive states, for example under acute drug administration or in a different context. The behavioural impulsivity tasks, on the other hand, provide an objective measure of impulsivity, suitable for repeated uses under various experimental paradigms.

Motor impulsivity

Impulsivity may derive from an inability to inhibit an inappropriate motor response. A variety of behavioural tasks has been developed to measure motor impulsivity. In both the Stop Signal Task (SST; Logan, 1994) and Go/No Go (GNG) task (Hogg, Evans, & Adrian, 1975) subjects respond to go-signals, and should inhibit their responses to stop-signals. Evidence suggests, however, that these tasks probe distinct processes i.e. 'action cancellation' (inhibition of an already initiated response) in the SST and 'action selection and restraint' (inhibition of a response before it has started) in the GNG (Dalley, Everitt, & Robbins, 2011; Eagle, Bari, & Robbins, 2008; Winstanley, 2011). Therefore, although both GNG and SST seem very similar at the behavioural level ("stopping impulsivity", Robinson et al., 2009; Dalley et al., 2011), these tasks are not equivalent and reflect different aspects of motor impulsivity.

The Continuous Performance Task (CPT) (Rosvold, Mirsky, Sarason, Bransome, & Beck, 1956) measures yet another feature of motor control; where subjects are required to scan through 5-digit sequences and respond when the number matches a target stimulus. Impulsive behaviour in the task is reflected in a high number of premature responses, which indicates that an individual has difficulty awaiting the correct signal; therefore, the term "waiting impulsivity" was coined (Robinson et al., 2009; Dalley et al., 2011). The Immediate and Delayed Memory Tasks (IMT, DMT) (Dougherty, Marsh, & Mathias, 2002) are also variants of the CPT used to study attention, memory, and impulsivity. Participants are presented sequentially with several-digit stimuli on the computer screen. In the IMT subjects need to indicate when the currently displayed number is identical to the preceding one, while in the DMT subjects should respond to a target number and ignore distractor numbers appearing in-between. The 5-Choice Serial

Reaction Time Task (5-CSRTT, Carli et al., 1983) is a task primarily developed to study waiting impulsivity in rodents, but recently also adapted to be used in humans (Sanchez-Roige et al., 2014; Voon et al., 2014). In this task, subjects are required to react to a stimulus which can occur in one of five locations. Impulsive behaviour is reflected in premature responses (i.e. before the stimulus appears).

Information regarding motor impulsivity is summarised in Figure 1.3.

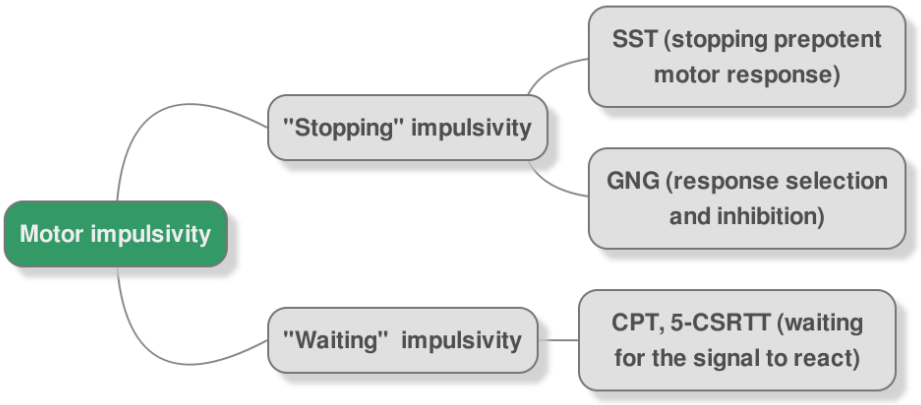

Figure 1.3 Motor impulsivity according to Robinson et al., 2009 and Dalley et al., 2011.

Reflection impulsivity

In everyday life, we encounter countless situations when we need to choose between several alternatives. In order to select the optimal one, we need to evaluate each of the options, as rash decisions may be maladaptive: impulsive individuals who make fast decisions also make more mistakes than reflective subjects who take longer to come to a conclusion (Clark et al., 2006; Kagan, 1965a, 1965b; Kagan, Rosman, Day, Albert, & Phillips, 1964). The tendency to make snap choices without gathering and evaluating information first has been referred to as 'reflection impulsivity' (Kagan, 1965a, 1965b; Kagan et al., 1964). Experimental measures of reflection impulsivity include the Information Sampling Task (IST) and Matching Familiar Figures Task (MFFT). The IST (Clark et al., 2006) assesses the uncertainty tolerance upon making decisions; in other words, it measures how much information an individual needs before making a decision. In the MFFT (Cairns & Cammock, 1978) participants compare several visual stimuli in order to decide which one is identical to the target image. The combination of fast and inaccurate responding is considered impulsive, whereas slower and accurate performance is regarded as reflective.

Impulsive choice

In daily life people face intertemporal choices of different outcomes at various time points: a slim figure in the future or enjoying a cake now, rewarding oneself with a night out

today or saving money to go for holidays in several months. Research indicates that sooner rewards are often preferred over delayed larger ones; however, impulsive individuals show a steeper discounting rate than those less impulsive (Ainslie, 1975; Kirby, Petry, & Bickel, 1999). Difficulty in delaying gratification, temporal impulsivity, can be assessed with pen-and-paper questionnaires or computerised tasks. The Monetary Choice Questionnaire (MCQ) and Delay Discounting Task (DD) (e.g. Kirby & MarakoviĆ 1996; Kirby et al., 1999) are both pen-and-paper tasks in which participants choose between hypothetical smaller immediate rewards (e.g. £19 today) and larger but delayed ones (e.g. £25 in 53 days). The tasks provide a measure of the delay discounting rate – a degree of a devaluation of future outcomes relative to present outcomes. It is worth noting, though, that through such questionnaires subjects report their preferences towards hypothetical rewards and delays that they do not experience in the laboratory. This raises the question whether such hypothetical decisions actually reflect choices when real rewards are used. Overall, research indicates that hypothetical rewards are discounted in the similar way to real rewards (Baker, Johnson, & Bickel, 2003; Bickel, Pitcock, Yi, & Angtuaco, 2009; Johnson & Bickel, 2002; Lagorio & Madden, 2005; Lawyer, Schoepflin, Green, & Jenks, 2011). Some evidence, however, suggests that real rewards are related to decreased temporal impulsivity compared with hypothetical gratification (Hinvest & Anderson, 2010).

The Single Key Impulsivity Task (SKIP) or Two Choice Impulsivity Paradigm (TCIP; Dougherty, Mathias, Marsh, & Jagar, 2005) have been developed to account for these issues. Both tasks are behavioural measures of how long one is willing to wait to obtain a reward. In these tasks, participants experience the delay towards the delivery of a reward in the form of points. In the SKIP participants press the mouse-button to obtain a point reward. The magnitude of the reward is dependent on the delay between consecutive responses: the longer the period individual waits, the more points they receive. In the TCIP subjects choose between two visual stimuli representing a smaller-immediate reward and larger-delayed reward. Participants choose the stimuli and receive points after the delay period elapses. Finally, the "Marshmallow Test" (MT; Mischel, Ebbesen, & Zeiss, 1972; Mischel, Shoda, & Rodriguez, 1989) is a delay of gratification measure used to study children. The procedure is straightforward: a child is offered a choice between one small treat (for example a marshmallow) provided immediately or two treats if they resist the temptation of eating it for a short period. Interestingly, data from longitudinal studies indicate that the ability to delay gratification in childhood is associated with a number of positive outcomes later in life, including better academic performance, improved social and emotional coping, better ability to deal with stress and frustration, less drug use, as well as decreased probability of becoming overweight (Ayduk et al., 2000; Mischel, Shoda, & Peake, 1988; Schlam, Wilson, Shoda, Mischel, & Ayduk, 2013; Seeyave et al., 2009; Shoda, Mischel, & Peake, 1990).

The temporal delay may devalue the significance of the gratification, but so can the uncertainty about the reward being delivered (probability discounting, Winstanley et al., 2010). Therefore, disadvantageous or risky decision-making is sometimes considered to be a part of impulsivity construct (e.g. Mazur, 1993; Rachlin, 1990; Richards et al., 1999 but see Holt et al., 2003; Shead and Hodgins, 2009). Whether temporal impulsivity and risk-taking/probability discounting are part of the same facet (choice impulsivity) or are distinct from each other is debatable (Broos et al., 2012; Fineberg et al., 2014; Fineberg et al., 2010; Holt, Green, & Myerson, 2003; Richards, Zhang, Mitchell, & de Wit, 1999; Shead & Hodgins, 2009; Winstanley et al., 2010).

A popular measure of decision-making deficit is the Iowa Gambling Task (IGT) (Antoine Bechara, Damasio, Damasio, & Anderson, 1994). IGT simulates real-life decision-making by involving conditions of reward, punishment and uncertainty. In this task participants select cards from four card decks to win money. Each selected card is associated with a monetary reward, but on some trials, penalties are also imposed. Two card decks (A and B) are related to high rewards but also high losses; therefore, choosing from these decks is disadvantageous in the long run. In contrast, the two other decks (C and D) yield smaller immediate gains but also smaller penalties; thus, they bring profit if played continuously. Performance in the gambling tasks is thought to depend on insensitivity to future consequences and punishment, as well as increased sensitivity to reward (Antoine Bechara et al., 1994).

A way of assessing risk-taking is the Balloon Analogue Risk Task (BART) (Lejuez et al., 2002). BART is a computer-based task, in which participants must “pump” virtual balloons as much as possible without popping any of them. With each pump, subjects are awarded points, but if the balloon pops, all points from that trial are lost.

The many ways of measuring impulsive behaviour summarised above indicate a variety of approaches to impulsivity research and show how complex a construct it is. The measures of ‘trait impulsivity’ (self-reports) ask participants to assess how they behave in different situations. Although this form allows examining real-life scenarios, it is not ideal as it requires honesty and good self-insight from the individual. Behavioural measures overcome these limitations; however, their relevance to everyday behaviours may be debatable. Therefore, a combination of both self-report and objective measurements is often used in research to encompass the wide range of impulsivity construct.

1.6 Brain circuits of impulsivity

The differences between distinct subtypes of impulsivity are further observed at the neuronal level: despite some overlap, different impulsivity subtypes show separate neuronal

correlates. This section provides a non-exhaustive overview of neuronal networks associated with different types of impulsivity.

1.6.1 Motor impulsivity

Functional magnetic resonance imaging (fMRI) studies revealed common neural circuits for "stopping" impulsivity including inferior and right middle frontal gyri, anterior cingulate, pre-supplementary motor area, right inferior parietal lobe, and left middle temporal cortex (Rubia et al., 2001). However, the GNG task was associated with bilateral, but predominantly left-hemisphere activation, whereas the SST was primarily related to the activation in the right hemisphere (D'Alberto, Funnell, Potter, & Garavan, 2017; Nikolaou, Critchley, & Duka, 2013; Rubia et al., 2001). These findings are further confirmed by lesion studies, which revealed that patients with left frontal damage showed intact response inhibition, whereas patients with right frontal lesions had increased motor impulsivity in the SST (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003).

Evidence suggests that neural circuitry underlying the "waiting" impulsivity is distinct from the "stopping" impulsivity described above. The ability to wait depends on the top-down interactions of the prefrontal cortex (PFC, including anterior cingulate cortex) with limbic structures (including the hippocampus, amygdala, and ventral tegmental area as well as the nucleus accumbens; reviewed in Dalley et al., 2011).

1.6.2 Reflection impulsivity

The underlying neural substrates of reflection impulsivity remain to be explored; however, an fMRI study found that increased uncertainty during gathering information before making a decision was associated with activity in the dorsal anterior cingulate cortex, whereas greater uncertainty while executing a decision was related to the lateral frontal and parietal activity (Stern, Gonzalez, Welsh, & Taylor, 2010). Moreover, greater reflection impulsivity, as indexed by lower information sampling in the IST, was associated with the bigger left dorsal cingulate cortex and right precuneus volumes (Banca et al., 2016).

1.6.3 Impulsive decision-making

Three distinct brain networks were proposed to be involved in temporal discounting (Peters & Büchel, 2011): (1) the ventral striatum, ventromedial prefrontal cortex (vmPFC) and substantia nigra/ventral tegmental area are involved in determining individual incentive values of rewards, (2) the lateral prefrontal- and cingulate cortices are associated with cognitive control, while (3) the medial prefrontal lobe network, comprising hippocampus, amygdala,

vmPFC, and posterior cingulate cortex, is implicated in imagery and prospective evaluation of future outcomes. Moreover, recent evidence indicated the role of the insular cortex in temporal decision-making (Frost & McNaughton, 2017; Sellitto, Ciaramelli, Mattioli, & di Pellegrino, 2016). Indeed, insular lesions have been related to decreased sensitivity to immediate rewards: Individuals with insular damage show less steep discounting rates than patients with lesions in other parts of the brain and healthy controls (Sellitto et al., 2016).

These brain areas were also identified to be involved in risky decision-making. Neuroimaging, as well as lesion evidence, indicate that prefrontal regions including the orbitofrontal cortex (OFC), medial and vmPFC, take part in decision-making under uncertainty, and the performance on gambling tasks depends on them (Clark et al., 2008; Clark, Manes, Antoun, Sahakian, & Robbins, 2003; Fukui, Murai, Fukuyama, Hayashi, & Hanakawa, 2005; MacPherson, Phillips, Della Sala, & Cantagallo, 2009; Rao, Korczykowski, Pluta, Hoang, & Detre, 2008; Zeeb & Winstanley, 2011). Taking a voluntary risk on the BART is also associated with activation of mesolimbic areas (Rao et al., 2008). Moreover, the nucleus accumbens activation was found to precede risky choices, while the anterior insula activation preceded safe choices in a financial decision-making task, suggesting the existence of two distinct neural circuits driving risk-seeking and risk-aversion respectively (Kuhnen & Knutson, 2005). Indeed, patients with insular cortex lesions consistently showed an increased level of betting on a gambling task compared to healthy controls and frontal lesioned patients, even when the odds of winning decreased, suggesting the role of the insular cortex in signalling the probability of aversive outcomes (Clark et al., 2008). Furthermore, animal studies also indicate the role of the amygdala in the risky decision-making. Rats with lesions of the basolateral amygdala showed more risky choice in the rat gambling task (Zeeb & Winstanley, 2011). Therefore, temporal discounting and risk-taking share underlying neural circuitry, providing evidence that they may be grouped into a single impulsivity subtype.

1.6.4 Similarities and differences in brain circuitry of different impulsivity subtypes

The brief summary of the brain circuitry involved in distinct impulsivity subtypes above suggests some level of specificity in brain areas underlying different constructs. For example, inferior frontal gyrus seems specifically vital for motor response inhibition. While an extensive network of brain areas is involved in impulsive decision-making, the activity of mesolimbic areas and insular cortex might be particularly vital for this impulsivity subtype. Nevertheless, there also seems to be some level of overlap between the circuits: the prefrontal regions and cingulate cortex may be common substrates across different types of impulsivity; however, future functional neuroimaging studies on reflection impulsivity are needed to confirm this.

Although this review focuses on healthy volunteers research, it is worth noting that bipolar disorder, which is associated with high levels of impulsivity and risk taking (American Psychiatric Association, 2013; Najt et al., 2007), is associated with altered functioning of prefrontal cortex, ventral striatum and amygdala (Mason, O'sullivan, Montaldi, Bentall, & El-Deredy, 2014; Phillips & Swartz, 2014), regions implicated in impulsive actions and decision-making.

1.7 Emotion and impulsivity in the brain

The relationship between emotions and impulsivity is supported by functional anatomical evidence. The key brain regions involved in emotion regulation (Figure 1.4), i.e. PFC, anterior cingulate cortex (ACC), amygdala, and basal ganglia (BG), also are important in impulsive and risky behaviours, as well as decision-making processes (Hinvest, Elliott, McKie, & Anderson, 2011; Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2004, 2002; Xie et al., 2011; Zeeb & Winstanley, 2011).

The role of the amygdala in emotional processing is well recognised. Evidence from both animal and human studies supports the critical role of the amygdala in feeling fear and fearful stimuli processing (LeDoux, 2000; Murphy et al., 2003; Phan et al., 2004, 2002). Moreover, some findings suggest that amygdala responds to emotionally salient stimuli regardless of valence (reviewed in Phan et al., 2002; Phan et al., 2004). Literature suggests that the amygdala plays a vital role also in impulsive behaviour; for instance, increased functional connectivity between the amygdala and other brain regions (thalamus, insula) in abstinent heroin addicts is associated with high impulsivity (Xie et al., 2011). Moreover, lesions of the amygdala in rats increase risky decisions in rat gambling tasks (Zeeb and Winstanley, 2011).

Various neuroimaging studies have demonstrated the importance of the fronto-basal-ganglia network in response inhibition, particularly successful stopping of the prepotent motor response on the SST (for example Aron 2007; Aron et al., 2007; Boehler et al., 2010; Nikolaou et al., 2013; Kim & Lee 2011). BG seem to also play a vital role in experiencing both happiness and disgust (Murphy et al., 2003; Phan et al., 2002). This seemingly contradictory activity of BG may be associated with the role of these structures in motor control and, thus, guiding the organism towards pleasant (happy) stimuli and away from unpleasant (disgusting) stimuli (Panksepp, 1998). Moreover, Sprengelmeyer et al., (1998) proposed a specific role for the basal ganglia in processing disgust, as the putamen activates during viewing facial expressions of disgust in healthy individuals. Furthermore, patients suffering from Huntington's disease (HD) and OCD, conditions characterised by neuropathology in the basal ganglia, show problems with recognising facial expressions, particularly disgust (Sprengelmeyer et al., 1997; Sprengelmeyer et al., 1996). Interestingly, both HD and OCD are associated with increased levels of

impulsivity and disinhibition (Boisseau et al., 2012; Kalkhoven, Sennef, Peeters, & van den Bos, 2014).

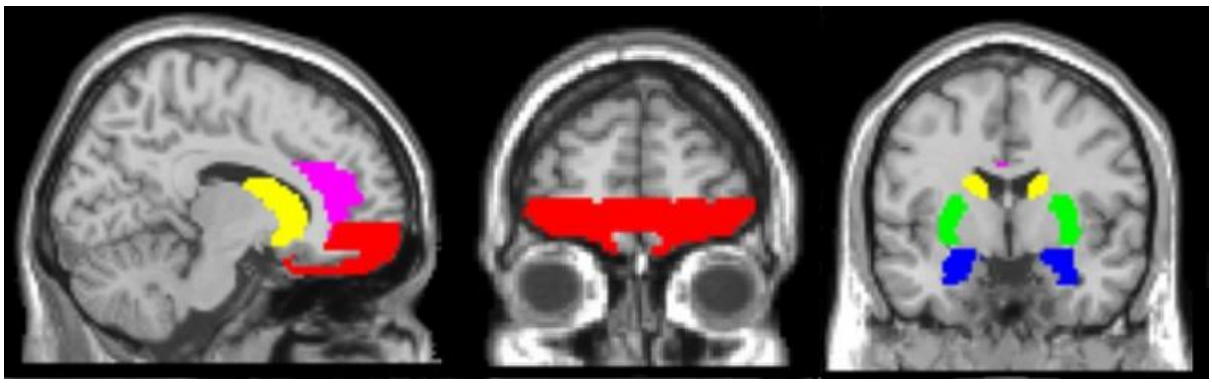

Figure 1.4 Brain regions implicated in both emotional experience and impulsive behaviour. Orbitofrontal cortex – red, amygdala – blue, anterior cingulate cortex – violet, caudate nucleus (basal ganglia) – yellow, putamen (basal ganglia) - green.

Another brain region which links impulsivity and emotions is the PFC. Fronto-cortical dysfunction, such as seen in substance abusers, is related to impaired inhibitory control (Jentsch & Taylor, 1999; Rogers et al., 1999). In particular, the ventromedial PFC, including subcallosal cingulate (BA 25) is implicated in a diminished inhibitory control reflected in impulsive behaviours in cocaine addicts (Volkow et al., 2010). Moreover, when making inter-temporal decisions, the activity of the prefrontal areas (PFC, ACC) correlated positively with participants' self-reported impulsivity and venturesomeness (Hinvest et al., 2011). Finally, lesions to the orbitofrontal sections of the PFC also result in decision-making deficits (Rogers et al., 1999). The PFC functioning is also strongly linked to emotional processing. Surgical lesions of the orbitofrontal cortex (OFC) and ACC are associated with deficits in emotion identification and changes in subjective emotional state (Hornak et al., 2003). While the lateral OFC seems to be more related to feelings of anger (Murphy et al., 2003), the medial PFC alongside with the ACC are often found to be activated across various emotions, without specificity towards any particular feeling, suggesting a general role in emotional processing (Phan et al., 2002; Phan et al., 2004). ACC, precisely the subcallosal cingulate cortex part, may be mainly involved in sadness and apathy (Murphy et al., 2003; Phan et al., 2002; Phan et al., 2004).

The evidence summarised here indicates that brain networks involved in emotional experience and impulsive behaviour largely overlap. Those shared neuronal correlates also suggest a mechanism via which affective states exert influence on impulse control.

1.8 Impulsivity and emotion

Having described the complex construct of impulsivity and the neural circuitry underlying both impulsive actions and emotional processing, in following sections, we now

discuss the research on the influence of mood states on different aspects of impulsive behaviour. Since in this review we are predominantly interested in the role of changeable states on impulsive behaviour and decision-making, we use terms ‘emotions’, ‘mood states’, and ‘affect’ interchangeably to refer to those transient emotional experiences.

1.8.1 Risk-taking

The influence of the affective state on risk-taking and decision-making has received substantial attention. For instance, in one study participants who received an unexpected gift before gambling (positive mood state induction) betted their study credits more conservatively than those in the control condition (no gift received), suggesting that people in a positive mood state may be risk aversive (Isen & Geva, 1987). Moreover, Isen & Patrick (1983) demonstrated that positive affect increases the tendency to take the real risk (a loss of course credits), but only in the situations where risk is relatively small. In contrast, in the hypothetical dilemma task, positive mood state increased risk-taking tendencies regardless of the risk level (Yuen & Lee, 2003). As an explanation for different results in the real risk versus hypothetical risk conditions Isen & Patrick (1983) suggested that individuals in a good mood state try to maintain their positive state and, therefore, do not engage in behaviours which carry a high risk of a loss (risk aversion). Accordingly, Nygren et al., (1996) observed that participants with induced positive mood state overestimated their probability of winning on a gambling task (optimism), but were less likely to gamble than controls when faced with the possibility of real losses (caution). These findings suggest that although people in a positive mood state view risky situations more optimistically, the decision-making process is more focused on avoiding potential losses, probably to maintain positive feelings (Isen & Geva, 1987; Isen & Patrick, 1983; Nygren et al., 1996).

Thus, it seems that while experiencing positive affect our tendency to take risk is decreased, at least in circumstances where high losses are probable. However, as decisions often need to be made in the stressful situations, it is important to understand how acute stress influences our choices. Increased negative affect and anxiety, related to anticipation of giving a public speech, was found to be associated with more risk-seeking tendencies in the task where participants are confronted with potential gains or losses (Pabst, Brand, & Wolf, 2013; Starcke, Wolf, Markowitsch, & Brand, 2008). However, the impact of stress on risky choice may depend on subjects’ gender (Lighthall, Mather, & Gorlick, 2009; van den Bos, Harteveld, & Stoop, 2009). For male participants, acute cortisol administration and a stress challenge were found to increase risky behaviours but decreased it among females (Lighthall et al., 2009; Putman, Antypa, Crysovergi, & van der Does, 2010). Together, these results indicate that acute

differences in stress reactivity (changes in stress hormone levels over time) affect decision-making process differently in men and women.

1.8.2 Temporal impulsivity

In everyday life, many decisions require finding a balance between the immediate pleasures and longstanding aims. Work by Tice et al., (2001) offers evidence that emotional distress can increase the tendency to seek immediate gratification due to a shift in priorities: from focusing on the long-term goals (e.g. slim figure and physical fitness) to short-term pleasures (self-indulgence).

Preschool children in whom a sad mood state was induced showed more delay discounting on the MT (i.e. chose the immediate reward significantly more often) than children in a happy or neutral mood state (Moore, Clyburn, & Underwood, 1976). These findings were also replicated in adult populations. Several studies showed that negative emotions, either naturally occurring (Koff & Lucas, 2011) or experimentally induced in participants by a presentation of aversive images (Augustine & Larsen, 2011), are related to higher discounting rates, suggesting that negative affect is associated with increased temporal impulsivity. Similarly, sadness, but not disgust, has been associated with more myopic financial decisions (Lerner, Li, & Weber, 2013). Also priming choices in the DD paradigm with fearful images resulted in much higher percentages of smaller-but-sooner choices compared with positive and neutral priming, again, indicating an increase in impulsive choice (Guan et al., 2015). Even imagining future events was shown to modulate delay discounting. Participants were more inclined to choose the delayed but larger rewards when they imagined positive future events than when they did not imagine anything; while participants were more inclined to choose the immediate but smaller rewards when they imagined negative future events than when they did not imagine events at all (Liu et al., 2013). Likewise, daily variabilities in self-reported mood state and arousal affect discounting rates: positive mood state and arousal were associated with a less impulsive choice on the DD task (Weafer, Baggott, & de Wit, 2013). Therefore, positive affect is associated with increased patience (lower levels of temporal impulsivity); whereas negative affect is related to near-sighted behaviours.

Considering such consistent findings from studies of the effects of mood state on delay discounting, it is quite surprising that research on the relationship between acute stress associated with decreased mood state and delay discounting reported mixed observations. Several studies failed to find any effects of stress on inter-temporal choice (Haushofer et al., 2013; Robinson, Bond, & Roiser, 2015). For example, in one study male subjects underwent a stress procedure in which participants are required to deliver a speech and perform mental arithmetic in front of an audience. Following the stress challenge procedure, participants were

asked to make intertemporal choices. Even though stress induction depleted mood state, no influence on discounting rate was found (Haushofer et al., 2013). Lempert et al., (2012), on the other hand, tested a large group of male participants who either experienced acute stress by anticipating giving a videotaped speech or underwent a control procedure. Following induction, subjects completed a DD task. Taking all subjects together, individuals who experienced an increase in salivary cortisol levels, regardless of the assigned condition, were more likely to select smaller, sooner rewards (a tendency towards impulsive choice). Yet, the relationship did not hold when only the stress induction group was considered. Instead, individual variation in the level of perceived stress was related to the performance in the task (Lempert et al., 2012). Similarly, in another study, following the same stress induction procedure, participants were divided into two groups depending on their cortisol secretion change in response to stress manipulation (Kimura et al., 2013). Stress manipulation was related to an increase in the tendency to discount future rewards but only in cortisol responders, indicating that temporal discounting can be affected by an acute increase in cortisol levels. It is worth noting, however, that high cortisol responders tended to have higher cortisol levels at baseline. Taken together this evidence suggests that individuals more sensitive to stress may be differentially affected in temporal discounting tasks than subjects with low reactivity to stress.

1.8.3 Motor impulsivity

The role of emotional states in impulsive choice received substantial attention, but little is known about the effects of mood state on impulsive actions. Some evidence suggests that negative emotions might be related to decreased impulse-control in everyday life, which is reflected in impulsive behaviours such as compulsive eating or procrastination (Tice et al., 2001). A large body of research consistently shows that emotionally loaded stimuli, particularly threatening ones, diminish response inhibition on the GNG and SST (De Houwer & Tibboel, 2010; Kalanthroff, Cohen, & Henik, 2013; Lindström & Bohlin, 2012; Pessoa, Padmala, Kenzer, & Bauer, 2013; Rebetez, Rochat, Billieux, Gay, & Van der Linden, 2015; Verbruggen & De Houwer, 2007; Wilson et al., 2016). In these studies, however, the mood state was not manipulated, but emotional images were presented while participants were performing the response inhibition task; therefore, the results may be explained via attentional capture. Incidental mood state changes may impact inhibitory control via a different mechanism. Research of the effects of mood state on motor impulsivity does not report consistent results. For instance, in one study no effects of daily variability in mood state were found on any of the motor impulsivity measures tested (SST, GNG, CPT) (Weafer et al., 2013). Likewise, sadness induction did not affect response inhibition on the GNG task (Chepenik, Cornew, & Farah, 2007; Smallwood, Fitzgerald, Miles, & Phillips, 2009). Similarly, a study performed on 30

female participants did not show any effects of stress on response inhibition in the go/stop task (Cackowski et al., 2014). Scholz et al. (2009), on the other hand, tested male participants on the GNG task and found the effect of stress on reaction time (slower responses following the stress manipulation), but no effect on the number of false alarms was observed. Schwabe et al. (2013) reported enhanced response inhibition in the SST following the stress induction, while Patterson et al. (2016) observed contradictory results.

Those opposing results might be explained by differences in methodology. In the study by Weafer et al. (2013), the affect was not manipulated; instead, daily variability in mood state was assessed. Possibly the changes in self-reported affect were not significant enough to have an impact on motor impulsivity in the laboratory setting. Cackowski et al. (2014) induced stress via simultaneous exposure of participants to various stressors, and used a go/stop procedure, a modification of CPT, in which participants not only respond to a target sequence of digits and ignore non-target sequences (waiting for the signal to occur), but also should refrain from responding if the colour of the target sequence changes (response inhibition; Dougherty et al., 2005). Schwabe et al. (2013) and Patterson et al. (2016) both used the SST, however, both studies used different mood state manipulation methods (socially evaluated cold pressor test and affective images presentation, respectively). Importantly, Schwabe et al. (2013) introduced a delay between stress-induction and behavioural testing so testing would take place during cortisol peak level after stressor occurrence, which might have an impact on the results. As discussed in the previous section subtypes of motor impulsivity are distinct from each other not only in the behavioural terms but also regarding underlying circuitry. Thus, mood state and stress might differentially affect subtypes of motor impulsivity.

In conclusion, data regarding the effects of incidental emotional states on motor impulsivity are limited and yield inconsistent results. To clarify the issue, future studies should compare the effects of mood state on different subtypes of motor impulsivity.

1.8.4 Reflection impulsivity

Little is known about the influence of mood state on reflection impulsivity. Messer (1970) found that children who experienced a success on a task showed a decrease in response time on the MFFT task in relation to children who experienced a failure on the task or did not undergo any manipulation. However, no differences between groups in task accuracy were found. These results indicate that good mood state associated with experiencing a success might affect efficiency in the decision-making process by decreasing deliberation time. Indeed, Isen and others found that subjects in whom positive mood state was induced, reached the decisions quicker than controls in the tasks which involved choosing one option from several alternatives (Isen & Means, 1983) or solving a clinical problem (Isen, Rosenzweig, & Young, 1991).

Participants in the positive mood state were less likely to review information they once analysed or considered unimportant for the task, which allowed them to be as accurate as the control group but reach the conclusion faster.

Taken together, these results indirectly suggest that positive and negative mood state might have opposite effects on reflection impulsivity by increasing and decreasing efficiency in the task, respectively. However, more research is needed to confirm this hypothesis directly using appropriate measures.

1.8.5 Inattention

Other studies revealed that participants in whom negative mood state was induced showed an increase in attention lapses (reflected in more incorrect responses in the sustained attention task) and reported a greater frequency of task-irrelevant thoughts (Smallwood et al., 2009). Therefore, it seems that while experiencing negative affect, individuals focus less on the task at hand and, thus, the time needed to complete the task increases, even if performance is not compromised.

Overall, results summarised here indicate that distinct subtypes of impulsivity are differentially influenced by emotional states. It seems though that some differences may be related to gender and individual differences in traits (e.g. stress sensitivity). These factors should be further investigated in future research. Moreover, most research looked at the role of affective states in decision-making; therefore, how exactly emotions shape other impulsivity subtypes (motor and reflection) yet need to be confirmed.

1.9 Physiological arousal and impulsivity

Emotional states are inextricably linked to physiological arousal. Certain emotional states, such as anxiety, anger or happiness, are related to an increased autonomic response, while others, such as sadness or contentment, with decreased response (Kreibig, 2010), but there is no unique physiological characteristic of discrete emotional state (Kreibig, 2010; Mauss & Robinson, 2009). Therefore, the level of physiological arousal may independently modulate impulsive behaviour. Indeed, early on it was argued that level of physiological arousal is related to impulsive behaviour. Several theories of personality claim that impulsivity is associated with under-arousal at rest and that impulsive individuals seek stimulation to obtain an optimal level of arousal (Barratt, 1985; H. J. Eysenck & Eysenck, 1985; Zuckerman, 1969). The optimal level of arousal is Hebb's concept whereby under-arousal produces an unpleasant state; therefore, people are motivated to maintain a certain level of arousal to feel comfortable (Hebb, 1955).

Data from both clinical and healthy populations seem to confirm the theories of under-arousal at rest in impulsive individuals. Under-arousal is at the core of Satterfield's & Dawson's

(1971) model of ADHD. According to this concept, symptoms of this disorder (i.e. inattention, hyperactivity, and impulsivity), arise from the under-aroused nervous system. Several studies found that highly impulsive but healthy individuals also show lower sympathetic arousal at rest (Fowles, 2000; Mathias & Stanford, 2003; Puttonen et al., 2008; Schmidt, Mussel, & Hewig, 2013). Similar results were also observed in children; those who showed high behavioural impulsivity had lower resting-state heart rate than less impulsive children (Bennett, Blissett, Carroll, & Ginty, 2014; Muñoz & Anastassiou-Hadjicharalambous, 2011). However, it is worth noting that some research focused on male participants only (Mathias & Stanford, 2003), or found that when male and female subjects were considered separately, the relationship between trait impulsivity and resting state arousal was significant for males only (Allen, Hogan, & Laird, 2009; Allen, Matthews, & Kenyon, 2000).

High impulsivity levels were also found to be related to blunted reactivity to stress. The relationship between poor response inhibition and diminished cardiac responses to acute psychological stress have been shown both in children (aged 7 – 11) and young adults (Bennett et al., 2014; Bibbey, Ginty, Brindle, Phillips, & Carroll, 2016). Blunted autonomic reactivity to stress has also been reported in impulsive adolescents and adults (Allen et al., 2009; Stankovic, Fairchild, Aitken, & Clark, 2014). However, Allen et al., (2009) reported that when male and female subjects were studied separately, the relationship was true for males only. Finally, Mathias & Stanford (2003) found that highly impulsive men showed greater initial autonomic reactivity under a challenge condition, but declining arousal following sustained stimulation. Since, low cardiovascular and catecholamine reactivity to stress has been related to many health conditions, for instance obesity, bulimia nervosa, gambling, drug abuse or ADHD (Carroll, Phillips, & Der, 2008; Ginty, Phillips, Higgs, Heaney, & Carroll, 2012; Koo-Loeb, Pedersen, & Girdler, 1998; Lovallo, Dickensheets, Myers, Thomas, & Nixon, 2000; Paris, Franco, Sodano, Frye, & Wulfert, 2010; Pesonen et al., 2011), these lowered physiological responses in impulsive subjects may reflect blunted autonomic reactivity to challenge which may be maladaptive and result in health problems.

Neuroimaging studies start to unveil the neural mechanisms linking arousal regulation and impulse control. Brown and colleges (Brown, Manuck, Flory, & Hariri, 2006), studied the relationship between individual differences in trait impulsivity and neural correlates of both behavioural arousal and inhibitory control, assessed via amygdala reactivity paradigm and GNG task. Impulsivity, as indexed by the BIS-11, was positively correlated with activity in the ventral amygdala, anterior cingulate cortex, and caudate, whereas it was negatively correlated with activity in the dorsal amygdala and ventral PFC. The activity of the amygdala and ACC is related to autonomic arousal (Critchley et al., 2003; Napadow et al., 2008), while the ventromedial PFC (vmPFC) plays a causal role in the regulation of physiological arousal (S. Zhang et al., 2014). The PFC is also known to be critical for successful response inhibition

(Horn, Dolan, Elliott, Deakin, & Woodruff, 2003). Therefore, these results suggest that impulsivity is affected by the functional interplay between the arousal and inhibitory control systems (Brown et al., 2006). Moreover, a recent study (S. Zhang et al., 2015) showed a positive association between trait impulsivity (measured with BIS-11) and skin conductance response to stop trials in the SST. Furthermore, high trait impulsivity was associated with decreased vmPFC regulation of physiological arousal in female but not male participants, suggesting altered arousal regulation in impulsive females. These gender differences may reflect the fact that some other dimension of trait impulsivity, which is not captured with the BIS, is related to arousal regulation in men (S. Zhang et al., 2015).

Some evidence also suggests that regulation of the state arousal may influence impulsive behaviour. Findings by Smith et al., (1991), for example, indicate that trait as well as the state of physiological arousal, may differently affect high and low impulsive individuals. While highly impulsive individuals showed a large increase in systolic blood pressure following caffeine administration, low impulsive subjects exhibited a drop in systolic blood pressure. The same study also found that impulsive individuals performed worse than low-impulsive subjects in the sustained attention task in the control (baseline) condition, but they obtained a greater benefit from caffeine than non-impulsive subjects; although their performance remained lower than less-impulsive individuals. As inattention is related to impulsive behaviours (de Wit, 2009), these findings suggest that manipulation of the physiological state may influence state impulsivity, especially in highly impulsive subjects. This is supported by clinical findings in ADHD patients, whereby treatment with stimulant drugs, which are known to increase arousal, leads to decreases in impulsive behaviour (Swanson, Baler, & Volkow, 2011). Similar observations were made in healthy populations. Schmidt et al., (2013) found that the lower the participants' physiological arousal at rest, reflected in decreased heart rate, the faster the responses and the riskier the behaviour in a gambling game, indicating diminished impulse control. Participants with low resting heart rate also perceived the risk options in the gambling task as less arousing and less risky compared to participants with higher resting heart rate. However, subjects tended to behave less risky in the gamble following physical exercise, compared to a resting condition.

Taken together, these findings provide support for the under-arousal theory of impulsivity. Moreover, summarised results indicate that increased state arousal may affect impulse control (decreased in impulsivity) offering support for the optimal level of arousal hypothesis (Schmidt et al., 2013).

1.10 Concluding remarks

The term ‘impulsivity’ refers to both a stable personality trait and a range of behaviours that are susceptible to modulation. Trait impulsivity is typically assessed using self-report questionnaires, while behavioural impulsivity is measured using laboratory tasks and paradigms. Both approaches view impulsivity as a complex construct consisting of several subtypes. Within the behavioural scope, three major subtypes can be differentiated, according to the stage at which they are expressed in the control of action (Caswell et al., 2015; Evenden, 1999a): reflection impulsivity occurs at the action preparation stage, motor impulsivity at the action execution stage, and temporal impulsivity at the action outcome stage. Additionally, decision-making under conditions of risk or uncertainty is also encompassed within conceptualisations of impulsivity, sometimes grouped with temporal impulsivity in a single construct of impulsive-choice (Fineberg et al., 2010, 2014; Winstanley et al., 2010).

Impulsivity is a familiar part of everyday life, yet it is also of central importance to many neuropsychiatric conditions, including addictions, personality disorders or attention deficit hyperactivity disorder (ADHD) (American Psychiatric Association, 2013). Recognition of the broad consequences of impulsive behaviour to society and the health of individuals has motivated a growing interest in impulsivity research, crucially directed at determining factors that might modulate behavioural impulsivity.

In this review, we discuss one potential regulator of impulsive behaviour: the affective state. We make the case that mood state exerts differential effects on impulsivity, depending on the subtype in question (summarised in Figure 1.5). The relationship between mood state and impulsive choice has received particular attention in the literature. People in a good mood state hold a more optimistic outlook on risky situations, but at the behavioural level show risk-avoidance, probably as a protective mechanism against losing positive feelings. Moreover, positive emotions increase our ability to wait for gratification, making us more patient. This role of mood state in behavioural inhibition remains ambiguous and, similarly, there is little research on the role of emotions on reflection impulsivity. However, available data suggest that negative affect is associated with increases in reflection impulsivity via decreases in the efficiency of task performance. Importantly, initial research on the neuronal circuits underlying emotional states and impulsive behaviours has indicated an overlap supporting further the relationship between emotions and impulsivity.

A further modulator of impulsive behaviour is physiological arousal. Indeed, several theories of personality argue that impulsivity is associated with under-arousal at rest, a greater increase in arousal following stimulation, and that impulsive individuals seek stimulation to obtain an optimal level of arousal (E. S. Barratt, 1985; H. J. Eysenck & Eysenck, 1985; Zuckerman, 1969). Thus, based on research summarised in this review, we propose a model to

account for how impulsive actions and decisions are affected by our current affective and physiological state. Moreover, we argue that internal states impact on behaviour through dependence on a particular set of factors: (1) the subtype of impulsivity in question, (2) individual differences (gender, trait anxiety, trait stress sensitivity), (3) the baseline (resting state) level of arousal.

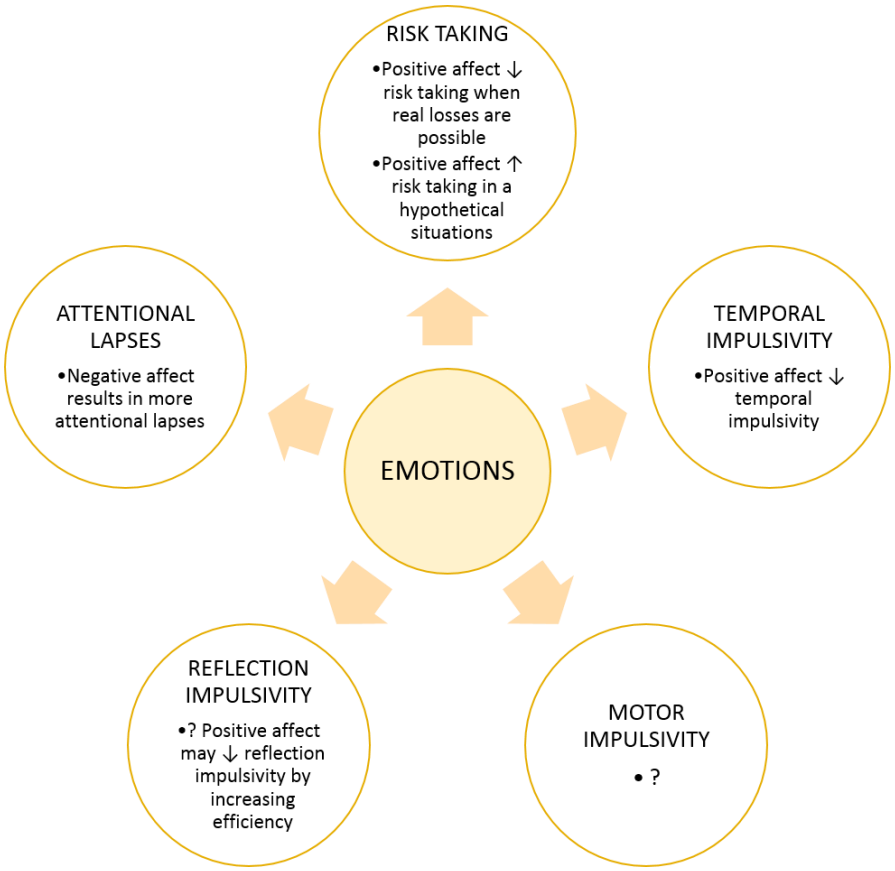

Figure 1.5 The effects of emotions on different subtypes of impulsivity.

Advances in understanding such modulators can potentially inform the development of fresh therapeutic approaches (reducing impulsivity levels) for impulsive people. To achieve translational impact, future studies should (1) clarify how different emotional states modulate distinct subtypes of impulsivity at both behavioural and neural levels; and (2) establish the relationship between the level of physiological arousal and impulsivity, perceived both as a stable trait and variable state. For example, it is important to characterise first, whether acute changes in physiological arousal modulate impulsive behaviour and second, whether highly impulsive individuals are more affected by changes in the bodily state than less impulsive individuals. Finally, (3) deeper insights will be gained from research defining the neuronal mechanisms underlying the interaction between affective and physiological states with impulsive action and decision-making.

1.11 Aims

From the evidence presented thus far, it is evident that there is a need for research examining the role of emotional and physiological states in modulating distinct impulsivity dimensions. In this way, we can identify which subsets of impulsivity are more prone to be influenced by bodily states. This information can further inform researchers and clinicians in developing better coping strategies for impulsive individuals and help impulse-control-related problems prevention efforts. Therefore, investigations in this thesis attempt to better characterise distinct impulsivity dimensions, focusing on their modulators. Specific aims of the current thesis are threefold:

1. To clarify the role emotions play in different dimensions of impulsive behaviours also considering the role of individual differences in this relationship.
2. To examine neural correlates underlying the impact of emotions on distinct subtypes of impulsivity.
3. To establish the relationship between impulsivity, both behavioural and trait, and physiological arousal.

To address these objectives, we conducted a set of experiments using a variety of methods including behavioural testing, physiological recordings, psychopharmacology and neuroimaging. This variety of methods employed allowed for a comprehensive understanding of the issues in question. To fulfil the first aim, we conducted two studies. Study 1 investigated how mood-induction affects impulsive performance in standard measures of impulsivity, including motor, temporal and reflection impulsivities. Study 2 built on findings from study 1, examining whether naturally occurring mood states and personality traits predict impulsive decisions. To address the second aim, study 3 used functional magnetic resonance imaging (fMRI) techniques, to identify neural substrates underpinning the emotional influences on the motor and temporal impulsivities. Specifically, the role of task-independent emotional context on tasks performance was investigated also considering individual differences in trait impulsivity. Finally, the subsequent two studies addressed the third aim. In study 4 we investigated the influence of increased physiological arousal, via pharmacological manipulation, on dimensions of impulsivity. In study 5 we further explored the relationship between resting-level of arousal and trait impulsivity as well as the link between sensitivity to one's bodily state (interoception) and trait impulsivity. Through these investigations this thesis attempts to characterise distinct impulsivity dimensions better, focusing on their modulators.

In the final chapter, Chapter 6, I summarise the main outcomes of this thesis and place our findings in a broader context. Chapter 6 will also include a consideration of the limitations; and future directions for studying the modulatory effects of internal bodily states on impulsivity.

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1.12 References

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CHAPTER 2.

STUDY 1.
KEEP CALM AND MANAGE YOUR IMPULSIVITY: MOOD AS A MODULATOR OF IMPULSIVE BEHAVIOUR

This article has been submitted to PloS One:

Herman, A. M., & Duka, T. Keep calm and manage impulsivity: Mood as a modulator of impulsive behaviour. *Plos One* (submitted).

Contribution

I contributed to the study design and the interpretation of the results. I collected and analysed the data as well as prepared the initial manuscript.

2.1 Abstract

This study investigated how different mood states affect distinct subtypes of impulsivity: motor impulsivity [measured with the Stop Signal (SST) and the 5-Choice Serial Reaction Time Task (5-CSRTT)], reflection impulsivity [assessed with the Information Sampling Task (IST)], and temporal impulsivity (the Delay Discounting Questionnaire). Eighty healthy volunteers completed two experimental sessions. During session 1, which served as a baseline measure, participants underwent a neutral mood induction procedure. In Session 2, they were randomly allocated to one of the mood-induction groups (Neutral, Positive, Sad, and Anxiety). Mood state ratings included bipolar visual analogue scales on mood (positive/negative), tension/relaxation and arousal (tired/active). No group effect was found on any of the impulsivity measures. Correlational analyses between mood changes (following the mood manipulation procedures) and behaviour in the tasks revealed that increased relaxation was related to increased information sampling in the IST (decreased reflection impulsivity). In addition, the more active subjects reported to be, the more likely they were to choose a delayed reward over the immediate one (decreased temporal impulsivity). These results indicate that subjective changes in mood state are associated with behavioural impulsivity levels. Importantly, distinct facets of impulsivity (reflection, motor and temporal) are differently affected by changes in mood state.

Keywords: Stop Signal Task, Delay Discounting, Information Sampling Task, 5-Choice Serial Reaction Time Task, Emotions

2.2 Introduction

Impulsivity is often described as a tendency to act rapidly without taking into account consequences of one's actions (Dalley et al., 2011). It is generally considered to be maladaptive as impulsivity is associated with risky sexual activities (Winters, Botzet, Fahnhorst, Baumel, & Lee, 2009), gambling (Hodgins & Holub, 2015; Lai, Ip, & Lee, 2011; Lawrence, Luty, Bogdan, Sahakian, & Clark, 2009), smoking (Mitchell, 1999) and binge drinking (Bø, Billieux, & Landrø, 2016; Sanchez-Roige et al., 2014). Furthermore, deficits in impulse control, both behavioural and trait characteristic, are related to several disorders such as attention deficit and hyperactivity disorder (ADHD), manic episodes of bipolar disorder, borderline personality disorder, Parkinson's disease, schizophrenia, eating disorders or substance abuse (American Psychiatric Association, 2013).

Given the importance of impulsivity both in everyday life and in clinical practice, it is vital to understand the modulators of impulsive behaviour. Numerous studies show that negative emotions exert a great impact not only on our actions but also on decision-making processes. Tice and colleagues (Tice et al., 2001) demonstrated that experiencing negative emotions leads to limited self-control, which in turn results in impulsive behaviours such as compulsive eating, reduced delayed gratification or procrastination. Experience of stress or anxiety has also been shown to lead to maladaptive behaviours including smoking, comfort-eating or drinking alcohol (Abrantes et al., 2008; Bekker et al., 2004; Cooper et al., 1995; Swendsen et al., 2000). Such activities are believed to serve as a coping mechanism. Episodes of binge eating and vomiting in patients with bulimia nervosa are related to prior states of increased self-reported negative mood, stress or feelings of anger (Engel et al., 2007; Smyth et al., 2007) and engagement in purging behaviours leads to decrease in negative emotions (Smyth et al., 2007).

On the other hand, the beneficial impact of positive affect in everyday life has been reported in several studies. For instance, people in a good mood state perform better at creative problem-solving tasks (Subramaniam, Kounios, Parrish, & Jung-Beeman, 2009) and show increased cognitive flexibility (Nadler, Rabi, & Minda, 2010). However, high levels of positive affect may also be associated with undertaking risky and impulsive behaviours such as heavy-drinking as part of celebrations (Del Boca, Darkes, Greenbaum, & Goldman, 2004; Peacock, Cash, Bruno, & Ferguson, 2015) or gambling (Cyders & Smith, 2008a).

The evidence summarised above provides support for the link between emotional states and impulsivity, as well as an interaction between the two in forming our actions and motivations contributing to addictive behaviours. However, little is known about how exactly emotional states impact the different facets of behavioural impulsivity. Therefore, the current experiment aimed to examine how incidental changes in mood state influence the distinct impulsivity subtypes using common laboratory tests.

Due to the multifaceted nature of impulsivity (Caswell et al., 2015; Evenden, 1999b; Sharma, Markon, & Clark, 2014; Whiteside & Lynam, 2001), several independent measures were used to capture a wider range of impulsivity dimensions: impulsive tendencies (personality traits), reflection, temporal, motor 'stopping' and 'waiting' impulsivity, and inattention. We hypothesised that negative emotional state might reduce inhibitory control, as worry and rumination are costly in terms of cognitive resources (Hirsch & Mathews, 2012). Since negative affect has been related to an increase in task-unrelated thoughts (Smallwood et al., 2009), we also hypothesised that sadness and anxiety might be related to increased impulsivity on the tasks which require attention. On the other hand, positive affect might decrease reflection impulsivity by improving efficiency (Isen & Means, 1983; Isen et al., 1991). Positive affect could also improve self-regulation (Tice, Baumeister, Shmueli, & Muraven, 2007) and, therefore, make individuals more likely to wait for their incentive (decrease temporal impulsivity).

2.3 Methods

2.3.1 Participants

Eighty-three volunteers (50 females) were recruited from the University of Sussex community, providing consent to participate in the study. Sample size was motivated by previous studies using similar methodologies (Smallwood et al., 2009; Tice et al., 2007, 2001; Yuen & Lee, 2003). Participants were informed that the study investigated the effects of experience on cognitive tasks performance. The inclusion criteria were following: age 18-35 years old, fluency in English, no current diagnosis of any mental or neurological disorders, and no current pharmacological treatment (except birth control). During the experiment participants' olfactory abilities were tested; therefore, additional exclusion criteria was anosmia, hay fever or cold. Data from this part of the procedure will be reported elsewhere. Participants were instructed not to consume any caffeine-containing products or any other substances which may affect their activity level on the days of testing. The study was approved by the local Ethics Committee. All participants were compensated for their time.

2.3.2 Materials

Nuffield Hospitals Medical History Questionnaire assessed demographic details, past and present health status (to confirm meeting study inclusion criteria), use of medications and recreational drugs, and an estimate of a number of cigarettes smoked per day.

2.3.3 Subjective ratings:

KUSTA Mood scale (Wendt, Binz, & Miuller, 1985) was used to asses mood state. To capture the crucial changes in affective state, only Kusta bipolar scales of Mood (a measure of valence, positive vs negative), Activity (a self-report measure of arousal) and Tension/Relaxation (a measure of stress, Ilona Papousek et al., 2010; Ilona Papousek, Schulter, & Premsberger, 2002; Iona Papousek & Schulter, 2001) were employed.

Alcohol Use Questionnaire (AUQ, Mehrabian & Russell, 1978): AUQ gives a measure of total units of alcohol consumed per week, binge score and alcohol use score.

Barratt Impulsiveness Scale (BIS-11; Patton, Stanford, & Barratt, 1995) consists of 30 items which assess a tendency for impulsive actions in everyday life. BIS is organised into three subscales: attentional, motor and non-planning impulsivity.

UPPS Impulsivity Scale (Whiteside & Lynam, 2001) consists of four subscales: Urgency (a tendency to act impulsively while experiencing strong negative emotions), Premeditation, Perseverance and Sensation Seeking.

Both scales are commonly used measures of trait impulsivity and were introduced to assess distinct aspects of impulsivity characteristics.

2.3.4 Tasks

The 5-Choice Serial Reaction Time Task (5-CSRTT; Sanchez-Roige et al., 2014) assesses motor impulsivity, particularly the ability to wait for a signal to respond (i.e. ‘waiting’ impulsivity). Participants were required to hold their index finger of the dominant hand on the "home button" at the bottom of the iPad (iOS 6 operating system; Apple Inc) screen until one of five blue circles moving on the screen in a "circular" fashion illuminated briefly (0.5s). Subjects respond to it by tapping the appropriate circle as fast as possible and return to the home button. Premature responses, occurring before stimulus onset, were considered a measure of poor inhibitory control and punished by a 5s time-out period. Following practice trials in which the stimuli were presented at fixed inter-trial intervals of 5s, in experimental trials targets were presented at variable inter-trial intervals (vITI) lasting for 2, 5, 10, or 15 seconds. The task lasted until 50 correct trials were completed or 10 minutes had elapsed, whichever came first. The variables of interest of this task were the number of premature responses made (No Premature) - high scores indicate high impulsivity and number of omissions (No Omissions) - high values indicate inattention.

The Monetary Choice Questionnaire (MCQ; Kirby, Petry, & Bickel, 1999) is a measure of temporal impulsivity. Volunteers are presented with 27 hypothetical choices between small, immediate rewards (SIR) and larger delayed rewards (LDR), for example, “would you prefer £54 today or £55 in 117 days?”. For each participant the discounting parameter (k) is calculated

using the formula: k = ((LDR-SIR)-1)/delay. High k values indicate high impulsivity (values were log transformed to improve distribution).

The Stop Signal Task (SST, Logan, 1994) assessed an ability to inhibit a pre-potent motor response. Participants respond with button presses to the direction of a green arrow (Go signal) displayed on a computer screen but are required to withhold this response whenever the arrow changes colour to red (a Stop Signal, occurring on 25% of trials). The difficulty of inhibition of pre-potent responses is reflected in heightened Stop Signal Reaction Time (SSRT; high scores indicate high impulsivity).

The Information Sampling Task (IST; Clark, Robbins, Ersche, & Sahakian, 2006) is a measure of reflection impulsivity. On each trial, a matrix of 5x5 grey squares is presented on a computer screen. Participants select a square by clicking with the mouse over the square, to reveal one of two colours until they are confident enough to decide which of the two colours is most frequent in the array. There are two conditions of the task:

(i) Fixed win condition (FW): participants win 100 points if they make the right decision (regardless of how many boxes they have opened); otherwise, they lose 100 points. Participants complete ten experimental trials.

(ii) IST reward conflict (RC): for every box opened, participants lose 10 points from a bank of 250. If a participant chooses correctly they win the remaining points from the bank; otherwise, they lose 100 points. Participants complete ten experimental trials.

The dependent variable for each condition (FW and RC) is the mean number of boxes opened (high values indicate low impulsivity).

2.3.5 Mood induction

Details on mood induction procedures can be found in Appendix 1. Briefly, the neutral, positive and sad mood was induced by presentation of emotional images (neutral, positive, or sad respectively) together with congruent emotional music to strengthen the effect. Participants in the anxiety group were simultaneously exposed to different types of stressors: emotional (pictures depicting anxiety-provoking images, e.g. snakes), acoustic (white noise), and cognitive (mental calculations under the pressure of time).

2.3.6 Procedure

Participants attended two experimental sessions 3-9 days apart (M = 6.09, SD = 1.80). Sessions took place between 9 am and 6 pm.

Session 1:

Participants were informed about the procedures of the experiment and before signing the consent to participate in the study, they were shown an example of a negatively valenced image used in the study to ensure they would not find it too distressing.

The aim of the first session was to ensure the mood-induction groups were well-matched and did not differ on any of the trait, mood or behavioural measures. Therefore, all participants completed the trait and AUQ questionnaires and underwent a neutral mood induction procedure (viewing neutral images while listening to music), to assess performance on the task under neutral conditions. Immediately before and after the mood induction, participants completed the VAS scales.

Next, participants completed a battery of cognitive tasks (SST, MCQ, 5-CSRTT and IST). Tasks were completed in a randomised order with short pauses in-between. During the breaks, a shortened mood induction procedure (1 minute only) was introduced to maintain the stable mood throughout the session.

Session 2:

Participants were semi-randomly (to ensure equal proportions of males and females in each group) assigned to one of the four conditions: neutral (control), positive, sad, or anxious mood. Their mood was assessed with VAS before and immediately after the procedure. As in the first session, participants completed the five cognitive tasks in a randomised order with 1 minute-mood induction periods in-between.

At the end, participants were debriefed and signed a form confirming their willingness for the data being used in the analyses.

2.3.7 Statistical analyses

To test whether the four groups were well-matched, baseline group demographics (age, smoking habit, alcohol use, and trait impulsivity measurements) as well as performance on the tasks during session 1, were compared using one-way ANOVA in SPSS, v22. Furthermore, to asses that groups did not differ in the way their mood ratings changed following the neutral mood manipulation at Session 1, a mixed ANOVA with time (pre- and post-manipulation) applied as a within-subject factor, and experimental condition (Control, Anxiety, Sad, Positive) as a between-subject factor was performed. Same mixed ANOVA was performed for session 2 to assess whether mood induction was successful. To examine the influence of mood state on impulsive behaviour during session 2 a series of ANOVAs were performed. As the perception of mood induction may differ across individuals, in addition, correlational analyses were

performed between changes in mood state ratings (post-induction score – pre-induction score) and performance indices in the tasks, at session 2.

2.4 Results

2.4.1 Exclusions

Two participants (one male) did not return for the second session. Moreover, one male volunteer was very inattentive throughout the first session of the study and failed to comply with the experimenter's instructions on three of the tasks; therefore, he was compensated for attending the first session and not invited to return for the second session and was excluded from the analyses completely. Thus, the final number of participants who completed both sessions of the study is 80 (49 females).

Nine participants (3 from the Control group, 3 Sad, 3 Anxiety) were excluded from the SST analyses for the first session and 9 (4 Control, 2 Positive, 2 Sad, 1 Anxiety) for the second session as they failed to follow task instructions (i.e. they were slowing down responses waiting for the stop signal to occur, which resulted in go accuracy below 90% and stop correct rate above 60%).

One participant (Anxiety group) was excluded from the IST FW analyses and another two individuals (Anxiety group) from the Reward Conflict condition for session 1 only, as they misunderstood the instructions (guessing rather than sampling information before making a choice or ignored changed instructions for the reward conflict condition). One participant was excluded from the IST FW condition and further three participants (Positive group) were excluded from the analyses of session 2, Reward conflict condition, due to continuous guessing on the task, rather than sampling information.

Two participants (1 Anxiety, 1 Control) were excluded from the MCQ analyses for the first session and 1 (Control) for the second session, because of highly inconsistent responses given (less than 75% consistency).

Due to technical problems, the 5-CSRTT was completed only by 56 participants during session 1 and 57 during session 2.

2.4.2 Session 1 (Control session)

Groups were well matched for their demographics, personality trait measurements and performance on the tasks (see Table 2.1 for details).

Repeated measures ANOVA with time (baseline vs post-mood induction 1) as a within-subject factor and group (Control, Anxiety, Sad, Positive) as a between-subject factor showed a

main effect of time, $F(1, 76) = 4{,}77$, $p = .032$, $\eta_p^2 = 0.059$, on activity self-rating score, indicating a decrease in activity following the induction. No other main effects were observed (time effect: $F(3, 76) \leq 2.63$, $p > .05$, $\eta_p^2 \leq .10$, group effect : $F(3, 76) \leq 0.81$, $p > .05$, $\eta_p^2 \leq .03$). Data related to mood state ratings are presented in Table 2.2 and Appendix 2. There were also no group differences regarding performance on any of the task measurements (p's > 0.5; see Table 2.3), suggesting that groups performed equally well on the tasks.

Table 2.1 Sample demographics and trait measurements for each of the mood manipulation groups.

Variable	**All**		**Control**		**Anxiety**		**Sad**		**Positive**		**One-way ANOVA**		
N (Female)	80(49)		20(12)		20(13)		21(13)		19(11)				
No of Smokers	13		2		3		4		4		1.04[1]	0.792[2]	
	Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**F**	**p**	**η^2**
Age	22.15	3.69	22.05	3.75	22.75	4.32	22.57	4.09	21.16	2.52	0.71	0.55	0.027
Alcohol Units per week	12.52	12.08	14.41	16.72	9.75	9.06	10.5	11.03	15.66	10.15	1.13	0.34	0.043
No of Cigarettes a day	0.60	1.68	0.45	1.61	0.45	1.28	0.86	2.35	0.63	1.42	0.35	0.79	0.014
BIS Total	64.07	9.00	63.75	8.61	63.75	11.22	65.00	9.29	63.58	7.35	0.10	0.96	0.004
Premeditation	21.34	4.63	21.3	4.26	20.3	4.45	21.91	4.21	21.53	5.78	0.43	0.73	0.017
Negative Urgency	28.73	5.61	27.45	4.82	28.15	6.04	30.38	6.23	28.68	5.39	1.01	0.39	0.038
Sensation Seeking	36.23	6.79	36.35	7.69	37.50	6.08	34.71	5.54	36.47	8.20	0.57	0.64	0.022
Perseverance	19.96	4.91	19.25	4.52	19.95	5.17	21.10	5.71	19.00	4.00	0.74	0.53	0.028

[1]X^2 test, [2]*p*-value

Table 2.2 Mood state ratings for each group for Session 1 and 2 for each of the mood manipulation groups.

Ratings		**Control**		**Anxiety**		**Sad**		**Positive**	
Session 1		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mood	Baseline	72.10	18.84	63.50	20.80	66.29	17.20	62.95	25.92
	Post-induction	66.25	19.22	60.20	19.89	63.76	18.71	62.89	23.14
Activity*	Baseline	60.70	26.09	56.50	24.54	59.43	21.94	51.16	21.25
	Post-induction	54.30	22.21	49.70	22.89	54.90	23.19	52.89	23.11
Relaxation	Baseline	75.45	19.36	67.50	22.15	73.33	18.34	68.84	25.92
	Post-induction	68.85	19.82	62.15	23.60	72.00	15.48	69.53	24.73
Session 2									
Mood[&]	Post-induction	74.85	17.19	**73.60**	18.64	**69.29**	15.30	**69.21**	22.30
	Baseline	70.95	16.75	**46.00**	24.62	**43.81**	14.61	**77.58**	13.16
Activity	Post-induction	69.55	21.02	67.05	21.66	59.81	20.11	56.74	22.20
	Baseline	64.60	23.39	55.15	26.45	51.81	20.02	62.05	21.73
Relaxation[&]	Post-induction	76.30	19.70	**67.33**	22.68	**62.14**	21.93	**64.37**	19.73
	Baseline	71.90	20.12	**40.35**	24.81	**49.71**	16.76	**72.37**	12.13

* a main time effect; [&]a group by time interaction indicating differential manipulation changes (relevant means in **bold**)

Table 2.3 Tasks performance during session 1 and session 2 for each of the mood manipulation groups.

Variables	**Control**			**Anxiety**			**Sad**			**Positive**			**One-way ANOVA**			
	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	F		p	η^2
Session 1																
SSRT	17	246.01	34.17	17	244.6	30.79	18	249.68	33.86	19	262.89	21.17	1.40		0.252	0.06
5-CSRRT No Omissions	15	1.60	1.92	10	0.60	0.84	17	1.00	1.54	14	0.79	1.42	1.07		0.369	0.06
5-CSRRT No Premature	15	3.40	2.90	10	2.50	2.42	17	3.00	2.60	14	1.71	0.91	1.37		0.261	0.07
IST FW No boxes opened	20	15.21	6.22	19	14.32	5.44	21	14.89	6.91	19	14.89	6.91	0.37		0.775	0.02
IST RC No boxes opened	20	9.54	3.24	18	9.73	4.19	21	9.72	4.84	19	9.72	4.84	0.17		0.915	0.01
Mean k-value (log transformed)	19	-4.83	1.55	19	-5.33	1.63	21	-5.00	1.53	19	-4.98	1.16	0.38		0.767	0.02
Session 2																
SSRT	16	246.25	29.19	19	248.78	39.28	19	242.76	26.93	17	240.15	46.71	0.16	[1]	0.920	0.01
5-CSRRT No Omissions	16	1.69	2.41	14	0.50	0.76	17	2.18	2.72	10	0.50	0.71	**2.96**	[1]	**0.049**	**0.12**
5-CSRRT No Premature	16	2.06	2.64	14	1.64	2.65	17	2.29	2.59	10	1.30	1.95	0.40		0.756	0.02
IST FW No boxes opened	20	12.70	6.40	20	10.70	3.35	21	13.42	6.47	18	12.46	5.97	1.33	[1]	0.279	0.03
IST RC No boxes opened	20	8.36	3.34	20	8.01	2.45	21	8.77	4.13	16	10.09	3.39	1.24		0.300	0.03
Mean k-value (log transformed)	19	-4.62	1.04	20	-4.92	1.29	21	-4.81	1.61	19	-5.11	1.64	0.40		0.754	0.02

[1]Welsh statistics

2.4.3 Session 2 (Mood Manipulation)

Mood

Repeated-measures ANOVA with time (baseline vs post 1) as a within-subject factor and mood induction group as a between-subject factor was conducted to assess the successfulness of mood manipulation (see Table 2.2 for descriptive statistics). The Anxiety and Sad groups showed significant decrease in mood ratings (increase in negative mood) following the induction, the Positive group showed an increase in mood ratings (increase in positive mood), while the Control group presented no significant change (time vs group interaction: $F(3, 76) = 15.26$, $p < .001$, $\eta_p^2 = .38$). Regarding the tension-relaxation scale, Anxiety and Sad groups showed a decrease in relaxation, Positive group showed an increase in relaxation, while the Control group did not change (interaction: $F(3, 76) = 9.09$, $p < .001$, $\eta_p^2 = .26$). There was also a marginal interaction effect in activity ratings ($F(3, 76) = 2.71$, $p = .051$, $\eta_p^2 = .097$): the Positive group showed an increase in activity, while the remaining groups did not present any significant changes. The brief mood inductions in-between the tasks were also successful at maintaining the desirable mood states throughout the duration of the session (see Appendix 2 for details).

Task performance

The assumption of homogeneity of variances (Levene's test p's $< .05$) was violated for several measures: SSRT, NoOmiss and IST FW; therefore, Welsh test was computed to compare the performance between groups on these measures. A main group effect was found only for the number of omissions in the 5-CSRTT, Welsh ($F(3, 28{,}51) = 2.96$, $p = .049$), reflecting a higher number of omissions in the Sad group (see Table 2.3). However, Games-Howell post-hoc test showed no significant differences between any of the groups' pairs (p's $> .05$). No other group effects were found.

Correlations

Subsequent correlational analyses were performed to explore the relationship between mood changes and performance on the tasks (see Table 2.4). There was a negative correlation between the tension-relaxation score change and SSRT, indicating that the more tense participants were, the more impulsively they behaved in the task. There were positive correlations between the tension-relaxation score change and the performance on the IST in both conditions, indicating that the more relaxed participants were, the more information they sampled (decreased reflection impulsivity).

Table 2.4 Correlation matrix between performance on the tasks during session 2 and changes in mood state ratings (Post-induction - Pre-induction). Correlations which survived the Bonferroni correction for multiple comparison ($p < .004$) are depicted in **bold**.

Variable		Mood	Activity	Relaxation
SST: SSRT	Pearson's r	-.050	-.140	-.270
	p-value	.664	.233	.023
	Upper 95% CI	.180	.090	-.040
	Lower 95% CI	-.280	-.370	-.470
5-CSRTT: No Omissions	Spearman's rho	.150	.030	-.050
	p-value	.270	.822	.711
	Upper 95% CI	.390	.290	.210
	Lower 95% CI	-.120	-.230	-.310
5-CSRTT: No Premature Responses	Spearman's rho	-.250	-.270	-.060
	p-value	.061	.047	.685
	Upper 95% CI	.010	-.040	.210
	Lower 95% CI	-.480	-.490	-.310
IST: FW No boxes	Pearson's r	.010	-.070	.230
	p-value	.968	.564	.039
	Upper 95% CI	.220	.160	.430
	Lower 95% CI	-.220	-.280	.010
IST: RC No boxes	Pearson's r	.100	-.140	**.400**
	p-value	.399	.217	**< .001**
	Upper 95% CI	.310	.080	.570
	Lower 95% CI	-.130	-.350	.190
MCQ: log k	Pearson's r	-.060	**-.330**	-.090
	p-value	.574	**.003**	.452
	Upper 95% CI	.160	-.120	.140
	Lower 95% CI	-.280	-.510	-.300

The change in the activity score was negatively correlated with the discounting rate (log k), suggesting that an increase in activity was related to a decrease in temporal impulsivity. Change in the activity score was also negatively correlated with the number of premature responses, indicating that increased activity was related to lower level of premature responses; therefore, decreased 'waiting' impulsivity.

With correction for multiple comparisons set at $p < .004$ only the relationships between activity score change and discounting rate, and the relationship between tension-relaxation score change and the performance in RC on the IST survived (see Figure 2.1).

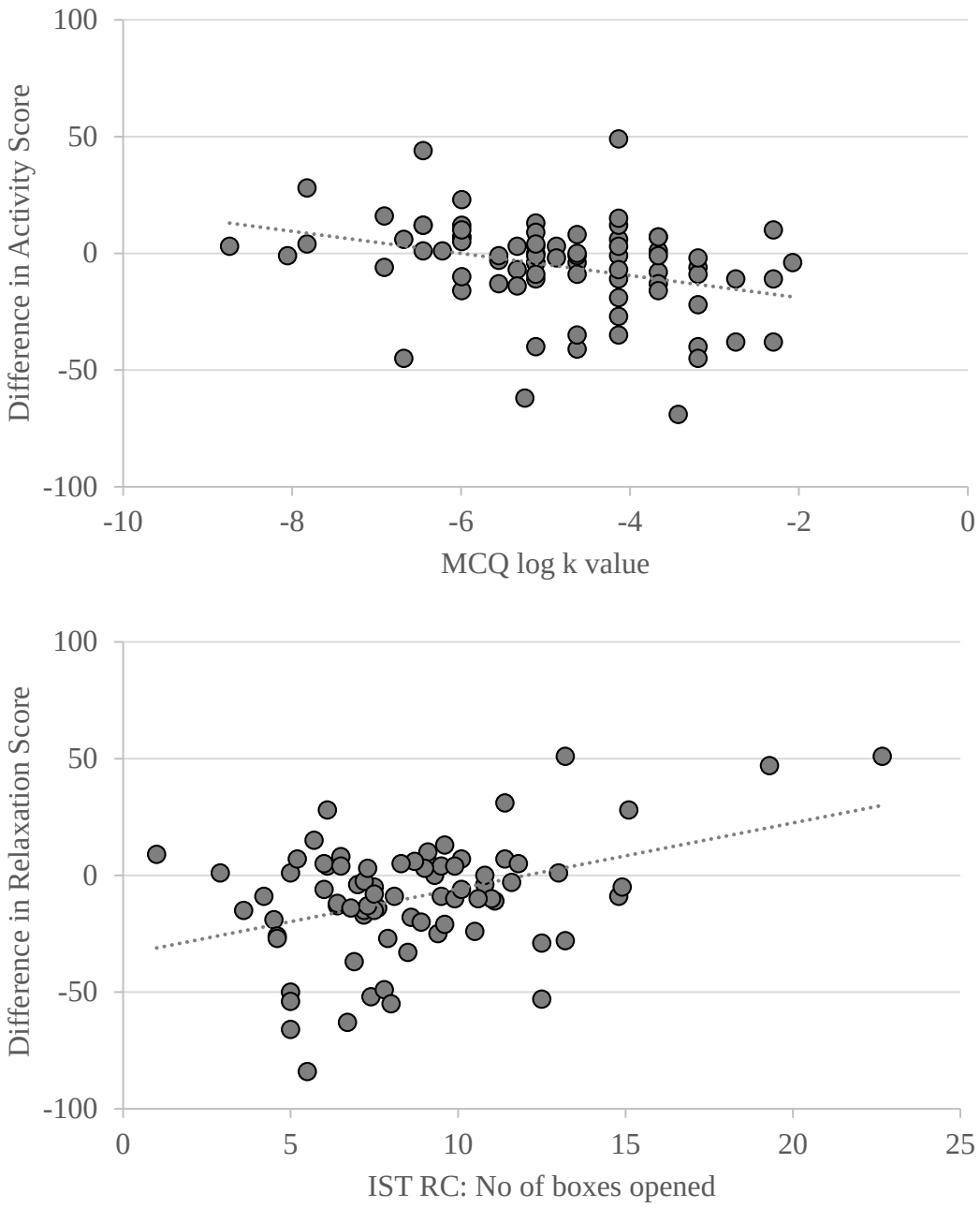

Figure 2.1 Plots showing significant association between post-induction changes in mood state and performance in the tasks during session 2. The top panel presents the relationship between the change in activity score (Post Activity – Pre Activity) and the discounting parameter (k value). The bottom panel presents the relationship between the change in Tension/Relaxation score (Post Relaxation – Pre Relaxation) and the performance on the information sampling task (IST), reward conflict condition (RC)

2.5 Discussion

The current study investigated the role of emotional state as a modulator of impulsive behaviour. Although no group differences in performance on the tasks were found, based on correlational analyses, we report relationships between behavioural impulsivity and subjective changes in mood state, irrespective of the group allocation. Specifically, increased relaxation (vs tension) was related to increased information gathering on the IST (decreased reflection

impulsivity), while increased activity (vs tiredness) was associated with lower levels of delay discounting (decreased temporal impulsivity). Together, our results suggest that distinct facets of impulsive behaviours are differentially affected by individual changes in mood state.

We predicted that increased positive affect might be related to decreased reflection impulsivity via enhanced task efficiency (Isen & Means, 1983; Isen et al., 1991). We found no relationship between either mood state (valence) or arousal (activity) measures, instead, increased relaxation state following the mood manipulation procedure was related to higher information sampling before deciding in the IST. This relationship was stronger for the reward conflict condition, in which participants sample information at a certain cost – the more boxes they open, the smaller the potential reward. This may indicate that changes across the tension-relaxation domain may be related to motivational changes. The "tension-relaxation" scale had proved to be a sensitive measure of subjectively experienced stress state in previous investigations (Ilona Papousek et al., 2010; Ilona Papousek, Schulter, & Premsberger, 2002; Iona Papousek & Schulter, 2001). Therefore, our results might be interpreted as the more stressed participants felt, the more impulsively they behaved on the IST RC.

We suspected that increased positive affective state might be associated with improved self-regulation, and therefore, decreased temporal impulsivity. We found no associations between temporal impulsivity and measures of either mood or tension/relaxation scales. The lack of findings linking mood scale (valence) contradicts previous research. For example, a study with preschool children also showed that pupils in whom a happy mood state was induced chose the larger delayed rewards significantly more often than those in a sad mood state (Moore et al., 1976). In contrast, participants who report high levels of negative affective state, show higher discounting rates (higher temporal impulsivity) than those low in a negative affective state (Koff & Lucas, 2011). Instead, our results indicate a specific relationship between temporal impulsivity and self-reported activity: Increased activity following the mood induction procedure was associated with low temporal impulsivity. Mental fatigue following completion of a cognitive task was associated with a diminished emotion regulation (Grillon, Quispe-Escudero, Mathur, & Ernst, 2015). Possibly the same mechanism applies to self-control on inter-temporal decisions in fatigued (decreased in activity) individuals resulting in short-sighted choices as shown in the present study.

Regarding motor impulsivity, there were significant group differences in the number of omissions on the 5-CSRTT. Post-hoc tests were insignificant, but judging by the mean values only, it appears that the Sad group was the most inattentive. This lends some support to our hypotheses that negative affective state might be related to attentional lapses. This conclusion also agrees with reports by Smallwood and colleagues (Smallwood et al., 2009): Relative to positive, negative mood state was associated with more attentional lapses, increased frequency of reports of task-irrelevant thoughts, and more difficulty to adjust behaviour following a lapse.

Moreover, there was a negative association between change in activity ratings and the number of premature responses, suggesting that individuals who felt more active following the mood induction, showed lower 'waiting' impulsivity. However, this correlation did not survive the correction for multiple companions; therefore, providing only tentative evidence for the relationship between mood state and ‘waiting’ impulsivity.

Similarly, our results lend some tentative evidence for the relationship between increased reports of tension (stress state) and impaired response inhibition. Noteworthy, past research on the role of emotional states on response inhibition yielded inconsistent results, with some studies reporting no effects of mood state (Cackowski et al., 2014; Weafer et al., 2013), some increased prepotent response inhibition following stress induction (Schwabe et al., 2013), yet another study found diminished inhibitory control following distress induction (Patterson et al., 2016). Possibly, some of these differences may be accounted for by different measures of ‘stopping’ impulsivity employed. Our findings agree with results by Patterson et al. (2016), who used a standard version of the SST, suggesting that acute stress state is associated with diminished motor response inhibition. Overall, the role of current emotional states on aspects of motor impulsivity remains unclear, and further research is necessary to resolve this issue.

Considering all findings together, we suggest that individual differences in perceived mood state or susceptibility to mood changes may play an essential role in situational impulsivity. In other words, individuals who are more prone to mood swings may also experience more mood-dependent changes in impulsive behaviour. Indeed, deficits in emotion regulation, which can lead to mood swings, have been linked to many impulse-related behaviours such as excessive food intake or substance and non-substance-related addictive behaviours (including alcohol, drug abuse, gambling disorder, video game addiction, and problematic Internet use) (de Campora & Giromini, 2015; Estévez, Jáuregui, Sánchez-Marcos, López-González, & Griffiths, 2017; Kelly et al., 2016; Williams, Grisham Jessica R, Erskine, & Cassedy, 2011). Moreover, in a study by Tice and colleagues, distress induction led to impulsive behaviours. However, ‘mood-freezing’ manipulation (i.e. leading people to believe that their mood state will not be affected) diminished the effect of distress on behaviour (Tice et al., 2001), suggesting that being in control (or a sense of control) over emotional reactions, simultaneously aids impulse control. Together, these findings imply that improved emotional regulation strategies may help reduce impulsive behaviours. Additionally, current results also pose some implications for research: current mood state should be considered when assessing behavioural impulsivity.

There were some limitations to the current study that should be considered. Our sample consisted of a narrow age range of individuals, the typical undergraduate sample of students, which restricts the generalisation of the findings. Mood inductions were successful, but as in previous studies (e.g. X. Zhang, Yu, & Barrett, 2014), it was easier to modulate negative

emotions (Sad and Anxiety groups) than positive emotions (Positive group). In fact, the Control and Positive groups showed similar mood ratings.

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2.7 Appendix 1: Mood induction – details

Neutral, positive and sad mood was induced by presentation of emotional images (neutral, positive, or sad respectively) taken from the International Affective Picture System (IAPS, Lang et al., 2005) combined with congruent emotional musical excerpts which proved to enhance emotional experience in the past research (Baumgartner, Lutz, Schmidt, & Jäncke, 2006; O. J. Robinson & Sahakian, 2009). Image selection was based on emotional ratings from previous studies (Lang, Bradley, & Cuthbert, 2008; Mikels et al., 2005b, 2005a, 2005c; J. C. Smith, Bradley, & Lang, 2005). Each image was displayed on the screen for 5 s. During the neutral induction, picture presentation was accompanied by the excerpt from The Planets, Op. 32: VII. Neptune, the Mystic by Gustav Holst. In the positive version, Serenade No. 13 KV 525 G Major: I. Serenade. Allegro by Wolfgang Amadeus Mozart was played, while in the sad mood induction, Adagio in G Minor by Tomaso Albinoni was played. The whole procedure lasted 5 minutes.

The anxiety induction procedure was based on the Mannheim Multicomponent Stress Test (Kolotylova et al., 2010; Reinhardt, Schmahl, Wüst, & Bohus, 2012). Participants were simultaneously exposed to different types of stressors (emotional, acoustic, and cognitive). In the first part of the induction (lasting 1 minute) participants viewed unpleasant emotional pictures while listening to white noise of increasing intensity (78 to 93 dB) to avoid habituation effect. Affective pictures were selected from the IAPS database (IAPS, Lang et al., 2005), based on their ratings of arousal and valence, as well as an ability to evoke feelings of anxiety and fear (Mikels et al., 2005b; J. C. Smith et al., 2005). Each picture was presented on the full screen for 5 seconds.

As a cognitive stressor a computerized version of the Paced Auditory Serial Addition Task (PASAT-C, Lejuez, Kahler, & Brown, 2003) was used. Numbers were sequentially presented in the middle of the screen, while affective images were displayed in the background. Participants were required to sum the number currently presented on the screen with the previous one and type the answer using a keyboard. Next, subjects had to ignore the sum and add the following number to the one presented before, etc. Each incorrect or too slow response was punished by an acoustic error signal. The mental calculation task consisted of two parts, lasting 2 min each. The time latency between the numbers in part 1 was 3 s and for the part 2 it was 2 s. The whole anxiety-induction procedure lasted 5 minutes.

Before the induction, participants completed a 10-trial practice run to familiarise themselves with the PASAT.

Table S2.1 presents selected images for each mood-induction condition. One-way analysis of variance (ANOVA) showed that there were significant differences between the categories of images on the valence ($F(3,396) = 2077.89$, $p < .001$) and arousal ($F(3,396) =$

171.28, $p < .001$) ratings. Bonferroni post-hoc test confirmed that Sad and Anxious categories were well matched regarding valence ratings ($p = 1$), but Anxious images were rated as more arousing ($p = .002$). In contrast, Positive and Sad categories were well matched on arousal ratings ($p = .251$), but Sad category has significantly lower valence ratings than Positive one ($p < .001$). There were significant differences between in all other comparisons (p's $< .05$). For details see Table S2.2 and Figure S2.1, which depict valence and arousal ratings for each group of images.

Table S2.1 IAPS images selected for each mood induction condition.

Sad:									
2053	2800	3150	6200	6530	9000	9140	9331	9440	9600
2205	2900	3160	6210	6561	9001	9160	9400	9470	9611
2590	3051	3180	6212	6570	9006	9180	9405	9490	9620
2691	3061	3220	6242	6571	9007	9181	9415	9500	9622
2700	3062	3230	6243	6821	9040	9182	9417	9520	9630
2710	3063	3261	6244	6830	9041	9220	9420	9530	9800
2722	3064	3300	6250	6831	9042	9250	9421	9560	9830
2750	3100	3350	6312	6940	9045	9253	9430	9561	9910
2751	3102	4621	6360	7361	9050	9265	9432	9570	9911
2753	3140	6010	6370	8230	9120	9280	9433	9571	9920
Positive:									
1440	1721	2091	2530	4660	5629	7260	7570	8190	8470
1460	1750	2150	2550	5260	5660	7270	7580	8200	8490
1463	1811	2160	2650	5270	5700	7280	8030	8210	8496
1500	1920	2165	2660	5450	5820	7330	8034	8300	8497
1510	1999	2170	4599	5460	5830	7350	8080	8350	8501
1540	2040	2260	4607	5470	5831	7400	8090	8370	8502
1590	2050	2311	4608	5480	5910	7430	8120	8380	8503
1600	2057	2340	4610	5600	5982	7470	8162	8400	8510
1610	2070	2341	4614	5621	7200	7480	8170	8420	8531
1710	2080	2391	4650	5623	7230	7502	8180	8461	8540
Neutral:									
1560	2570	2880	5532	7000	7034	7140	7205	7490	7820
1670	2580	2890	5533	7002	7035	7150	7207	7491	7830
2020	2620	4000	5534	7004	7040	7160	7217	7500	7950
2190	2702	4571	5731	7006	7050	7170	7224	7550	8010
2200	2752	5120	5900	7009	7060	7175	7233	7560	8160
2210	2810	5500	5920	7010	7080	7180	7234	7590	8311
2220	2830	5510	5940	7020	7090	7182	7235	7620	9070
2351	2840	5520	5950	7025	7100	7183	7237	7640	9210
2381	2850	5530	6150	7030	7110	7185	7283	7700	9360
2440	2870	5531	6900	7031	7130	7187	7351	7710	9402
Anxious:									
1050	2692	3102	3550	6244	6550	8230	9180	9430	9620
1120	2710	3140	6020	6250	6560	8480	9181	9433	9621
1201	2722	3150	6190	6260	6561	9001	9182	9440	9622
1300	2800	3160	6200	6312	6570	9040	9250	9470	9630
1301	3051	3180	6210	6313	6571	9041	9253	9490	9800
1302	3061	3261	6212	6350	6821	9042	9265	9500	9910
1930	3062	3280	6230	6360	6830	9050	9400	9570	9911
1931	3063	3350	6241	6370	6831	9120	9405	9571	9912
2120	3064	3500	6242	6510	6940	9140	9420	9600	9920
2691	3100	3530	6243	6530	7361	9160	9421	9611	9921

Table S2.2 Descriptive statistics for valence and arousal ratings for groups of images selected for each condition.

Ratings	Group of images	N	Mean	SD	SE	95% Confidence Interval		Min	Max
						Lower Bound	Upper Bound		
Valence	Sad	100	2.57	0.54	0.05	2.46	2.67	1.40	3.75
	Positive	100	7.47	0.36	0.04	7.40	7.54	6.96	8.34
	Neutral	100	5.04	0.44	0.04	4.96	5.13	4.03	5.99
	Anxious	100	2.66	0.66	0.07	2.53	2.79	1.40	4.21
Arousal	Sad	100	5.46	0.75	0.08	5.31	5.61	3.52	6.60
	Positive	100	5.22	0.81	0.08	5.06	5.38	3.98	7.35
	Neutral	100	3.38	1.07	0.11	3.17	3.59	1.72	6.97
	Anxious	100	5.89	0.71	0.07	5.75	6.03	3.52	7.35

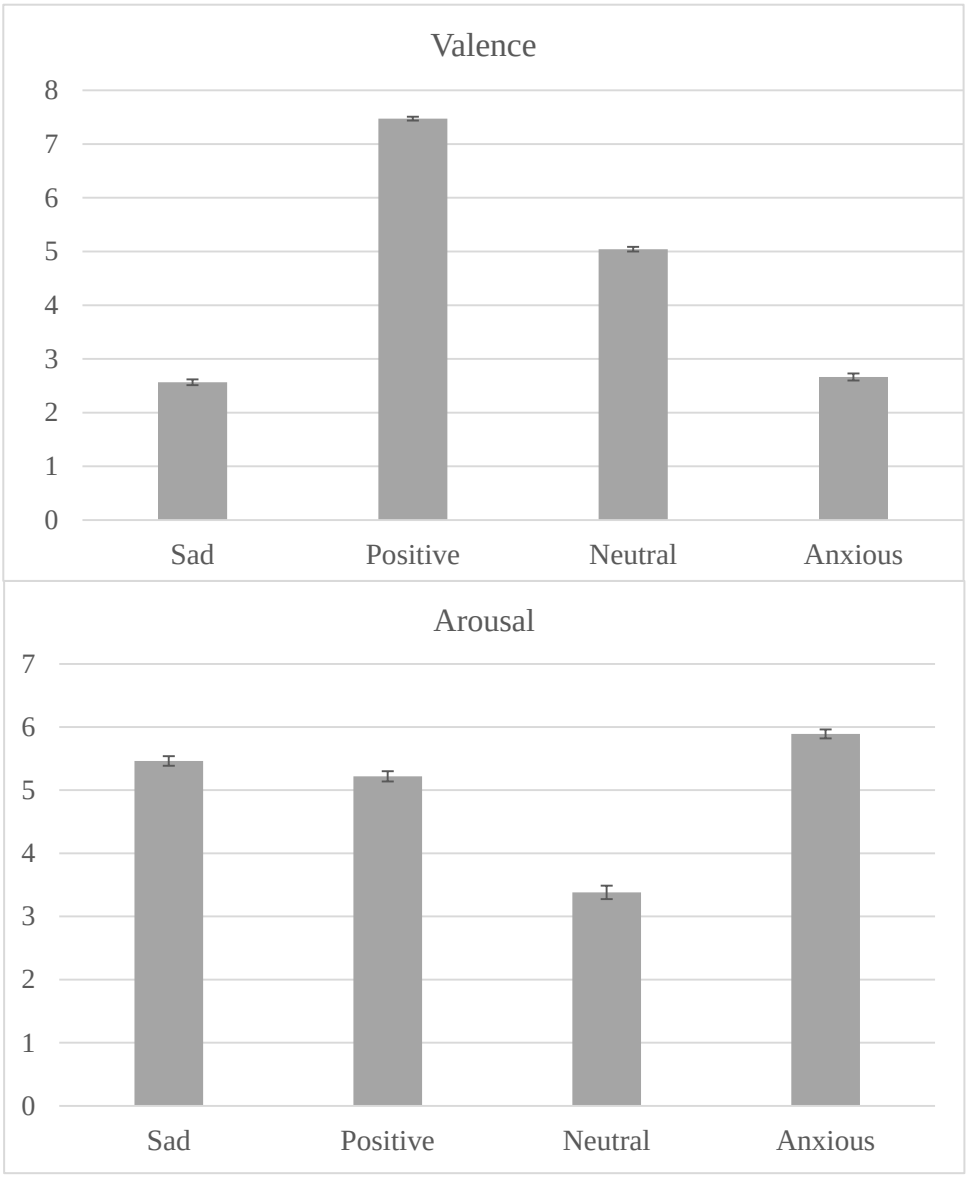

Figure S2.1 Ratings of each group of images on valence (upper panel) and arousal (bottom panel). Error bars represent standard error of the mean.

2.7.1 References

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2.8 Appendix 2: Supplementary figure

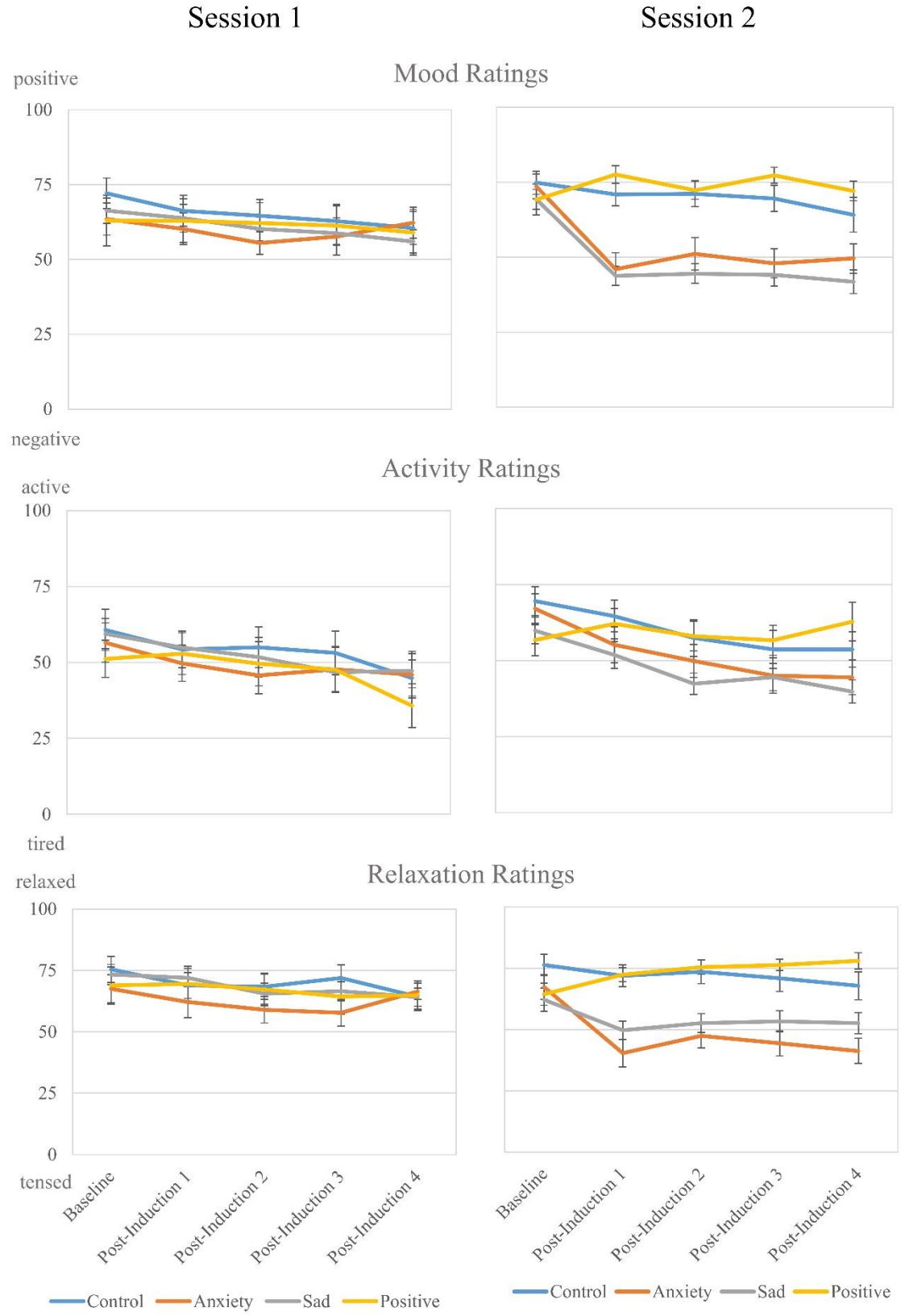

Figure S 2.2 Kusta mood state ratings for sessions 1 and 2 for each group. Error bars represent standard error of the mean.

CHAPTER 3.

STUDY 2.
RISK-TAKING AND IMPULSIVITY; THE ROLE OF MOOD STATES AND INTEROCEPTION

This article has been submitted to the Frontiers in Psychology:

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Contribution

I contributed to the study design and the interpretation of the results. I collected and analysed the data as well as prepared the initial manuscript.

3.1 Abstract

Objectives: The consequences of impulsive decisions and actions represent a major source of concern to the health and well-being of individuals and society. It is, therefore, crucial to understand the factors which contribute to impulsive behaviours. Here, we examined how personality traits of behavioural tendencies, interoceptive sensibility as well as transient mood states predict behavioural performance on impulsivity and risk-taking tasks.

Method: 574 (121 males; age 18-45) individuals completed self-report personality measures of impulsivity, reward sensitivity, punishment avoidance as well as interoceptive sensibility, undertook a mood assessment and performed a set of cognitive tasks: delay discounting (temporal impulsivity), probability discounting (risk-taking), and reflection impulsivity task. Data were interrogated using principal component analysis, correlations and regression analyses to test mutual relationships between personality traits, interoceptive sensibility, mood state and impulsive behaviours.

Results: We observed a clear separation of measures used, both trait and behavioural. Namely, sensation-seeking, reward sensitivity and probability discounting reflected risk-taking. These were separate from measures associated with impulsivity, both trait (negative and positive urgency, premeditation, perseverance) and behavioural (delayed discounting and reflection impulsivity). This separation was further highlighted by their relationship with the current emotional state: positive affect was associated with increased risk-taking tendencies and risky decision-making, while negative emotions were related to heightened impulsivity measures. Interoceptive sensibility was only associated with negative emotions component.

Conclusions: Our findings support the proposal that risk-taking and impulsivity represent distinct constructs that are differentially affected by current mood states. This novel insight enhances our understanding of impulsive behaviours.

Keywords: UPPS-P, Sensation Seeking, Delay Discounting, Probability Discounting, Reflection Impulsivity, Interoceptive Sensibility, Emotional State.

3.2 Introduction

Impulsivity describes a set of behaviours characterized by relative dominance of spontaneity over consideration. Examples include a preference towards obtaining immediate gratification over a delayed (yet ultimately more profitable) outcome, making 'snap decisions' before evaluating available information, or having difficulty waiting one's turn, withholding a reaction, or aborting an initiated motor response (Daruna & Barnes, 1993; Moeller *et al.*, 2001). Although spontaneous actions may be adaptive, for example when the matter is of little importance or when there is little time to make a decision (Dickman, 1990), high levels of impulsivity often result in negative consequences. Correspondingly, impulsivity is associated with poor academic achievement and impaired psychometric performance on reasoning tasks (Schweizer, 2002; Lozano *et al.*, 2014). A high degree of impulsivity is also related to risky driving (Pearson *et al.*, 2013), violent behaviour when under the influence of alcohol (Klimkiewicz *et al.*, 2014), diminished self-control and an increased food intake (Guerrieri, Nederkoorn, & Jansen, 2007; Guerrieri, Nederkoorn, Stankiewicz, *et al.*, 2007; Meule & Kübler, 2014), especially while experiencing negative emotions (Van Blyderveen *et al.*, 2016). The importance of impulsivity is increasingly recognized in a clinical setting: Many neuropsychiatric conditions, including addiction, bipolar disorder, and Attention-Deficit Hyperactivity Disorder are characterized by elevated impulsivity (American Psychiatric Association, 2013). Risk-taking is also closely related to impulsivity and predicts the initiation of drug and alcohol use and the pursuit of other hazardous behaviours (e.g. unprotected sex) (Donohew *et al.*, 2000; Ríos-Bedoya *et al.*, 2008).

Impulsivity may determine the integrity of our health and how everyday life flows or falters. It is, therefore, crucial to understand the factors that underlie impulsive behaviour and its expression. Moreover, impulsivity is a multidimensional construct (Whiteside & Lynam, 2001; Caswell *et al.*, 2015; Herman *et al.*, 2018), so it is also vital to investigate what factors might differentially influence distinct impulsivity subtypes. Ultimately, improved understanding of modulators of impulsive behaviour can enable us to develop better-coping strategies to help impulsive individuals and promote more advantageous decision-making in everyday life. Finally, impulsivity research to date focuses either on university students or certain target populations, e.g. substance abusers or binge drinkers. Hence broad information about the general population is lacking, yet much needed.

One likely modulator of impulsive behaviour is affective state (for discussion see Herman *et al.*, 2018). Indeed, people show diminished impulse control (i.e. behave more impulsively) when experiencing negative affect (Tice *et al.*, 2001). However, it is unknown if subtypes of impulsivity are equally affected by emotional states or whether impulsive behaviour is particularly sensitive to

specific emotions. Moreover, the role of characterological features contributing to 'behavioural style', for example, personality traits or sensitivity to internal bodily signals (interoception), is not to be underestimated, as these may shape how impulsively individuals respond while experiencing various mood states.

Implicitly one would assume that a measure of trait impulsivity would reflect the degree to which an individual behaves impulsively. However, typically very weak relationships are observed between various trait impulsivity (questionnaire) measures and objective performance on impulsivity tasks (Caswell et al., 2015; Cyders & Coskunpinar, 2011; Franken, van Strien, Nijs, & Muris, 2008; Shen, Lee, & Chen, 2014). Possibly, interoceptive ability, enabling more accurate detection of internal bodily sensations, e.g. heart rate (Craig, 2009), may determine why and when we behave impulsively. Physiological cues may guide behaviour particularly when a potential risk is involved (Damasio, 1996; Bechara *et al.*, 1997; Katkin *et al.*, 2001). For example, in a classic study by Bechara *et al.*, (1997), healthy individuals playing a gambling task generated anticipatory skin conductance responses whenever they considered a choice that turned out to be risky, before they developed an explicit knowledge that the choice was risky. In addition, more recently, good interoceptive ability was found to be associated with more advantageous choices in the Iowa Gambling Task (Werner *et al.*, 2009) and predicted profitable decisions in London financial traders (Kandasamy *et al.*, 2016). Since disadvantageous decision-making is considered a part of impulsivity construct (Winstanley, 2011; Herman *et al.*, 2018), this evidence could suggest that more impulsive individuals may lack interoceptive sensitivity. Alternatively, since highly impulsive individuals appear also to have lower resting levels of arousal compared to peers (Fowles, 2000; Mathias & Stanford, 2003; Puttonen *et al.*, 2008; Schmidt *et al.*, 2013), and engagement in impulsive or risky actions may be a maladaptive way of reaching an 'optimal' level of arousal (Zuckerman, 1969; Barratt, 1985; Eysenck & Eysenck, 1985), impulsive individuals may have normal interoceptive sensitivity to changes in their internal state, yet engage in impulsive actions as a means of regulating their arousal level.

Within the current study, we sought to examine the relationship between personality traits of impulsive tendencies, reward sensitivity and punishment avoidance, subjective interoceptive traits (interoceptive sensibility; Garfinkel *et al.*, 2015), current emotional states with behavioural impulsivity. In particular, we were interested which of these variables would be the best predictor of task performance. The UPPS-P impulsive behaviour scale (Cyders & Smith, 2007; Whiteside & Lynam, 2001) was used to assess aspects of impulsive tendencies. This scale was selected as it incorporates several dimensions of impulsivity based on personality measures with addition of tendencies for impulsive behaviours while experiencing strong emotions (urgency subscales).

Additionally, the Behavioural Inhibition System/Behavioural Activation System Questionnaire (Carver & White, 1994) was employed as a measure of reward sensitivity and punishment avoidance. The Body Perception Questionnaire (Porges, 1993) was used to score general subjective sensitivity to bodily processes (interoceptive sensibility; Garfinkel *et al.*, 2015). The Positive Affect/Negative Affect Scale (Watson *et al.*, 1988) and the Depression, Anxiety, Stress Scale (Henry & Crawford, 2005) were used to assess self-reported emotional state. Risk-taking behaviour was assessed from performance on a probability discounting task (Madden *et al.*, 2009). Distinct facets of impulsive behaviour were measured with the Monetary Choice Questionnaire (Kirby *et al.*, 1999), which assesses the ability to delay gratification (temporal impulsivity), and performance of the Matching Familiar Figures Task (Cairns & Cammock, 1978), which measures the degree of information seeking before making a decision (reflection impulsivity).

Since impulsivity is a term which encompasses a wide range of behaviours (Herman *et al.*, 2018), we hypothesized that distinct behavioural dimensions would be predicted by distinct factors. First, as interoception is linked to risk-taking and advantageous decision-making (Werner *et al.*, 2009; Kandasamy *et al.*, 2016), we predicted that individual differences in interoceptive sensibility would predict risk-taking. Second, extending earlier observations (Tice *et al.*, 2001), we predicted that negative emotional states compromise self-control, and thus increase behavioural impulsivity. Third, we predicted that components of the UPPS-P scale, which include emotion-based impulsivity components, would predict objective aspects of behavioural impulsivity.

To test our hypotheses, we conducted an online survey study of participants extending into the general population, providing a more demographically representative sample of the UK population than earlier studies. Participants completed self-report personality questionnaires, state-mood assessment and interoceptive sensibility questionnaires, and performed specific behavioural tasks to obtain an objective measure of impulsivity and risk-taking.

3.3 Material and methods

The study was approved by the University of Sussex Ethical board. Volunteers had to be at least 18 years old to participate. The study was conducted online via Qualtrics platform (https://www.qualtrics.com/) between May and October 2016. To make the results generalizable to a broad population, we wanted to obtain information from people with different backgrounds, educational levels, age, and not just university students. Therefore, participants were recruited via social media, websites (www.reddit.com, www.craiglist.org, and www.callforpartcipants.com), mailing lists, as well as posters advertising the study on Campus, cafes and community centres

around Brighton. Inclusion in a £25 prize draw or a possibility to earn two study credits for Psychology undergraduate students were offered as an incentive for participation.

3.3.1 Procedures

After reading study information, volunteers confirmed that they understood all information and then consented to their willingness to take part in the study. After completing the survey, participants were debriefed. The completion of the study took approximately 20 minutes (based on a pilot study during which participants completed the study uninterrupted).

3.3.2 Questionnaires

Basic demographics questionnaire was used to determine age, sex, education, smoking habits and recreational drug use.

Alcohol Use Questionnaire (AUQ) (Townshend & Duka, 2002) provided an estimate of a number of alcohol units consumed a week.

UPPS-P Impulsive Behaviour Scale (Whiteside & Lynam, 2001; Cyders & Smith, 2007) is a 59-item self-report measure of five dimensions of impulsivity: negative urgency (NU) – a tendency to act on impulse while experiencing strong negative emotions, (lack of) premeditation (LPrem)– a tendency to act without taking into account the consequences, (lack of) perseverance (LPe) – difficulty completing tasks which may be tedious or difficult, sensation seeking (SS) – a pursue of excitement and novelty, and positive urgency (PU) – a tendency to act on impulse while experiencing strong positive emotions.

Behavioural Inhibition System/Behavioural Activation System (BIS/BAS) Questionnaire (Carver & White, 1994) consists of 20 items organized into two main scales: BIS, which evaluates punishment sensitivity, and BAS which assesses reward sensitivity. BAS is further divided into three subscales: BAS Reward (anticipation or the occurrence of the reward), BAS Drive (the pursuit of desired goals), and BAS Fun Seeking (desire for new rewards and willingness to approach them).

Body Perception Questionnaire (BPQ) Very Short Form (Porges, 1993) consists of 12 items rated on a five-point scale and provides a measure of general awareness of bodily processes (high values indicate high awareness of bodily sensations).

Depression, Anxiety, Stress Scale (DASS) (Henry & Crawford, 2005) consists of three 7-item self-report scales that measure the extent of depression, anxiety, and stress experienced over the last week.

Positive Affect/Negative Affect Scale (PANAS) (Watson *et al.*, 1988) is a 20-item measure of self-reported positive (PA), and negative affect (NA) experienced at the present moment.

3.3.3 Tasks

Matching Familiar Figures Task (MFFT) (Kagan *et al.*, 1964; Cairns & Cammock, 1978) is a measure of reflection impulsivity. Participants need to identify an image identical to a target one, out of six possible options. The dependent variable is an Impulsivity Score (IS), which reflects quick responses and a high number of errors (high values indicate high reflection impulsivity).

Monetary Choice Questionnaire (MCQ) (Kirby *et al.*, 1999) is a measure of temporal impulsivity. It consists of a list of 27 choices between pairs of smaller immediate rewards (SIR) and larger but delayed rewards (LDR). The dependent variable is the discounting parameter (k) calculated for each participant using the formula: k = ((LDR-SIR)-1)/delay (log-transformed to reduce skewness). Large k values indicate high temporal impulsivity.

Probability Discounting task (PD) (Madden *et al.*, 2009) is a measure of risk-taking. It consists of a list of 30 choices between smaller certain rewards and uncertain larger gains. The dependent variable is h parameter, which reflects a degree of probability discounting at the indifference between two outcomes (a point at which the certain and probabilistic rewards are of equivalent subjective value). The h-parameter was calculated for each participant using the formula: h = (ProbabilisticReward/CertainReward -1)/OddsAgainsWinning) (ln-transformed to reduce skewness). Large h values indicate discounting of probabilistic rewards (risk aversion).

3.3.4 Data analysis

Data analysis was conducted using Statistical Package for Social Sciences (SPSS) version 22. First, principal component analysis (PCA) with pairwise deletion was conducted to reduce the number of variables for further analysis. PCA was carried out with Varimax rotation with Kaiser Normalization. Next, exploratory correlations between identified components were computed to better characterize their mutual relationship. Finally, multiple regression models were constructed to investigate which components best predict each subtype of impulsive behaviour.

3.4 Results

3.4.1 Participants

603 individuals completed the online questionnaire (132 males; age 18-74 24.39 ± 9.26), of whom 183 were 1st or 2nd-year psychology students who took part in the study in exchange for course credits. Due to such variability in age and a small fraction of older volunteers, we decided to focus on a subset of younger participants (≤ 45 years old). Therefore, the final sample size was constrained to 574 (121 males; age 18-45, 22.83 ± 6.06). 474 participants were non-smokers.

3.4.2 Exclusions

The following exclusion criteria were employed: for the MCQ and PD, participants with low response consistency (<75%) were excluded from the analysis (23 and 6 excluded, respectively), as low consistency makes it difficult to establish the discounting parameters reliably. Due to the specific character of the study and limited control over circumstances participants were completing the tasks, for the MFFT, for which response time is important for calculating the dependent variable IS, we excluded participants whose reaction times were outside the range observed in the previous study performed in our lab with a large sample size (N = 160) (Caswell *et al.*, 2015) (46 excluded).

3.4.3 Principle Component Analysis

Eighteen variables were included in the PCA: mean k value (log10-transformed to correct issue of non-normality), mean h value (ln-transformed), MFFT IS, NU, PU, LPrem, LPe, SS, BIS, BAS Fun, BAS Reward, BAS Drive, BPQ, Depression, Anxiety, Stress, PA, NA.

The total sample size of 574 participants for the 18 items exceeds the suggested minimum ration of 5 participants per item (Gorsuch, 1983). Chi-square was used to evaluate the fit between the model and the data. Components with eigenvalues >1 were retained, yielding six components, with the total of 67% of variance explained, which seemed to fit the data well. The Kaiser-Meyer-Olkin measure of sampling adequacy was .757, above the commonly recommended value of .6, and Bartlett's Test of Sphericity was significant (χ^2 (153) = 3107.60, p < .001), indicating that the null hypothesis that the correlation matrix is an identity matrix can be rejected. Finally, the communalities were all above .4, further confirming that each item shared some common variance with other items. Three items (PA BAS reward, and BPQ) cross-loaded on two factors above .4. Overall, PCA was deemed to be suitable for all 18 items. For details see Table 3.1.

The first component represented items related to the negative emotional state including Depression, Anxiety, Stress and NA. Component 2 included items related to how behaviours are motivated by the pursuit of rewards and excitement as well as positive feelings (namely all three BAS subscales, SS and PA). Component 3 contained items related to trait impulsivity (PU, NU, LPe, LPrem; all subscales of UPPS-P impulsivity scale but SS), and PA. Component 4 included punishment avoidance trait (BIS) and BAS reward, and factor 5 contained discounting parameters (k and h) and BPQ. Finally, factor 6 contained BPQ and MFFT IS.

Removal of PA and SS from component 2, resulted in more reliable BAS factor ($\alpha = .721$), therefore, for the further analysis, we chose to use BAS separately from SS and PA. Likewise, deletion of PA from component 3 resulted in higher reliability score ($\alpha = .751$); therefore, the new Impulsive Personality Trait (IPT) component was computed. The components 4, 5 and 6, had low-reliability scores; thus, these items were kept separately.

The complete list of variables used in subsequent analyses together with descriptive statistics is presented in Table 3.2.

Table 3.1 Component loading and reliability scores for components identified with the PCA.

	RC 1	**RC 2**	**RC 3**	**RC 4**	**RC 5**	**RC 6**
Anxiety	0.85	-0.03	0.07	0.06	0.12	-0.07
BAS Drive	0.10	0.77	-0.04	-0.04	-0.06	0.08
BAS Fun	-0.04	0.81	0.29	-0.01	0.03	0.00
BAS Reward	-0.07	0.67	-0.24	0.49	0.03	0.01
BIS	0.17	-0.13	-0.05	0.87	-0.03	0.01
BPQ	0.20	0.10	-0.12	0.14	0.57	-0.50
Depression	0.80	-0.10	0.20	0.08	-0.09	0.03
MCQ log k	0.06	0.09	0.17	-0.06	0.61	0.05
MFFT IS	0.09	0.07	0.05	0.05	0.17	0.86
NA	0.80	0.07	0.02	-0.08	0.03	0.05
Negative Urgency	0.36	0.32	0.59	0.32	0.11	0.07
Positive Affect	0.09	0.45	-0.50	-0.36	0.17	0.06
LPer	0.14	-0.22	0.78	-0.03	0.03	0.01
Positive Urgency	0.28	0.40	0.62	-0.09	0.11	0.03
LPrem	0.02	0.18	0.77	-0.19	0.04	0.08
PD ln h	-0.08	-0.25	-0.05	-0.01	0.57	0.18
SS	-0.13	0.67	0.14	-0.36	-0.09	-0.09
Stress	0.86	0.04	0.10	0.17	0.02	0.01
Cronbach's Alpha	0.86	0.55	0.67	0.34	0.14	0.10
Variance Explained [%]	17.30	15.60	13.65	8.13	6.35	5.87

Table 3.2 Final variables identified based on PCA, descriptive statistics and gender scores comparisons.

	All			Female			Male			Levene's Test		t-test		
	N	M	SD	N	M	SD	N	M	SD	*F*	*p*	*t*	df	*p*
BPQ	574	2.91	0.93	453	2.92	0.91	121	2.89	1.00	3.90	0.05	0.30	177.44	0.761
SS	574	31.99	7.42	453	31.44	7.46	121	34.07	6.94	1.44	0.23	3.50	572.00	< .001
BIS	574	22.27	3.75	453	22.83	3.55	121	20.20	3.75	0.31	0.58	7.14	572.00	< .001
BAS	574	38.58	5.66	453	38.56	5.78	121	38.68	5.19	4.03	0.05	0.22	206.60	0.827
PA	574	26.67	9.00	453	26.30	8.87	121	28.06	9.36	0.68	0.41	1.91	572.00	0.056
Negative Emotions	574	17.36	7.59	453	58.49	32.08	121	54.99	29.10	0.65	0.42	1.09	572.00	0.278
MCQ log k	551	-2.05	0.76	432	-2.11	0.74	119	-1.80	0.77	0.79	0.37	4.00	549.00	< .001
PD ln h	568	0.69	0.99	448	0.71	0.98	120	0.60	1.01	0.00	0.97	1.13	566.00	0.260
MFFT IS	533	-0.02	1.36	419	0.01	1.34	114	-0.15	1.43	0.15	0.70	1.15	531.00	0.251
IPT	574	99.72	20.53	453	99.23	20.91	121	101.59	19.04	0.78	0.38	1.12	572.00	0.262

3.4.4 Correlations

The correlational analysis was conducted to explore further and better characterize the relationship between items identified via PCA. Since impulsivity-related traits decrease with age (Steinberg *et al.*, 2008) and our sample had a large age-range (18-45), correlations between all the variables and age were computed. PD h parameter was positively correlated with age, indicating increased discounting of probabilistic rewards with age (risk-avoidance), $r(566) = .118$, $p = .005$. Similarly, SS was negatively correlated with age, $r(572) = -.142$, $p = .001$, indicate a decrease in SS with age. MFFT IS score slightly decreased with age, also indicating a decrease in reflection impulsivity with age, $r(531) = -.09$, $p = .032$. IPT was also negatively correlated with age, $r(572) = -.113$, $p = .007$, suggesting a decrease in trait impulsivity with age. Lastly, positive affect was positively correlated with age, $r(572) = .119$, $p = .004$.

We also wanted to account for possible sex differences in the identified components. Significant differences were found in SS, BIS scores, and temporal impulsivity (Table 3.2); namely, females reported higher punishment avoidance (higher BIS score), but lower SS, than males. Females also discounted delayed rewards less steeply than males (i.e. showed lower temporal impulsivity).

Therefore, partial correlations were computed between all variables used in the further analysis controlling for age and gender (see Table 3.3 for details). Bonferroni correction for multiple comparisons was set at $p \leq .001$.

3.4.5 Mood and impulsivity

IPT, as well as BIS, were significantly correlated with PA and the Negative Emotional state indicating that individuals higher on self-reported impulsivity and punishment aversion also reported lower levels of positive affect and higher levels of negative mood state. The reverse was true for SS – increased sensation seeking, which was related to higher positive affect and lower negative emotions. Similarly, BAS was positively correlated with PA, suggesting that individuals

Table 3.3 Pearson partial correlations, controlling for age and gender, between identified variables.

		SS	BIS	BAS	Positive Affect	Neg Emotions	IPT	MCQ log k	PD ln h	MFFT IS
BPQ	*r*	-0.007	0.055	0.070	0.058	0.179 ***	0.013	0.094 *	0.047	-0.050
	p	0.877	0.193	0.094	0.168	< .001	0.750	0.027	0.260	0.251
	df	570	570	570	570	570	570	547	564	529
SS	*r*		-0.302 **	0.494 ***	0.250 ***	-0.119 **	0.167 ***	-0.007	-0.109 **	-0.012
	p		< .001	< .001	< .001	0.004	< .001	0.865	0.009	0.781
	df		570	570	570	570	570	547	564	529
BIS	*r*			-0.028	-0.190 ***	0.209 ***	-0.003	0.022	0.008	-0.020
	p			0.506	< .001	< .001	0.952	0.614	0.856	0.638
	df			570	570	570	570	547	564	529
BAS	*r*				0.300 ***	0.018	0.230 ***	0.079	-0.140 ***	0.060
	p				< .001	0.669	< .001	0.064	0.001	0.169
	df				570	570	570	547	564	529
Positive Affect	*r*					-0.030	-0.166 ***	0.035	-0.018	0.009
	p					0.479	< .001	0.411	0.663	0.840
	df					570	570	547	564	529
Neg Emotions	*r*						0.359 ***	0.104 *	-0.027	0.086 *
	p						< .001	0.015	0.525	0.047
	df						570	547	564	529
IPT	*r*							0.183 ***	-0.035	0.134 **
	p							< .001	0.401	0.002
	df							547	564	529
MCQ log k	*r*								0.005	0.091 *
	p								0.916	0.041
	df								545	508
PD ln h	*r*									0.045
	p									0.307
	df									524

* $p <$ .05, ** $p <$ .01, *** $p \leq$ .001, **in bold** are presented correlations that survived the correction for multiple comparison ($p \leq .001$).
BPQ – Body perception questionnaire score, SS – Sensation Seeking, BIS – Behavioral Inhibition Scale score, BAS – Behavioral Approach Scale score, Neg Emotions – Negative Emotional State (DASS and NA), IPT – Impulsive Personality Trait, MCQ log k – Monetary Choice Questionnaire log transformed k parameter, PD ln h – Probability Discounting ln transformed parameter h, MFFT IS – Matching Familiar Figures Task Impulsivity Score.

high in reward sensitivity experience more positive affect. Temporal discounting and MFFT IS were correlated with the Negative Emotional state indicating that increased negative state was related to an increased temporal and reflection impulsivity. However, these correlations did not survive Bonferroni correction for multiple comparisons.

3.4.6 The relationship between behavioural and trait measures:

MCQ and MFFT only correlated with IPT, indicating increased temporal and reflection impulsivity in high-trait impulsivity individuals. PD, on the other hand, correlated with SS and BAS, suggesting that high SS (did not survive the Bonferroni correction) and BAS was related with impulsive decisions in the PD task (choosing the riskier option).

3.4.7 The relationship between personality traits:

SS was negatively associated with BIS, indicating that individuals who were high in sensation seeking report low punishment avoidance. Instead, SS, BAS and impulsive personality were all positively inter-correlated.

3.4.8 Interoceptive sensibility and impulsivity:

BPQ was positively correlated with Negative Emotions component indicating that self-reported bodily awareness is related to increased negative mood. Moreover, BPQ was also weakly positively correlated with MCQ, meaning that individuals high on impulsive personality also reported high self-perceived bodily awareness, however, this correlation did not survive Bonferroni correction.

3.4.9 Regressions

Multiple linear regressions were conducted with performance on the three behavioural tasks as dependent variables. Sex, mean-centred age and items identified with the factor analysis served as independent variables.

ANOVA indicated that all three regression models provided a good fit for the data (MCQ log k: $F(9, 541) = 5.10$, $p < .001$; PD ln h: $F(9, 558) = 2.91$, $p = .002$; MFFT IS: $F(9, 523) = 2.41$, $p = .011$). Tests to see if the data met the assumption of collinearity indicated that multicollinearity was not a concern (for all the dependent variables: Tolerance > .06, 1 < VIF <1.7).

It was found that trait impulsivity and sex were both significant predictors of the MCQ k parameter. Increased delay discounting (higher temporal impulsivity) was predicted by male sex and higher impulsive personality trait. None of the measures of mood were predictors; however, BPQ approached significance. Age and BAS were significant predictors of h parameter, indicating that younger age and higher reward sensitivity were predictive of more risky behaviour on the probability discounting task. Trait impulsivity turned out to be the only significant predictor of the MFFT IS, suggesting that high trait of impulsive personality is predictive of reflection impulsivity. Details are presented in Table 3.4.

3.5 Discussion

The current study investigated the role of personality traits (impulsive tendencies, reward sensitivity, punishment avoidance, and interoceptive sensibility) and emotional states as potential modulators of distinct subtypes of impulsive and risky behaviours. In accordance with our hypotheses, we first confirmed that trait impulsivity (IPT; positive and negative urgency and lack of premeditation and perseverance components of the UPPS-P scale) predicted temporal and reflection impulsivity. Moreover, reward sensitivity (BAS) best predicted risk-taking in a probability discounting task. However, contrary to our initial predictions, affective state did not predict any behavioural dimensions and no link was found between subjective interoception (interoceptive sensibility) and risk-taking.

We hypothesised that negative emotional state would relate to decreased self-control and therefore more impulsive behaviour. Although mood state was not a predictor of any of the behavioural tasks, we found correlational evidence providing tentative support for our hypothesis. Specifically, negative emotional state was related to both more short-sighted monetary decisions (increased temporal impulsivity) and more rushed decisions in the MFFT (increased reflection impulsivity). Although these relationships were weak, they nevertheless added to evidence form earlier studies which suggested that the experience of emotional distress, drives people to treat themselves to immediate pleasures, such as indulgent foods over healthy options, as a means of regulating one's mood (Moore *et al.*, 1976; Tice *et al.*, 2001; Lerner *et al.*, 2013; Gardner *et al.*, 2014). Experience of emotional distress is also considered a major trigger in substance use relapse. For example, stressful events increase the urge to drink alcohol and chances of relapse in treated alcoholics (Sinha *et al.*, 2009; Sinha, 2012). Increasingly, research also suggests that people drink alcohol to enhance positive or manage negative emotional state, and reduce tension (Conger, 1956; Cooper *et al.*, 1995; Zack *et al.*, 2002). Together, these findings support the importance of emotional state in impulsive choice and suggest that negative emotions bias behaviour toward

rushed and more near-sighted decisions, which can further lead to detrimental consequences both regarding finance (e.g. self-indulgence to improve one's mood instead of saving) and health (obesity, the risk of cardiovascular disorders, substance misuse).

Table 3.4 Results of the multiple regression.

Dependent variable	Predictors	B	SE	Beta	t	Sig.	R	R Square
MCQ log k	(Constant)	-2.11	0.04		-58.96	< .001	0.279	0.078
	IPT	0.01	0	0.19	3.92	< .001		
	Gender	0.3	0.08	0.17	3.76	< .001		
	BPQ	0.06	0.03	0.08	1.85	0.065		
	Positive Affect	0.01	0	0.07	1.46	0.144		
	BAS	0.01	0.01	0.04	0.84	0.402		
	Age	0	0.01	0.03	0.69	0.492		
	Neg Emotions	0	0	0.01	0.27	0.784		
	BIS	0	0.01	0.01	0.17	0.869		
	SS	-0.01	0.01	-0.07	-1.38	0.167		
PD ln h	(Constant)	0.31	0.02		15.37	< .001	0.212	0.045
	BAS	-0.01	0	-0.12	-2.39	0.017		
	Age	0.01	0	0.1	2.37	0.018		
	BPQ	0.03	0.02	0.06	1.46	0.144		
	Gender	-0.06	0.05	-0.06	-1.35	0.179		
	SS	0	0	-0.07	-1.31	0.19		
	Neg Emotions	0	0	-0.05	-1.07	0.284		
	Positive Affect	0	0	0.03	0.75	0.454		
	IPT	0	0	0.03	0.58	0.565		
	BIS	0	0.01	0	-0.07	0.944		
MFFT IS	(Constant)	0.01	0.07		0.15	0.88	0.198	0.039
	IPT	0.01	0	0.12	2.37	0.018		
	Age	-0.02	0.01	-0.08	-1.79	0.074		
	BPQ	-0.1	0.06	-0.07	-1.53	0.127		
	SS	-0.01	0.01	-0.08	-1.49	0.138		
	BAS	0.02	0.01	0.06	1.21	0.228		
	Neg Emotions	0	0	0.05	1.08	0.281		
	BIS	-0.02	0.02	-0.05	-0.94	0.348		
	Gender	-0.13	0.15	-0.04	-0.86	0.391		
	Positive Affect	0	0.01	0.03	0.53	0.594		

BPQ – Body perception questionnaire score, SS – Sensation Seeking, BIS – Behavioral Inhibition Scale score, BAS – Behavioral Approach Scale score, Neg Emotions – Negative Emotional State (DASS and NA), IPT – Impulsive Personality Trait, MCQ log k – Monetary Choice Questionnaire log transformed k parameter, PD ln h – Probability Discounting ln transformed parameter h, MFFT IS – Matching Familiar Figures Task Impulsivity Score.

A relationship was also observed between emotional state and trait measures: High levels of positive affect were associated with high levels of sensation seeking and reward impulsivity (SS and BAS) and low levels of both BIS and impulsive traits (IPT). The reverse was true for high levels of negative emotions. The fact that self-reported trait measures were related to state mood-measures merits comment since they are usually considered to be stable personality traits, unaffected by

changes in mood (Weafer *et al.*, 2013). The positive association between self-reported impulsivity and negative emotions corroborates with findings from clinical populations indicating increased impulsive tendencies in depressed individuals (Peluso *et al.*, 2007; Tomko *et al.*, 2015). Moreover, similarly to previous research (Sperry *et al.*, 2016), higher sensation seeking (SS) ratings were associated with higher positive affect.

However, since these are correlational measures, causality cannot be assumed. Nevertheless, it is plausible that while experiencing negative emotions, individuals may recall events when they behaved impulsively (memory bias) and be primed to behave the same way. Alternatively, engaging in impulsive actions may serve as a way of regulating one's mood (Tice *et al.*, 2001). Thus, it seems that emotional state is a consideration when assessing trait impulsivity.

It is noteworthy that the impulsive personality trait (IPT; as identified here) was related to negative emotions, whereas levels of sensation seeking (SS) were associated with positive affect. This dissociation between impulsive and risk-taking traits was further supported by component loadings within the principal component analysis, which separated SS from the remaining UPPS-P subscales. Indeed, although sensation seeking is encompassed within some constructs of impulsivity (Zuckerman, 1984; Whiteside & Lynam, 2001), other research suggests a differentiation between these two concepts (Magid *et al.*, 2007). Our findings also show that sensation seeking is distinct from trait impulsivity.

Delay discounting and reflection impulsivity were both predicted by the self-reported impulsivity (IPT), while risk-taking (probability discounting) was explained solely by BAS. Indeed, although early research suggests that delay and probability discounting are both facets of impulsive choice, sharing underlying processes (e.g. Mazur, 1993; Rachlin, 1990; Richards et al., 1999), more recent work argues that these two concepts are distinct from each other (Holt *et al.*, 2003; Madden *et al.*, 2009; Shead & Hodgins, 2009). Our findings agree with the latter, suggesting that delay and probability discounting reflect distinct aspects of decision-making, indexing delayed gratification and risk-taking/reward sensitivity respectively.

In agreement with an earlier report (Silverman, 2003), we observed that males showed significantly more delay discounting than females. The reason why gender may play such a role, what the mechanisms and potential consequences are, should be a subject of the future research.

Impulsive personality traits, which include facets of emotional impulsivity, predicted performance on the delay discounting task, supporting our hypothesis. It is worth noting that in both delay and probability discounting, our models explained only a small fraction of the variance, which suggests that other factors are contributing to discounting which are yet to be identified.

The MFFT task has been widely used to study reflection impulsivity in children and other target populations (Kagan, 1965; Verdejo-García *et al.*, 2008; Carretero-Dios *et al.*, 2009). However, it has been heavily criticised as a measure of behavioural impulsivity (e.g. Block et al., 1974) and suggested to be more related to cognitive performance more generally rather than behavioural impulsivity (Block *et al.*, 1986; Perales *et al.*, 2009). Our results indicate that impulsive personality trait is the best predictor of performance on the MFFT task, also supporting the classification of MFFT performance as a measure of reflection impulsivity (Caswell *et al.*, 2015).

In contrast to our expectations, no relationship was found between subjective interoceptive sensibility (BPQ) and probability discounting. This is distinct from previous research which reported the relationship between risk-taking or disadvantageous decision-making and individual differences in interoception (Werner *et al.*, 2009; Kandasamy *et al.*, 2016). These discrepancies may be due to methodological aspects of the measures employed. In the current study, we used a probability discounting task, which is an explicit measure of risk-taking. Using a more implicit measure of risk-taking, e.g. a gambling task, alongside a dimensional approach to quantifying (subjective objective and metacognitive) interoceptive abilities (Garfinkel *et al.*, 2015) could provide much finer grained insight into how interception relates to impulsivity, extending previous findings. Instead, we found a trend for bodily awareness to predict temporal discounting, indicating that heightened subjective sensitivity to bodily sensations (i.e. higher interoceptive sensibility, often characteristic of more anxious individuals) may result in increased temporal impulsivity. Similarly, the observed relationship between BPQ and negative emotions is also consistent with the association between interoception and anxiety (e.g. Pollatos *et al.*, 2009; Dunn *et al.*, 2010; Stevens *et al.*, 2011; Garfinkel *et al.*, 2015).

3.5.1 Limitations

Some study limitations merit comment. Firstly, this study relied on survey data obtained via an online questionnaire. There was consequently little experimental control over the circumstances in which participants completed the study, which should be considered. Future research may benefit from more controlled environments, e.g. as a typical lab-based study, to validate these findings. Secondly, despite recruiting participants online, our sample consisted mainly of female participants and a very small proportion of older adults. In the future, a more gender-balanced sample also including elderly should be studied to confirm these findings.

3.5.2 Conclusions

Our results indicate that impulsive personality traits predict temporal and reflection impulsivity, while reward sensitivity predicts risk-taking behaviour (probability discounting). This separation between measures of impulsivity and risk-taking suggests that the two concepts are distinct. The dissociation between measures of impulsivity and risk-taking was further highlighted by their relationship to the current emotional state: While increased negative emotions were predictably associated with increased impulsivity, increased positive affect was associated with increased measures of risk-taking. This interesting finding has important consequences for research since it suggests that the same person may show different levels of trait impulsivity in a positive (less impulsive) than a negative (more impulsive) mood state. Thus, future research into trait impulsivity should attend to concurrent mood states of participants. Marginal findings of the present study also motivate areas of further research: The fact that negative emotions were related to increased temporal impulsivity may indicate at least partly why people in a positive mood are likely to make commitments, such as keeping to a diet or exercising regularly – that is when they can oversee long-term goals over immediate goals. Consequently, in a negative emotional state, perception shifts towards immediate gratification (e.g. comfort food, watching television series instead of going to the gym). Moreover, our findings with the BPQ link subjective body awareness to temporal impulsivity suggesting the need for in-depth understanding of the relationship between interoceptive ability and decision-making.

Conflict of Interests

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

Author Contributions

AH collected and analysed data and wrote the initial manuscript. AH and TD interpreted the results. TD provided a guidance throughout. All authors contributed to the experimental design and the final version of the manuscript.

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CHAPTER 4.

STUDY 3.
THE ROLE OF EMOTIONAL CONTEXT AND IMPULSIVE TRAITS ON SELF-CONTROL AND ITS NEURAL SUBSTRATES

Methods and partly results from this study have been published in the European Journal of Neuroscience:

Herman, A. M., Critchley, H. D., & Duka, T. (2018). Binge drinking is associated with attenuated frontal and parietal activation during successful response inhibition in fearful context. *European Journal of Neuroscience* (in press). https://doi.org/10.1111/ejn.14108

Contribution

I contributed to the study design and the interpretation of the results. I collected and analysed the data as well as prepared the initial manuscript.

4.1 Abstract

The capacity for self-control is highly adaptive and fundamental to completing many daily tasks. However, negative emotions may deplete self-control resources, leading to an increase in impulsive actions and decisions. However, the neural mechanisms through which negative emotions alter self-control are not fully understood. The current study quantified the effect of negative (fearful) emotional context on prepotent response inhibition and delay discounting in a group of university students (N = 30) and used functional neuroimaging to identify neural correlates. We further tested how trait impulsivity related to functional connectivity within resting-state networks. During successful response inhibition, activation of prefrontal and parietal cortices was amplified in individuals with higher trait impulsivity. Fearful, compared to neutral, affective context further enhanced this effect, consistent with the need of impulsive individuals to engage more neural resources for successful inhibitory control in a negative emotional context. Temporal discounting was unaffected by emotional context and trait impulsivity. Resting-state functional connectivity analysis revealed that trait impulsivity was related to weaker coupling between lateral occipital cortex and the Somatomotor Network. This suggests that the coordination between sensory (visual, somatosensory) representation and behavioural output (motor actions) may be disrupted in highly impulsive individuals, resulting in maladaptive behaviours and suboptimal decisions. Together, our findings provide fresh insight into the neural mechanisms of successful response inhibition, highlighting a need for impulsive individuals to recruit greater neural resources, particularly in negative emotional context, potentially to compensate for decreased functional connectivity of the Somatomotor Network.

Keywords: Trait impulsivity, Stop Signal Task, Delay Discounting, Emotions, fMRI, Resting-State Functional Connectivity

4.2 Introduction

Self-control allows people to make plans for the future, choose the best option out of several alternatives, control impulses, inhibit unwanted thoughts, and regulate behaviours and emotions (Kelley *et al.*, 2015). However, emotional distress and negative affective states deplete limited self-control resources and lead to impulsive actions and decisions (Muraven & Baumeister, 2000; Heatherton & Wagner, 2011; Kelley *et al.*, 2015). Indeed, the tendency for people to engage in impulsive actions while experiencing emotional distress may reflect an attempt to regulate present mood state at the cost of suboptimal future consequences (Tice *et al.*, 2001).

Behavioural self-control is not only altered by the profound experience of distress, but also by task-unrelated emotional context. For example, being surrounded by anxious individuals may be sufficient to affect the way we make decisions: a negative context is associated with steeper temporal discounting of delayed rewards (i.e. more impulsive decisions with increasing impatience; Augustine & Larsen, 2011; Guan *et al*., 2015).

Research on emotional effects on behavioural response inhibition (i.e. motor impulsivity) does not always yield consistent results. Some studies suggest that neither task-independent emotional context nor emotional primes affect response inhibition in modified versions of commonly used motor impulsivity tasks (Sagaspe *et al.*, 2011; Brown *et al.*, 2012; Guan *et al.*, 2015; Chester *et al.*, 2016; Littman & Takács, 2017). Other research, however, observes impaired inhibitory control in the fearful compared to neutral contexts (Verbruggen & De Houwer, 2007; Kalanthroff *et al.*, 2013; Patterson *et al.*, 2016). Moreover, the context of anger seems to improve response inhibition in male participants (Pawliczek *et al.*, 2013).

Neuroimaging has contributed towards understanding the relationship between emotions and self-control. Failures in self-regulation appear to be the result of diminished 'top-down' prefrontal control over subcortical centres for reward and emotion (e.g. nucleus accumbens and amygdala; Heatherton & Wagner, 2011). Correspondingly, lesions to the medial orbitofrontal cortex lead to diminished self-control with an increased preference for immediate gratification despite its being more advantageous to wait for a larger reward (temporal impulsivity; Peters & D'Esposito, 2016; Sellitto *et al*., 2010). However, the hypothesis that the functional integrity of prefrontal cortices also underpins the impact of negative emotional contexts on impulsive behaviours, including difficulty in delaying gratification, remains untested.

In motor impulsivity, successful deployment of behavioural inhibitory control also requires recruitment of more lateral orbitofrontal and prefrontal regions (Fassbender *et al.*, 2006; Aron, 2007; Aron *et al.*, 2007; Deng *et al.*, 2017). However, the effects of negative emotion on motor inhibition are inconsistent, both for behavioural and neuroimaging findings. On the Go/No Go (GNG) task, a measure of action selection and restraint, with task-irrelevant

threatening or neutral images, response restraint in the emotional relative to neutral context was related to an increased recruitment of areas associated with visual attention and conflict resolution with no differences on behavioural performance (Brown *et al.*, 2012). In the Stop Signal Task (SST), inhibitory control is enhanced in the context of anger primes, linked to enhanced recruitment of right pre-supplementary motor area (pre-SMA), right middle frontal cortex and left inferior parietal cortex (Pawliczek *et al.*, 2013). However, in the same (SST) task, equivalent inhibitory control in a fearful, compared to a neutral, context is associated with *reduced* activation of the right inferior frontal gyrus (IFG) (using region of interest approach; Sagaspe *et al*., 2011). Reduced activity in prefrontal cortex (PFC) and lateral parietal cortex is also reported during successful response inhibition in the SST following presentation of fearful emotional primes (Patterson *et al.*, 2016).

Possibly, small samples sizes and individual differences may account for some of these inconsistencies in the literature. For example, certain individuals (e.g. those showing high trait impulsivity) may be more strongly affected by emotional contextual information at both behavioural and neural levels. Indeed, negative urgency describes the propensity to act impulsively while experiencing strong negative emotions. Participants who score high for negative urgency show greater recruitment of inhibitory brain regions when exposed to a negative context during response restraint on the GNG task compared to individuals who score low for negative urgency (Chester *et al.*, 2016). On the other hand, Pawliczek *et al*., (2013) observed that individuals displaying high trait anger are more impaired on the SST than those showing lower trait anger which was accompanied by attenuated activation in brain regions involved in response inhibition, including the pre-supplementary motor area and motor cortex. However, they found no interactions between trait aggression and emotional context (angry faces) on either behavioural or neural level.

4.2.1 Resting State Functional Connectivity

Past studies usually employed task-related functional magnetic resonance imaging (fMRI) to understand transient fluctuations in self-control in different emotional contexts. Although it is well suited to capture momentary brain activity changes in response to various conditions, this traditional approach may be insufficient to capture more tonic aspects of self-control (Kelley *et al.*, 2015). A global whole-brain network approach provides a means to understand how individuals execute self-control over longer timescales. Moreover, measurement of functional connectivity (FC) across ‘resting-state’ (RS) networks provides a valuable tool to address the mechanisms underlying neurocognitive processes and neuropsychiatric disorders which goes beyond activation–dependent modular inferences from task-related changes in regional brain activity (for example Cole *et al.*, 2014; De Luca *et al.*, 2006; Dipasquale *et al.*, 2015; van den

Heuvel & Hulshoff Pol, 2010). Indeed, studies using FC to investigate the interactions between distinct brain regions at rest have been used to study impulsivity and executive functioning in children (Inuggi *et al.*, 2014) and young adults (Davis *et al.*, 2013; Reineberg *et al.*, 2015; Weafer *et al.*, 2015). However, a study looking at associations between trait impulsivity and within- and between-network FC is missing.

4.2.2 Aims

An understanding of the brain mechanisms underlying self-regulation can provide valuable insights into how people regulate and control their thoughts, behaviours, and emotional states and what happens on those occasions when this regulation fails (Kelley *et al.*, 2015). The current study built on previous findings to investigate how emotion-laden conditions (negative affective context) affect response inhibition and temporal decision-making in healthy individuals who differ in their levels of trait impulsivity. We predicted that fearful context might disrupt self-control mechanisms at the behavioural level resulting in more impulsive behaviours, especially in individuals who show increased levels of trait impulsivity. At the neural level, we hypothesised that successful response inhibition in a fearful context would be supported by increased activity in the prefrontal cortex (Sagaspe *et al.*, 2011). Moreover, based on previous findings, we suspected that internal architecture of the default mode (Inuggi *et al.*, 2014), frontoparietal and attentional networks (Reineberg *et al.*, 2015) might be affected by trait impulsivity.

4.3 Materials and Methods

4.3.1 Participants

Thirty volunteers (9 men) were recruited from staff and students of the University of Sussex. Participants were required to be between 18 and 40 years old and right-handed. Exclusion criteria included history of any mental or neurological disorders, head injury, current treatment for any psychological or physical condition (including use of inhalers; excluding the contraceptive pill), pregnancy or breastfeeding, clinically significant impairment of vision, taking any psychoactive substances 48 hours before testing, and any MRI contradictions (claustrophobia, having any metal implants, teeth braces or bridges, or cardiac pacemakers).

All participants provided written informed consent. The study was approved by the Brighton and Sussex Medical School Research Governance and Ethics Committee.

4.3.2 Questionnaires

Participants completed the *Barratt Impulsiveness Scale* (BIS; Patton et al., 1995) and *UPPS-P Impulsive Behaviour Scale* (Whiteside & Lynam, 2001; Cyders & Smith, 2007), which are established self-report measures of trait impulsivity levels. Both questionnaires were used as UPPS-P contains measures of emotion-based impulsivity (i.e. positive and negative urgency), which assess the tendency to act impulsively while experiencing strong emotional states. For this study, our variables of interest were BIS Total score and UPPS Negative Urgency subscale.

4.3.3 Tasks

For the task-based fMRI investigation, we used an event-related fMRI paradigm. Before the fMRI session, all volunteers also underwent training outside the scanner to familiarise them with the tasks and to ensure they follow the instructions correctly.

During scanning, stimuli were back-projected onto a mirror mounted on the head coil and presented centrally against a homogeneous grey background. We used Cogent 2000 (Wellcome Dept., London, UK) in MATLAB (Mathworks Inc.) for stimulus presentation, the timing of stimuli and response events, and synchronisation with fMRI image acquisition. In both tasks, the emotional context was task-irrelevant.

Affective Stop Signal Task (ASST)

The ASST was based on a modified version of the SST based on previous work (Sagaspe *et al.*, 2011; Pawliczek *et al.*, 2013) with timings taken from the standard version of the task used in the laboratory, as described previously (Nikolaou *et al.*, 2013). Instead of arrows, participants were presented with facial expressions from the FACES database (Ebner *et al.*, 2010) of males and females (50% each) displaying either fear or neutral expression (50% each).

Each trial started with a central fixation cross for 1200-1500ms (jittered). Presentation of the Go-stimulus (a facial expression surrounded by a white frame) followed, which on the Go-trials remained on the screen for the total stimulus display duration of 800ms. On the Stop-trials, the Go-stimulus was replaced by the Stop Stimulus (the same picture surrounded by a yellow frame) after a variable stimulus onset asynchrony (SOA) period (see Figure 4.1). Initial SOA was 200ms and was adjusted according to a staircase procedure depending on individual performance separately for each emotional condition, to obtain a probability of stopping 0.5 for each condition. SOA increased 50ms every time the participant inhibited their response (Stop Success, SS) or decreased by 50ms every time the participant was unable to withhold their response (Stop Fail, SF). The Stop-Signal Reaction Time (SSRT) was calculated separately for neutral (NeuSSRT) and fearful (FeaSSRT) trials by subtracting the mean SOA from the average

reaction time (RT) to correct Go-trials (GoC; neutral or fearful, respectively). Further, dependent variables included Go RT and Go Accuracy.

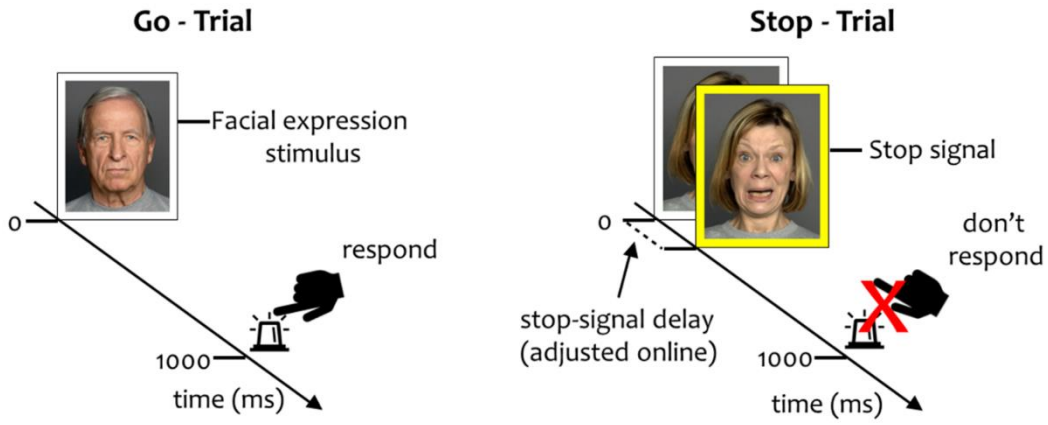

Figure 4.1 The Affective Stop Signal Task. The panel on the left shows an example of a Go trial (neutral condition), during which participants had to indicate with the appropriate button-press the gender of the face presented in the picture, irrespective of emotional expression. Participants had up to 1000ms to respond. The panel on the right shows an example of the Stop trial (fearful condition). The sudden change in the colour of the frame surrounding the picture (the Stop signal) meant that participants had to withhold (inhibit) their response (indicating perceived gender) and not press any buttons. The timing of the change in the frame's colour during Stop-trials (stop-signal delay) was adjusted online in accordance with the participants' performance: after a successful response inhibition, on the next Stop trial of the same emotional condition, the delay period was increased, making it more difficult to stop, while following an unsuccessful Stop trial, the delay was decreased, making it easier to withhold a response.

On the Go-trials, participants were instructed to respond with an appropriate button-press to indicate whether the face displayed on the screen was male or female (implicit emotional context) as quickly as possible and to try and withhold their responses when the frame surrounding the picture changed colour (Stop-trials). Participants were informed that speed and accuracy on task are equally important and that they should not be delaying their responses to see whether the frame would turn yellow.

Participants completed two runs of 160 trials each separated by a 1-minute break to allow them to relax. In total there were 120 Go Neutral, 120 Go Fearful, 40 Stop Neutral, and 40 Stop Fearful trials.

Affective Delay Discounting Task (ADD)

The second task was a modified delay discounting task, which measures the ability to delay gratification. Participants were presented with black and white facial expressions of (50% male, 50% female, 50% neutral, 50% fearful) from the NimStim (Tottenham *et al.*, 2009) and Radbound Faces (Langner *et al.*, 2010) Databases. Each trial started with a 1200-1500ms (jittered) central fixation cross. Then, a facial expression was presented in the centre of the screen for 2 seconds, followed by a different face of a congruent emotional expression (fearful or neutral) accompanied beneath by a question with two possible answers, displayed below the image, for example, "Would you prefer: £10 now, or £25 next week?" (Figure 4.2). The order of the immediate and the delayed options display was randomised. Participants were required to

respond by pressing an appropriate button. The trial was terminated after a response button was pressed or 7s has elapsed, whichever came first. Moreover, the participants were instructed to pay attention to each facial expression presented on the screen and imagine that the person in the image asks the question displayed below. Participants completed one run of 54 trials (27 neutral, 27 fearful trials in a randomised order) each. 27 items were taken from the Monetary Choice Questionnaire (Kirby *et al.*, 1999) and another 27 questions were adapted version matched for k values was developed (see Appendix). For each emotional condition, a k value (log transformed) and average decision RT for each condition were computed.

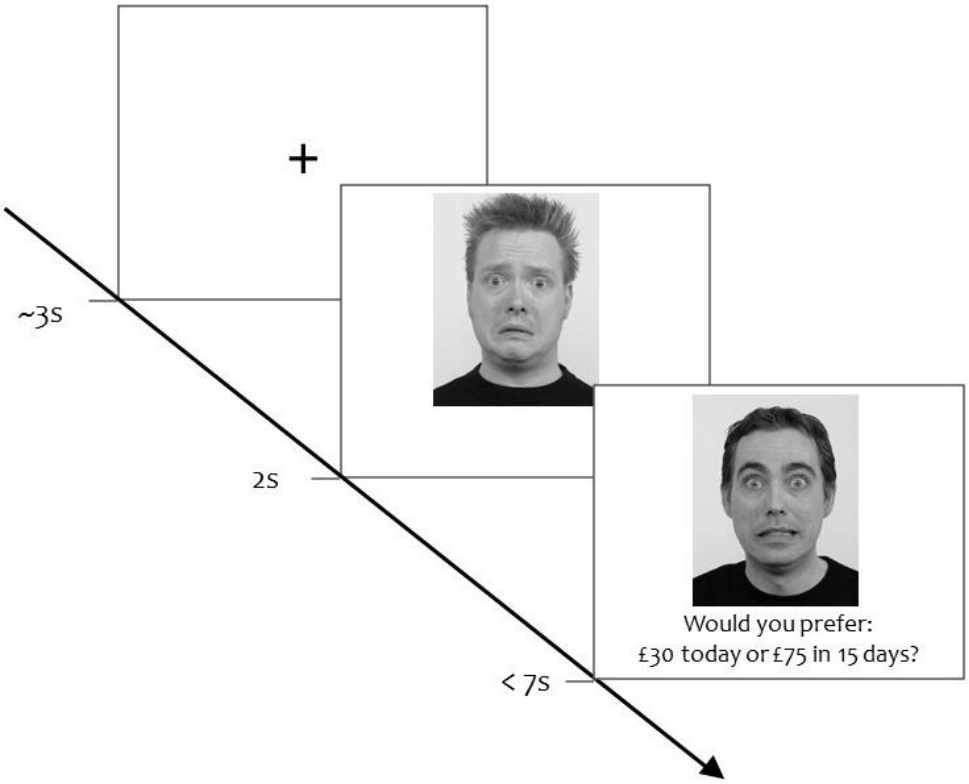

Figure 4.2 The Affective Delay Discounting Task. Each trial began with the presentation of a fixation cross (jittered between 1.2-1.5s). Next, a facial expression was presented on a screen for 2s, followed by a presentation of a different face depicting the same emotion (fearful or neutral) accompanied by a question; asking the participants to choose between a smaller monetary reward available immediately and a larger reward available after a delay. Participants were required to make a choice by pressing an appropriate button. They had up to 7s to decide.

4.3.4 MRI experiment design

In the MRI scanner, first, a structural scan was obtained followed by a 7-minute resting-state scan (165 volumes) during which participants were instructed to rest with their eyes open focusing on a fixation cross in the centre of the screen without thinking of anything and not falling asleep. Subsequently, ASST and ADD were completed. The total time spent in the

scanner by each participant did not exceed 50 minutes. All participants were tested between 2 pm and 6 pm to control for possible time of day effects on an attentional level.

MRI Acquisition

MRI was performed on a 1.5-Tesla MAGNETOM Avanto scanner (Siemens AG, Munich, Germany). Structural volumes were obtained using the high-resolution three-dimensional magnetisation prepared rapid acquisition gradient echo sequence. Functional data sets used T2*-weighted echo planar imaging sensitive to blood oxygenation–level-dependent signal (repetition time = 2.52 seconds, echo time = 43 ms, flip angle = 90°, 34 slices, 3-mm slice thickness, field of view = 192 mm, voxel size = 3 × 3 × 3 mm). Slices were angled -30° in the anteroposterior axis to reduce the signal loss in orbitofrontal regions (Deichmann *et al.*, 2003; Weiskopf *et al.*, 2006).

4.3.5 Statistical Analysis

Behavioural and trait measures

The differences in performance between the fearful and neutral conditions were investigated using paired-samples t-tests. Additionally, the potential differences in decision RTs on the ADD were analysed with repeated measures analysis of variance (ANOVA). To test the interaction between trait impulsivity and the difference in performance between the emotional conditions, we calculated subtraction scores (FeaSSRT-NeuSSRT, Fealogk-Neulogk) and computed correlation scores with trait impulsivity (BIS total and negative urgency). The analysis was conducted in SPSS v22.

fMRI Data Preprocessing

Imaging analysis was performed using FEAT (FMRI Expert Analysis Tool) version 6.00, a part of FMRIB Software Library (FSLv6.0, Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012). Pre-processing steps included (1) skull stripping of structural images with Brain Extraction Tool (BET), (2) removal of the first four functional volumes to allow for signal equilibration, (3) head movement correction by volume-realignment to the middle volume using MCFLIRT, (4) global 4D mean intensity normalization, (5) spatial smoothing (6mm full-width half-maximum), and (6) noise signals removal, (7) temporal high-pass filtering (90s cut-off for task-related data, and 100s for resting-state data).

FMRI datasets were co-registered to the participant's structural image using affine boundary-based registration as implemented in FSL FLIRT (Jenkinson & Smith, 2001; Jenkinson *et al.*, 2002) and subsequently transformed them to MNI152 standard space with 2mm isotropic resolution using non-linear registration through FSL FNIRT (Andersson *et al.*,

2010). Noise signals were identified individually and removed using ICA-AROMA toolbox (Pruim *et al.*, 2015). ICA-AROMA incorporates probabilistic Independent Component Analysis (ICA) on the partly pre-processed single-subject fMRI data (following spatial smoothing and normalisation but before high-pass filtering), identifies independent components (ICs) representing motion artefacts and removes them from the fMRI time-series using linear regression.

Task-related fMRI analysis methods

Statistical analyses were performed using the general linear model as implemented in FEAT. Customized square waveforms representing each event type and the duration of stimulus presentation were convolved with a double-gamma hemodynamic response function, and a high pass filter (90 s) was applied to remove low-frequency artefacts. For the ASST, events were modelled at the onset of the Go-stimuli. Several types of events were distinguished for the ASST for each condition (Neutral and Fearful): go correct (NeuGoC and FeaGoC), go incorrect (NeuGoI and Fea GoI), stop success (NeuSS and FeaSS), stop fail (NeuSF and FeaSF). For the ADD, three event types were identified for each emotional condition: face presentation (Neutral or Fearful), immediate (NeuImm and FeaImm) and delayed option selected (NeuDel and FeaDel).

Functional MRI data were subsequently analysed using voxel-wise time series analysis within the framework of the General Linear Model. Mixed-effects analysis of group effects was carried out using the FMRIB Local Analysis of Mixed Effects (FLAME). Final Z statistical images were thresholded using Gaussian random field–based clusters determined by $Z > 2.3$ (family-wise error corrected) and a cluster significance threshold of $p < 0.05$ across the entire brain (Worsley, 2001; Heller *et al.*, 2006).

Since there was a broad age range within our population (18-37yrs) and more females participated in the study, in all reported analyses gender and mean-centred age were added as covariates of no interest at the second level group analysis. Subsequently, we repeated all the analysis with the BIS total score and, separately, Negative Urgency as a covariate of interest to investigate whether more impulsive individuals showed changes in brain activity in the tasks.

Several contrasts of interest were computed. Specifically, for the ASST the main contrast of interest regarded the emotional context vs successful response interaction term ([FeaSS-FeaGoC]-[NeuSS-NeuGoC]). For completeness, we also computed the successful response inhibition regardless of the emotional context (SS>GoC) contrast; however, since our main focus was on the role of the emotional context, these results are reported in the Appendix. The main contrast for the ADD was the interaction term of brain activity related to choosing a delayed and immediate reward in fearful vs neutral context ([FeaDel-FeaImm]-[NeuDel-NeuImm]). Additional contrasts [i.e. making a decision relative to just passive facial expression

viewing regardless of the emotional context (Choosing-Face) and choosing larger delayed versus smaller immediate rewards irrespective of the emotional context (Del-Imm)] are described in the Appendix.

4.3.6 Resting state-data

Independent components analysis

The RS data preprocessing and analysis pipeline is summarised in Figure 4.3. To decompose the RS data into various independent spatiotemporal components, Probabilistic Independent Components Analysis (PICA) was performed on the preprocessed functional scans using Melodic version 3.14 (Beckmann & Smith, 2004). A dimensionality estimation using the Laplace approximation to the Bayesian evidence of the model order (Beckmann & Smith, 2004) produced 11 spatiotemporal components. Following an approach described in Reineberg *et al.* (2015), we statistically compared the spatial map of each independent component (IC) to a set of 7 reference RS networks from a previous large-scale RS analysis (Yeo *et al.*, 2011). We used FLS's "fslcc" tool to calculate Pearson's r for each pairwise relationship and kept only those ICs that yielded a significant spatial correlation (Pearson's r > .3) with one of the reference networks. This procedure identified and helped label ten target ICs (see Table 4.1 for details). Upon visual inspection, the remaining 1 IC was considered noise and was not subjected to further analysis.

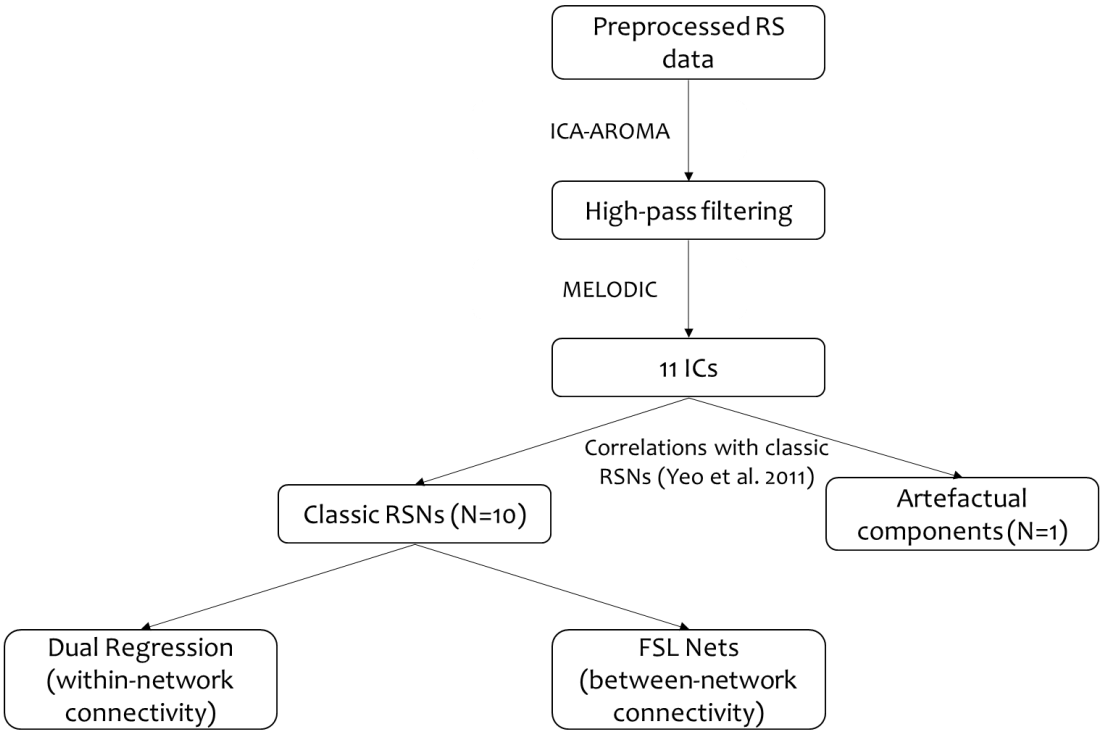

Figure 4.3 Resting-state functional fMRI data preprocessing and analysis pipeline. RS – Resting state, ICA - Independent Component Analysis, ICs – Independent Components, RSNs – Resting State Networks.

Table 4.1 Identified Independent Components (IC Number) and their characteristics. DMN – Default Mode Network.

IC Number	Matching Template Network	Correlation with the Template (Pearson's r)	Regions	Lateralisation	Number of Voxels
1	Visual	0.745	Cuneal Cortex, Intracalcarine Cortex, Occipital pole	bilateral	1138587
2	DMN	0.746	Precuneus, Lateral Occipital Cortex, Middle Frontal Gyrus	bilateral	761539
3	Dorsal Attention/ Visual	0.579/0.359	Lateral Occipital Cortex, Occipital Pole, Middle Frontal Gyrus, Middle Temporal Gyrus, Precentral Gyrus, Precuneus	bilateral	1003173
4	DMN	0.469	Frontal Pole, Precuneus, Middle Temporal Gyrus, Subcallosal Cortex, Superior Frontal Gyrus	bilateral	266631
5	DMN	0.548	Frontal Pole, Angular Gyrus, Supramarginal Gyrus, Frontal Orbital Cortex, Inferior Frontal Gyrus, Middle Frontal Gyrus, Cerebellum	bilateral	670689
6	Ventral Attention	0.454	Supramarginal Gyrus, Inferior Frontal Gyrus, Frontal Pole, Latreal Occipital Cortex, Precentral Gyrus, Frontal Operculular Cortex, Insula, Cingulate Gyrus	bilateral	181331
7	Somatomotor	0.746	Postcentral Gyrus, Precentral Gyrus, Insula, Lateral Occipital Cortex, Cingulate Gyrus	bilateral	898845
8	Frontoparietal	0.329	Middle Frontal Gyrus, Lateral Occipital Cortex, Occipital Fusiform Gyrus, Middle Temporal Gyrus, Frontal Pole	left	944938
9	Frontoparietal	0.513	Middle Frontal Gyrus, Lateral Occipital Cortex, Middle Temporal Gyrus, Cerebellum, Paracingulate Gyrus, Cingulate, Frontal Pole, Insular Cortex	right	689400
10	Ventral Attention	0.301	Frontal Pole, Paracingulate Gyrus, Cerebellum, Superior Frontal Gyrus, Frontal Opercular Cortex, Juxtapositional Lobule, Insular Cortex, Occipital Fusiform Gyrus	bilateral	211073

Dual regression

Next, we performed dual regression to generate subject-specific spatial maps and time courses from un-thresholded group-level ICs maps (Beckmann *et al.*, 2009; Filippini *et al.*, 2009). The dual regression consists of (1) a spatial regression of the group-average set of ICs, which produces a set of subject-specific time series, one per group-level component, and (2) a

temporal regression of those subject-specific time series, resulting in a set of subject-specific spatial maps, one per group-level component.

We quantified the within-network variation in functional connectivity (FC), depending on BIS total score and subject-specific ICs, using Randomise, FSL's nonparametric permutation testing tool (Winkler *et al.*, 2014), with 5000 permutations and threshold-free cluster enhancement (TFCE) with an alpha level of 0.05 to correct for multiple comparisons. The permutation testing procedure was run for each set of subject-specific ICs (one for each group-level ICs of interest); thus, the resulting statistical images reveal how variation in RS FC predict differences in trait impulsivity. Following studies using similar procedures (Uddin *et al.*, 2013; Nomi & Uddin, 2015; Reineberg *et al.*, 2015; de Bézenac *et al.*, 2017), further correction for multiple component testing was not applied.

Between-network connectivity: FSL Nets

To examine the relationship between trait impulsivity and between-network FC, we employed the FSL Nets package implemented in Matlab (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSLNets). This analysis involved correlation of the participants' time courses from the dual regression analysis and subjects them to between-network comparisons to determine how they are correlated with each other (Smith *et al.*, 2013). BIS total score was then used to predict full and partial correlation values using FSL randomise with 5000 permutations.

4.4 Results

4.4.1 Exclusions

No participant was removed due to extensive motion in the scanner. Two participants showed no discounting (consistently chose the delayed reward), i.e. they lacked events for delayed trials. Therefore, these datasets were excluded from the fMRI and behavioural analysis for the ADD task entirely. As such, the sample for the ADD task consisted of 28 participants (9 males). No one was excluded from the ASST.

4.4.2 Behaviour:

ASST

There were no differences in the SSRTs or Go RTs between the fearful and neural conditions (see Tables 4.2 and 4.3 for details). However, paired-samples *t*-test indicated that participants were significantly less accurate (e.g. committed more errors) on the Fearful Go trials than Neutral Go trials, $t(29) = 3.30$, $p = .003$, indicating that participants were less

accurate at identifying the gender of fearful faces compared to neutral faces. Accordingly, participants showed higher stop accuracy on the fearful vs neutral trials, indicating it was easier to withhold response in the fearful context, $t(29) = 2.57$, $p = .016$ (see Tables 4.2 and 4.3 for details). Next, subtraction scores between the conditions (FeaSSRT - NeuSSRT) were correlated with trait measures. There were no significant correlations (BIS: $r(30) = -.209$, $p = .269$; Negative Urgency: $r(30) = -.326$, $p = .079$); therefore, we conclude that performance on the task was not dependent on trait features.

Table 4.2 Performance on the ASST and ADD tasks.

Task	Variable		Fearful		Neutral	
		N	Mean	SD	Mean	SD
ASST	SSRT [ms]	30	299.67	44.72	305.77	35.08
	Go RT [ms]	30	573.61	60.81	570.06	57.01
	Go Correct [%]	30	90.06	5.28	92.11	5.21
	Stop Correct [%]	30	52.08	2.87	50.75	4.11
ADD	log k	28	-2	0.98	-1.77	0.83
	Choice Del RT [ms]	28	1547.08	384.5	1620.05	455.58
	Choice Imm RT [ms]	28	1536.92	447.19	1547.51	456.7

Table 4.3 Comparison of performance in the Fearful and Neutral Conditions in ASST and ADD tasks.

					95% Confidence interval	
Variable	t	df	p	Cohen's d	Lower	Upper
SSRT [ms]	-0.65	29	0.522	0.12	-0.24	0.48
Go RT [ms]	1.39	29	0.176	0.25	-1.68	8.77
Go Correct [%]	-3.3	29	0.003	-0.6	-3.33	-0.78
Stop Correct [%]	2.57	29	0.016	0.47	0.27	2.39
log k	-1.22	27	0.232	-0.23	-0.6	0.15

ADD

There were no differences between conditions in discounting parameters (see Tables 4.2 and 4.3 for details). There was also no main effect of decision type (Imm vs Del; $F(1, 27) = 3.06$, $p = .092$, $\eta_p^2 = .10$) or emotion-decision type interaction ($F(1, 27) = 1.07$, $p = .310$, $\eta_p^2 = .04$). However, repeated measures ANOVA revealed a marginally significant effect of emotion on RT ($F(1, 27) = 3.99$, $p = .056$, $\eta_p^2 = .13$), with shorter responses in the fearful context. There were no correlations between the difference in performance on the tasks (Feak - Neuk) and trait measures (BIS: $r(28) = -.19$, $p = .339$; Negative Urgency: $r(28) = .005$, $p = .981$).

4.4.3 fMRI

ASST

There was no emotion vs successful inhibition interaction ([FeaSS-FeaGoC]>[NeuSS-NeuGoC]; no suprathreshold voxels), mirroring behavioural results.

Next, we went on to explore the role of personality traits in the neural correlates of successful inhibitory control. Regression analysis revealed a response type versus emotional context interaction ([FeaSS>FeaGoC]>[NeuSS>NeuGoC]) indicating higher BIS score was associated with increased activity in the right superior parietal lobule, postcentral gyrus and lateral occipital cortex (see Table 4.4 and Figure 4.4). This suggests that more impulsive individuals need to engage greater neural resources to inhibit prepotent motor responses in the fearful environment successfully.

In contrast, regression analysis with Negative Urgency showed no voxels that met threshold criteria for interaction between emotional contexts versus response type interaction.

Table 4.4 Local maxima details and coordinated in MNI space for each cluster of regions identified for the ASST interaction contrast [(FeaSS-GoC) > (NeuSS-GoC)] regressions with BIS Total score. Cluster index refers to a group of voxels encompassing multiple brain areas. 'Voxels' refer to the number of voxels within each cluster. The Harvard-Oxford cortical and subcortical probabilistic atlases were used to identify each region.

Cluster Index	**Voxels**	**P**	**Z-MAX**	**Z-MAX X (mm)**	**Z-MAX Y (mm)**	**Z-MAX Z (mm)**	**Region**	**Side**
1	514	0.004	3.85	20	-38	56	Postcentral Gyrus	R
1			3.76	28	-48	70	Superior Parietal Lobule	R
1			3.46	30	-62	62	Lateral Occipital Cortex	R
1			3.38	24	-56	58	Superior Parietal Lobule	R
1			3.29	18	-40	62	Postcentral Gyrus	R
1			3.23	34	-48	70	Superior Parietal Lobule	R

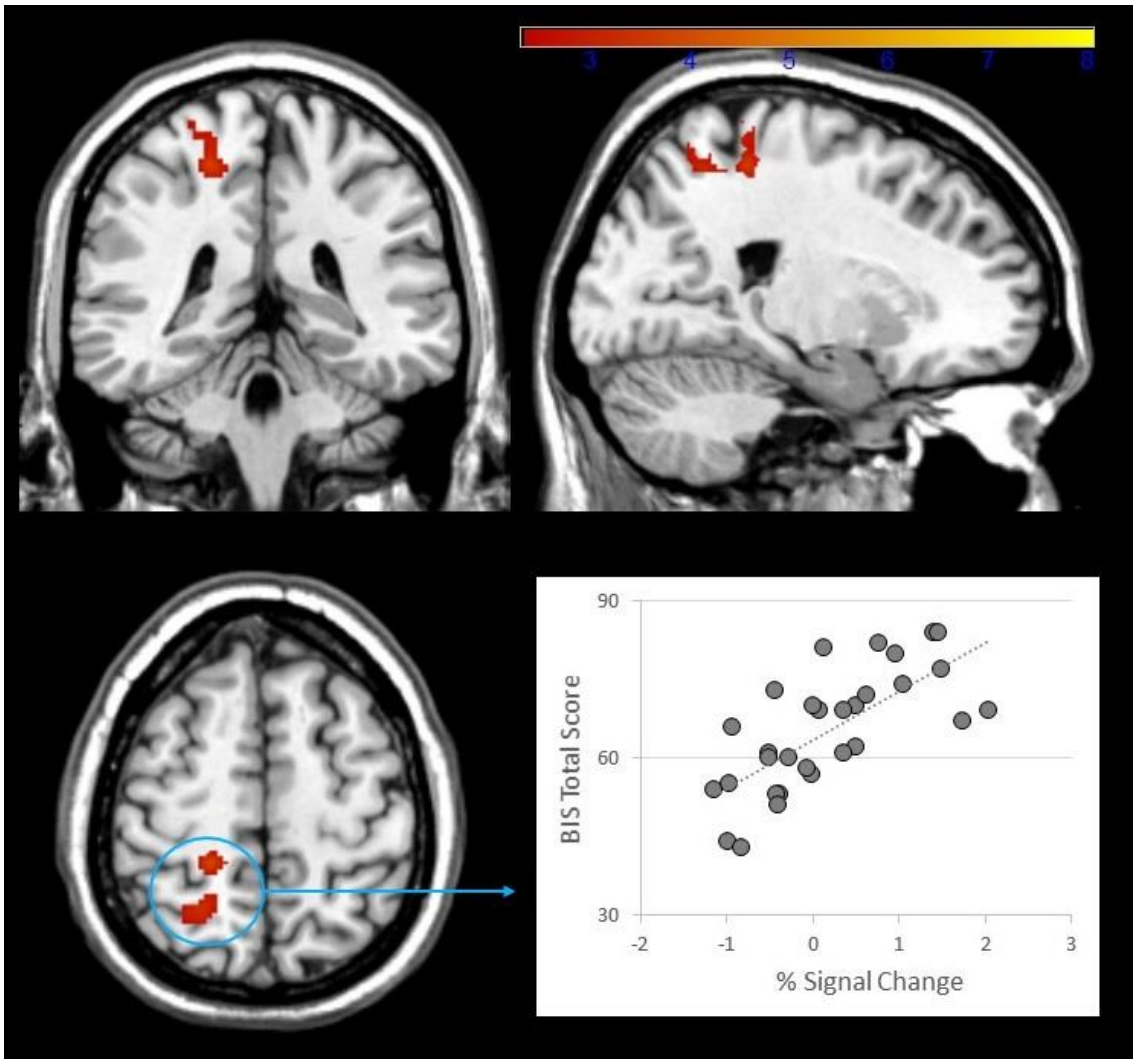

Figure 4.4 Brain regions which showed a significant positive association between BIS Total score and successful response inhibition in the Fearful vs Neutral context (FeaSS-GoC) > (NeuSS-GoC) on the ASST. In the bottom right corner, the illustration of the correlation between the BIS score and the percentage signal change extracted from the region surrounded by the circle. Images are presented in the radiological convention. The colour bar represents Z scores ranging from 2.3 to 8. X = 20 Y = -38 Z = 56

ADD

We observed no suprathreshold neural effects reflecting decision vs emotion interaction ([FeaDel-FeaImm]-[NeuDel-NeuImm]) neither with nor without including trait impulsivity measures into the model.

4.4.4 Resting State Functional Connectivity

Within-network connectivity

Greater self-reported impulsivity (BIS score) was associated with lower coupling of the right lateral occipital cortex with IC7, a network that correlated significantly with Somatomotor template network (peak mm 46/-70/16, FWE 1-*p* = 0.981) (Figure 4.5).

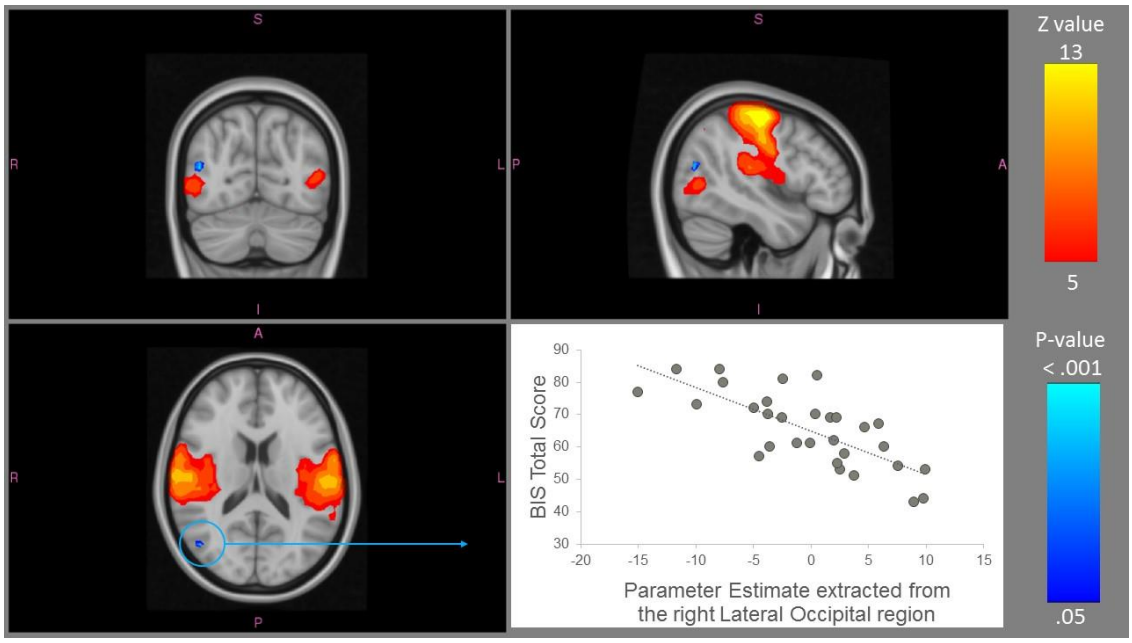

Figure 4.5 Differences in resting-state functional connectivity within IC 7 (Somatomotor Network) associated with individual differences in trait impulsivity (BIS Total Score). The IC overlay derived at the group level is depicted in warm colours, and the region of decreased coupling with the network associated with increased BIS total score is depicted in blue. In the bottom right corner, the illustration of the correlation between the BIS score and the parameter estimates extracted from the lateral occipital cortex region. X = 46 Y = -70 Z = 16. Images are presented in the radiological convention. A-anterior, I-inferior, L-left, P-posterior, R-right, S-superior. IC – Independent Component.

Between-network connectivity

Using BIS or Negative Urgency score as predictors, no significant between-network differences in connectivity were found (Figure 4.6).

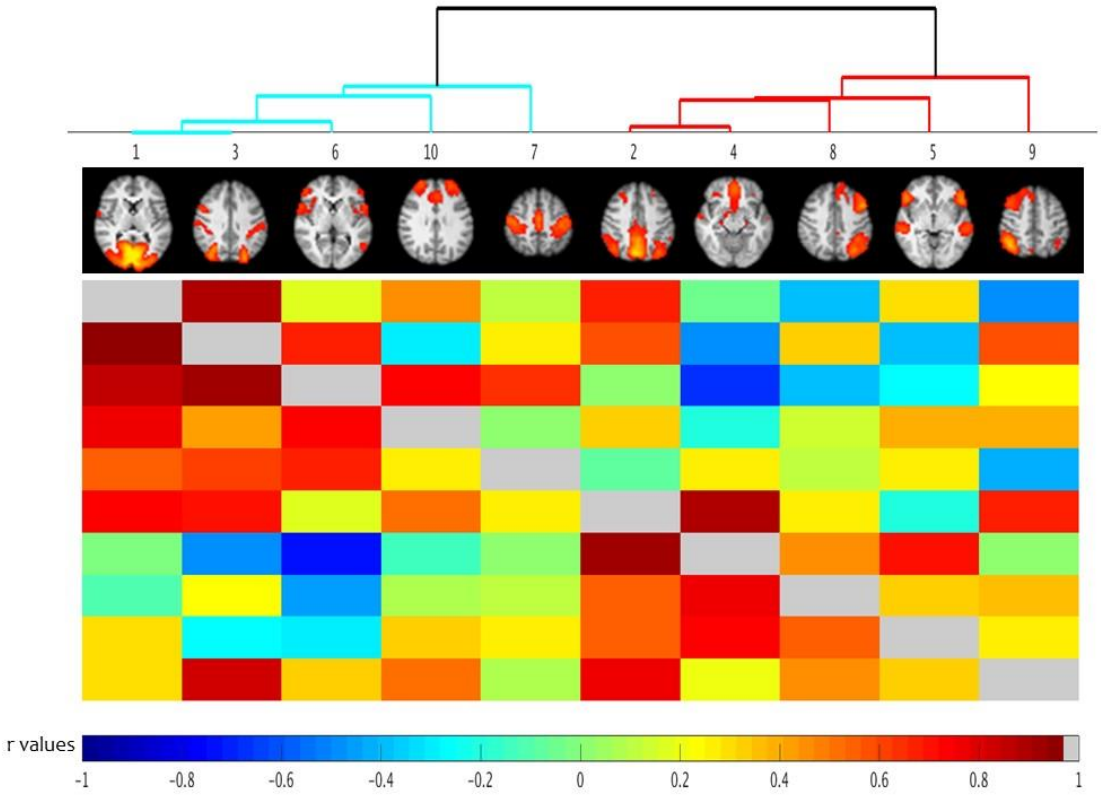

Figure 4.6 FSL Nets between network correlations at the group level (N = 30). Full correlations are shown below the diagonal line (in grey) with partial correlations shown above the diagonal line. Numbers indicate specific independent components as described in Table 4.1.

4.5 Discussion

This study tested the impact of task-irrelevant emotional context (fearful and neutral facial expressions) on behavioural control during performance of motor and temporal impulsivity tasks. We predicted that the context of fear would result in increased impulsive behaviour in both tasks, and correspondingly evoke increased activation of the prefrontal brain regions in support of top-down cognitive control. We also hypothesised that these effects would be enhanced for more impulsive individuals. In fact, our results showed no differences at the behavioural level in either motor response inhibition or temporal discounting between neutral and fearful contexts, contradicting our primary hypothesis. However, brain imaging provided evidence for the role of individual differences in trait impulsivity with regard to the magnitude of recruitment needed to implement response-inhibition successfully. Importantly this effect was enhanced in the presence of the negative emotional context: More impulsive individuals had to engage more neural resources, indicative of a compensatory mechanism.

4.5.1 ASST-behaviour

In agreement with many previous reports, we did not find a direct effect of emotional context on response inhibition measure (i.e. SSRT) (Sagaspe *et al.*, 2011; Brown *et al.*, 2012;

Guan *et al.*, 2015; Chester *et al.*, 2016; Littman & Takács, 2017). Our behavioural data, however, revealed that participants were less accurate at gender discrimination when fearful faces were presented (an implicit emotion processing task). This is in line with previous findings reporting decreased gender discrimination accuracy of fearful vs happy faces (Stockdale *et al.*, 2015) and reduced accuracy on trials preceded by negative in contrast to neutral images (Littman & Takács, 2017). Threat-related stimuli capture attention more than neutral or nonthreat-related stimuli (Pourtois *et al.*, 2004). Even though we did not find significant differences in reaction times between neutral and fearful trials, we did observe that participants showed higher stop accuracy on the fearful compared to neutral stop trials, supporting the attention-capture effect.

4.5.2 ASST-fMRI

We also did not find evidence for a direct effect of emotion on the prepotent response inhibition at the neural level. This may be because we employed an ASST paradigm in which gender categorisation was implicit. Indeed, previous event-related potential findings using an emotional GNG paradigm indicated that the action inhibition stage is modulated by emotional facial information, but only when facial expressions are processed explicitly not implicitly (Yu *et al.*, 2014).

However, we found evidence for excessive neural recruitment during successful inhibitory control in more impulsive individuals, as characterised by their BIS Total score and Negative Urgency score (see the Appendix for details). Importantly, the effect of neural hyper-activation with increased BIS score was stronger in the fearful relative to neutral context, but no such effect was found regarding negative urgency. A stronger activation was observed in the right postcentral gyrus, superior parietal lobule (SPL) and lateral occipital cortex, areas involved in somatosensory processing, visual attention, working memory (Corbetta & Shulman, 2002; Yantis *et al.*, 2002) and object recognition (Grill-Spector *et al.*, 2001). The postcentral gyrus is a primary somatosensory cortex. Previously, an increased postcentral gyrus, parahippocampal and visual cortical activity in post-traumatic stress disorder (PTSD) patients during response inhibition tasks has been interpreted as a state of hyperactive sensory processing during inhibitory control (Falconer *et al.*, 2008). Similarly, enhanced somatosensory and lateral occipital areas activation during successful response inhibition in the fearful versus neutral context in more impulsive individuals in the current study may also reflect increased sensory vigilance in response to fear cues in more impulsive individuals. Given previous reports of ‘compensatory’ prefrontal recruitment during response restraint in individuals scoring high for Negative Urgency in the emotional GNG task (Chester *et al.*, 2016), the fact that we did not observe a similar association between Negative Urgency and inhibitory control in the emotional

context was unexpected. Arguably, this discrepancy may be a result of different tasks employed – a GNG task (Chester *et al*., 2016), which assesses response selection and restraint, and a version of the SST, a measure of prepotent response inhibition, in the current study. The commonalities and differences between these two measures of motor impulsivity and their relationship to BIS and Negative Urgency should be explored in future research.

4.5.3 ADD

We found no differences in temporal discounting at the behavioural level between emotional and neutral conditions. We offer two explanations of these findings. First, the negative emotional context may not affect temporal impulsivity, which would be in contrasts with previous reports (Augustine & Larsen, 2011; Guan *et al.*, 2015). Alternatively, the fearful facial expression may have been insufficiently threatening or arousing to evoke changes at the behavioural level. However, we did observe marginally faster decisions in the fearful relative to neutral context, suggesting that emotional condition did affect the decision-making process at the level of information processing. Possibly if real financial decisions were at stake, the decision-outcomes (delayed and immediate options) would also be affected.

Contrary to expectations, there was also no effect of emotional context on temporal discounting. This matched our behavioural results, where we found no differences in the discounting rate between the conditions. The lack of impact of emotional context on temporal discounting may again be due to the type of stimuli employed (facial expressions), which arguably were not strong enough to impact temporal discounting. Future studies are needed to investigate this matter further.

4.5.4 Functional connectivity

We showed that individual differences in trait impulsivity, assessed with BIS Total Score, are associated with altered aspects of the functional architecture of the Somatomotor RS network. Specifically, higher trait impulsivity was linked to decreased coupling between the lateral occipital cortex and the Somatomotor Network. Surprisingly, we did not find any significant differences in the network functional architecture of default mode or frontoparietal networks associated with impulsivity as has been reported previously (Inuggi *et al.*, 2014; Reineberg *et al.*, 2015). However, it is important to note that previous research used different measures of impulsivity. Therefore, those inconsistent findings might merely reflect a heterogeneous nature of impulsivity and underlying neural mechanisms (Caswell *et al.*, 2015; Herman *et al.*, 2018).

The finding of disrupted FC within Somatomotor RS network in relation to trait impulsivity level corroborates previous studies. Using graph theory approach, Davis *et al*.,

(2013) studied the relationship between impulsivity, reflected in BIS score, and the functional segregation ("modularity") of whole-brain resting state architecture. The analysis revealed shifts in the functional connectivity between visual, sensorimotor, cortical, and subcortical structures across the impulsivity range.

The lateral occipital cortex is involved in visual perception and multisensory integration (Grill-Spector *et al.*, 2001; Beauchamp, 2005). However, the visual cortices may contribute to impulsivity (Davis *et al.*, 2013) and disorders commonly associated with impulsivity, such as ADHD (Castellanos & Proal, 2013). The sensorimotor network consists of both motor cortices, known to play a critical role in response inhibition (Li *et al.*, 2006; Duque *et al.*, 2012; Rae *et al.*, 2014), and somatosensory areas, which are vital for sensory integration and show altered activity in inhibitory control in diseased states (Falconer *et al.*, 2008; van Rooij *et al.*, 2014) or under pharmacological interventions (Schmidt *et al.*, 2017). Therefore, this 'decoupling' of Somatomotor and visual areas may reflect itself in a less effective integration of perceptual information, visual and somatosensory, in behavioural control manifesting itself in impulsive behaviours.

Finally, we did not find any differences in between-network connectivity that could be related to elevated impulsivity levels. Possibly, this is because our sample consisted of highly functioning young adults, all university students, and significant differences in between-network connectivity may only reveal themselves in more disinhibited individuals. Nevertheless, somatosensory cortex and lateral occipital cortex showed increased activation during response inhibition in the fearful context and showed disrupted RS FC in more impulsive individuals. Therefore, these areas revealed by the analysis of a normative population might be crucial to the definition of predictive biomarkers for impulse-control disorders.

4.5.5 Limitations

In the current study, we did not find a robust direct effect of fearful context on either response inhibition or temporal discounting behaviour. Possibly no impact on behaviour is due to the specific stimuli we employed – facial expressions of fear. Heightened emotional arousal can influence response inhibition (Verbruggen & De Houwer, 2007); however, images depicting fearful facial expressions may be insufficiently potent to evoke the requisite level of emotional arousal. Indeed, this may also account for null findings in previous studies of this sort (Sagaspe *et al.*, 2011). Habituation and affective adaptation may also play a role since regions that respond preferentially to emotionally valenced faces, including the amygdala, also rapidly habituate to these stimuli (Breiter *et al.*, 1996). Thus, the length of the study may have attenuated the impact of emotional effects here.

4.5.6 Conclusions

Our results show that impulsive individuals engaged more neural resources in order to implement inhibitory control successfully than less impulsive people. Impulsive individuals also seemed to be more affected by the emotional context, showing raised prefrontal and parietal activation during successful response inhibition in the fearful settings. Interestingly, we observed a dissociation between measures of Negative Urgency and BIS score – the latter proved to be more sensitive to differences between emotional contexts. Therefore, implementing motor self-control in the negative emotional context may be more difficult for persons showing elevated levels of BIS impulsiveness. Nevertheless, emotional facial expressions did not seem to affect measures of temporal impulsivity, regardless of the trait impulsivity levels. In the brain, higher BIS Total was also associated with altered RS FC within the Somatomotor Network. Specifically, impulsive individuals showed greater 'decoupling' between the lateral occipital cortex and the Somatomotor Network. Importantly, both RC FC analysis as well as task-based analysis (ASST) indicated associations between trait impulsivity and activation within the lateral visual and somatosensory cortices. This strengthens the evidence to support the use of these regions as biomarkers for impulse-control problems.

4.6 References

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4.7 Appendix: Supplementary Results and Discussion

4.7.1 Supplementary Results

ASST

We first identified the brain regions engaged in successful response inhibition regardless of the emotional context (SS > GoC). This contrast evoked an expected pattern of activation including superior, middle and inferior frontal gyrus, insular cortex, frontal operculum and dorsal striatum, predominantly in the right hemisphere (see Table S4.1, Figure S4.1).

Next, we went on to explore the role of personality traits in the neural correlates of successful inhibitory control. Regression analysis revealed that individuals with higher BIS Total scores exhibited increased activity within the paracingulate gyrus and supramarginal gyrus, anterior cingulate, middle and inferior frontal gyrus, during successful inhibitory control (SS > GoC). These findings indicate that more impulsive individuals need to engage more neural resources to inhibit motor responses successfully (see Table S4.1, Figure S4.2).

Similarly to the analysis using BIS Total score, regression analysis with Negative Urgency, also revealed that more impulsive individuals show elevated activity in the superior frontal/paracingulate gyrus, superior parietal lobule and frontal pole on the right side, during successful inhibitory control (SS > GoC; Table S4.2, Figure S4.3).

ADD

Choosing an option when passively viewing a facial expression (Choosing-Face viewing), irrespective of the portrayed emotion, activated prefrontal regions (bilateral inferior frontal gyrus, right frontal orbital cortex and frontal pole) and adjacent left insula and frontal opercular cortex (See Table S4.3, Figure S4.4). There were no suprathreshold voxels for main decision type contrast (Del vs Imm).

Regarding the role of impulsive traits, there were no suprathreshold changes in any of the contrasts that correlated with BIS Total score. However, we did observe a main effect of decision type (Del > Imm) with relation to Negative Urgency, suggesting that individuals reporting higher Negative Urgency presented elevated activation in the occipital pole while making delayed responses relative to immediate ones (Table S4.4, Figure S4.5). There were no other significant results.

Table S 4.1 Local maxima for each cluster of regions identified in the ASST successful response inhibition contrast (SS>GoC), controlling for Age and Sex. Cluster index refers to a group of voxels encompassing multiple brain areas. 'Voxels' states the number of voxels within each cluster. The Harvard-Oxford cortical and subcortical probabilistic atlases were used to identify each region.

Contrast: SS > GoC								
Cluster Index	**Voxels**	**P**	**Z-MAX**	**Z-MAX X (mm)**	**Z-MAX Y (mm)**	**Z-MAX Z (mm)**	**Region**	**Side**
6	30272	< .001	5.48	60	-38	0	Middle Temporal Gyrus	R
6			5.46	18	-72	58	Lateral Occipital Cortex	R
6			5.33	44	-46	52	Supramargnal Gyrus	R
6			5.26	26	-72	58	Lateral Occipital Cortex	R
6			5.17	-14	-70	56	Lateral Occipital Cortex	L
6			5.1	50	-44	44	Supramargnal Gyrus	R
5	15111	< .001	5.76	38	48	30	Frontal Pole	R
5			5.46	36	52	30	Frontal Pole	R
5			5.22	34	60	-12	Frontal Pole	R
5			5.02	40	58	-10	Frontal Pole	R
5			4.98	58	18	16	Inferior Frontal Gyrus	R
5			4.84	36	40	40	Frontal Pole	R
4	2683	< .001	4.41	-36	36	28	Middle Frontal gyrus	L
4			4.37	-30	60	-8	Frontal Pole	L
4			4.26	-32	40	40	Frontal Pole	L
4			4.03	-22	56	-12	Frontal Pole	L
4			3.97	-20	50	-14	Frontal Pole	L
4			3.91	-28	64	16	Frontal Pole	L
3	1546	< .001	4.22	-18	10	-6	Putamen	L
3			4.09	-44	18	-8	Frontal Orbital Cortex	L
3			3.94	-8	8	4	Caudate	L
3			3.92	-50	6	34	Precentral Gyrus	L
3			3.83	-32	26	0	Frontal Orbital Cortex	L
3			3.82	-34	20	14	Frontal Operculum Cortex	L
2	614	0.001	4.04	-28	0	58	Middle Frontal gyrus	L
2			3.82	-32	-4	58	Middle Frontal gyrus	L
2			3.79	-18	6	70	Superior Frontal Gyrus	L
2			3.69	-16	2	72	Superior Frontal Gyrus	L
2			3.27	-14	-4	74	Superior Frontal Gyrus	L
2			3.24	-12	-8	70	Superior Frontal Gyrus	L
1	396	0.019	3.99	10	4	4	Caudate	R
1			3.94	6	-2	12	Thalamus	R
1			3.85	18	8	14	Caudate	R

Table S 4.2 Continued.

Contrast: SS > GoC Regression with BIS								
Cluster Index	**Voxels**	**P**	**Z-MAX**	**Z-MAX X (mm)**	**Z-MAX Y (mm)**	**Z-MAX Z (mm)**	**Region**	**Side**
5	31497	< .001	5.78	42	-46	52	Superior Parietal Lobule	R
5			5.7	62	-38	2	Middle Temporal Gyrus	R
5			5.59	16	-72	56	Lateral Occipital Cortex	R
5			5.57	50	-30	-2	Superior Temporal Gyrus	R
5			5.56	26	-72	56	Lateral Occipital Cortex	R
5			5.53	54	-22	-6	Middle Temporal Gyrus	R
4	16763	< .001	5.74	38	48	30	Frontal Pole	R
4			5.39	30	60	-12	Frontal Pole	R
4			5.36	52	22	4	Inferior Frontal Gyrus	R
4			5.33	58	18	16	Inferior Frontal Gyrus	R
4			5.31	34	58	-12	Frontal Pole	R
4			5.24	20	16	64	Superior Frontal Gyrus	R
3	4730	< .001	4.59	-30	60	-8	Frontal Pole	L
3			4.51	-34	58	-8	Frontal Pole	L
3			4.47	-34	36	28	Middle Frontal Gyrus	L
3			4.46	-32	40	40	Frontal Pole	L
3			4.33	-44	18	-8	Frontal Orbital Cortex	L
3			4.23	-20	10	-4	Putamen	L
2	748	< .001	4.13	-28	0	58	Middle Frontal Gyrus	L
2			3.95	-18	6	70	Superior Frontal Gyrus	L
2			3.86	-18	4	76	Superior Frontal Gyrus	L
2			3.44	-14	-4	74	Superior Frontal Gyrus	L
2			3.22	-36	0	68	Middle Frontal Gyrus	L
2			2.79	-6	-8	68	Juxtapositional Lobule Cortex	L
1	470	0.006	4.02	6	-2	12	Thalamus	R
1			3.99	10	0	14	Caudate	R
1			3.97	10	4	4	Caudate	R
1			3.87	18	8	14	Caudate	R
1			2.85	22	8	4	Putamen	R
1			2.69	18	12	-4	Putamen	R

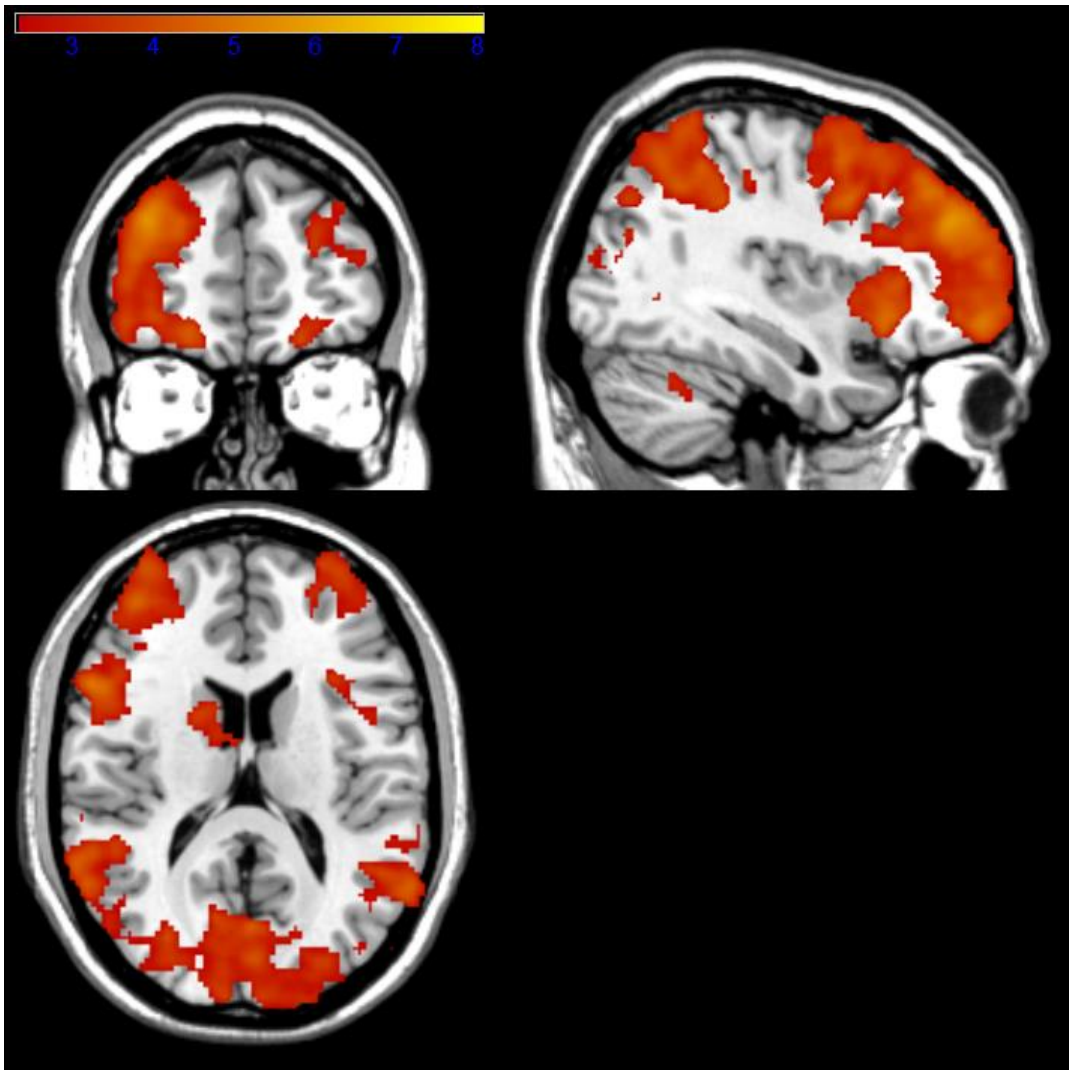

Figure S 4.1 Brain activations evoked by the SS > GoC contrast in the ASST. Images are presented in the radiological convention. The colour bar represents Z scores ranging from 2.3 to 8. X = 36 Y = 49 Z = 16

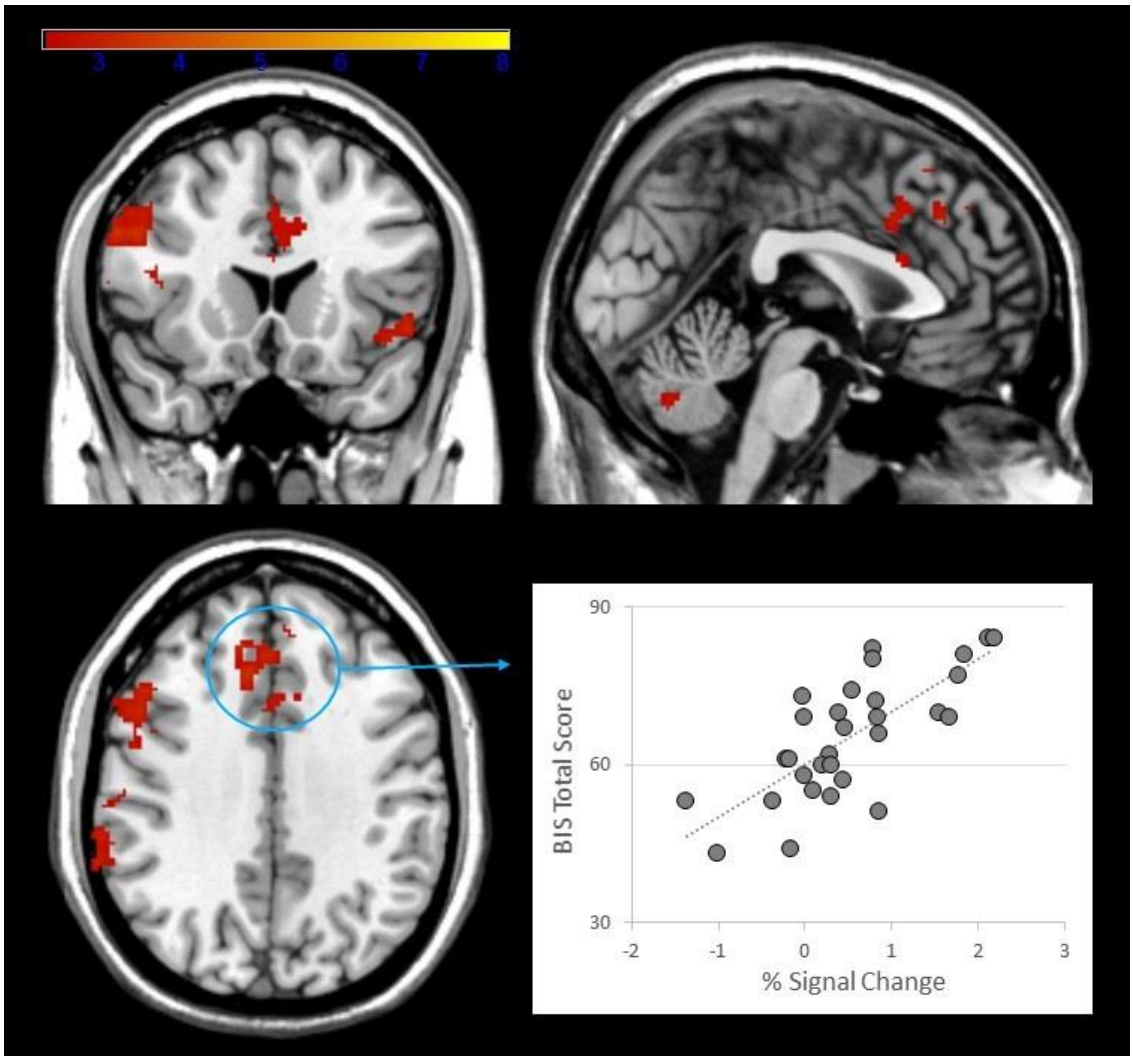

Figure S 4.2 Brain regions which showed significant association between BIS Total score and successful response inhibition (SS > GoC) in the ASST. In the bottom right corner, the illustration of the correlation between the BIS score and the percentage signal change extracted from the region surrounded by the circle. Images are presented in the radiological convention. The colour bar represents Z scores ranging from 2.3 to 8. X = -1 Y = 18 Z = 36

Table S 4.3 Local maxima for each cluster of regions identified for the ASST successful response inhibition contrast (SS>GoC) regressions with Negative Urgency Score. Cluster index refers to a group of voxels encompassing multiple brain areas. 'Voxels' refer to the number of voxels within each cluster. The Harvard-Oxford cortical and subcortical probabilistic atlases were used to identify each region.

Cluster Index	**Voxels**	**P**	**Z-MAX**	**MNI coordinates (mm)**			**Region**	**Side**
				Z-MAX X	**Z-MAX Y**	**Z-MAX Z**		
4	697	< .001	4.05	6	36	42	Superior Frontal gyrus	R
4			3.97	6	40	40	Superior Frontal gyrus	R
4			3.84	12	40	28	Paracingulate Gyrus	R
4			3.37	4	38	32	Paracingulate Gyrus	R
4			3.09	8	30	30	Paracingulate Gyrus	R
3	551	.002	3.85	40	-48	62	Superior Parietal Lobule	R
3			3.38	42	-48	54	Superior Parietal Lobule	R
3			3.16	62	-52	50	Angular Gyrus	R
3			3.15	50	-58	56	Lateral Occipital Cortex	R
3			3.15	44	-56	66	Lateral Occipital Cortex	R
2	520	.003	4.44	18	72	18	Frontal Pole	R
2			3.79	20	66	16	Frontal Pole	R
2			3.43	26	72	6	Frontal Pole	R
2			3.29	28	68	6	Frontal Pole	R
2			2.83	26	72	14	Frontal Pole	R
2			2.75	28	64	12	Frontal Pole	R
1	341	.040	3.77	24	18	66	Superior Frontal gyrus	R
1			3.52	24	18	70	Superior Frontal gyrus	R
1			3.41	36	14	64	Middle Temporal Gyrus	R
1			3.34	22	32	50	Superior Frontal gyrus	R
1			2.71	22	6	64	Superior Frontal gyrus	R

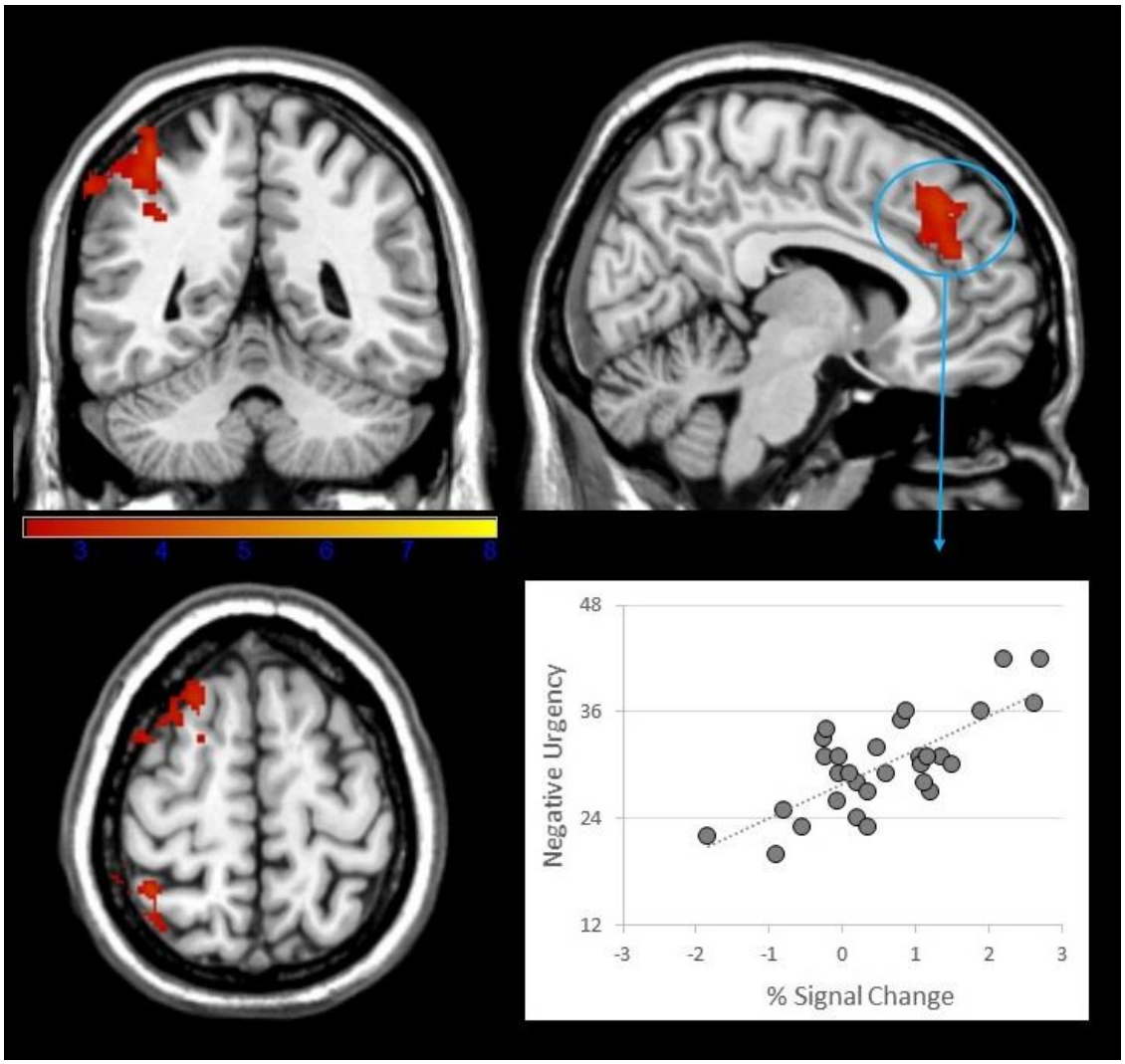

Figure S 4.3 Brain regions which showed significant association between Negative Urgency and successful response inhibition (SS > GoC) on the ASST. In the bottom right corner, the illustration of the correlation between the Negative Urgency score and the percentage signal change extracted from the region surrounded by the circle. Images are presented in the radiological convention. The colour bar represents Z scores ranging from 2.3 to 8. X = 6 Y = -48 Z = 62

Table S 4.4 Local maxima for each cluster of regions identified for the ADD task evoked by Choice (Choosing-Face viewing) contrast, controlling for age and sex. Cluster index refers to a group of voxels encompassing multiple brain areas. 'Voxels' refer to the number of voxels within each cluster. The Harvard-Oxford cortical and subcortical probabilistic atlases were used to identify each region.

Cluster Index	Voxels	P	Z-MAX	Z-MAX X (mm)	Z-MAX Y (mm)	Z-MAX Z (mm)	Region	Side
1	540	.001	4.63	-52	18	-6	Inferior Frontal Gyrus	L
1			3.33	-44	18	6	Frontal Operculum Cortex	L
1			3.19	-42	30	0	Inferior Frontal Gyrus	L
1			3.17	-60	16	-2	Inferior Frontal Gyrus	L
1			2.82	-44	6	-6	Insular Cortex	L
1			2.68	-58	16	6	Inferior Frontal Gyrus	L
2	629	< .001	4.59	50	20	-6	Inferior Frontal Gyrus	R
2			3.62	46	22	-14	Frontal Orbital Cortex	R
2			3.40	50	40	0	Frontal Pole	R
2			3.02	62	14	0	Precentral Gyrus	R
2			3.01	42	48	2	Frontal Pole	R
2			2.79	54	30	12	Inferior Frontal Gyrus	R

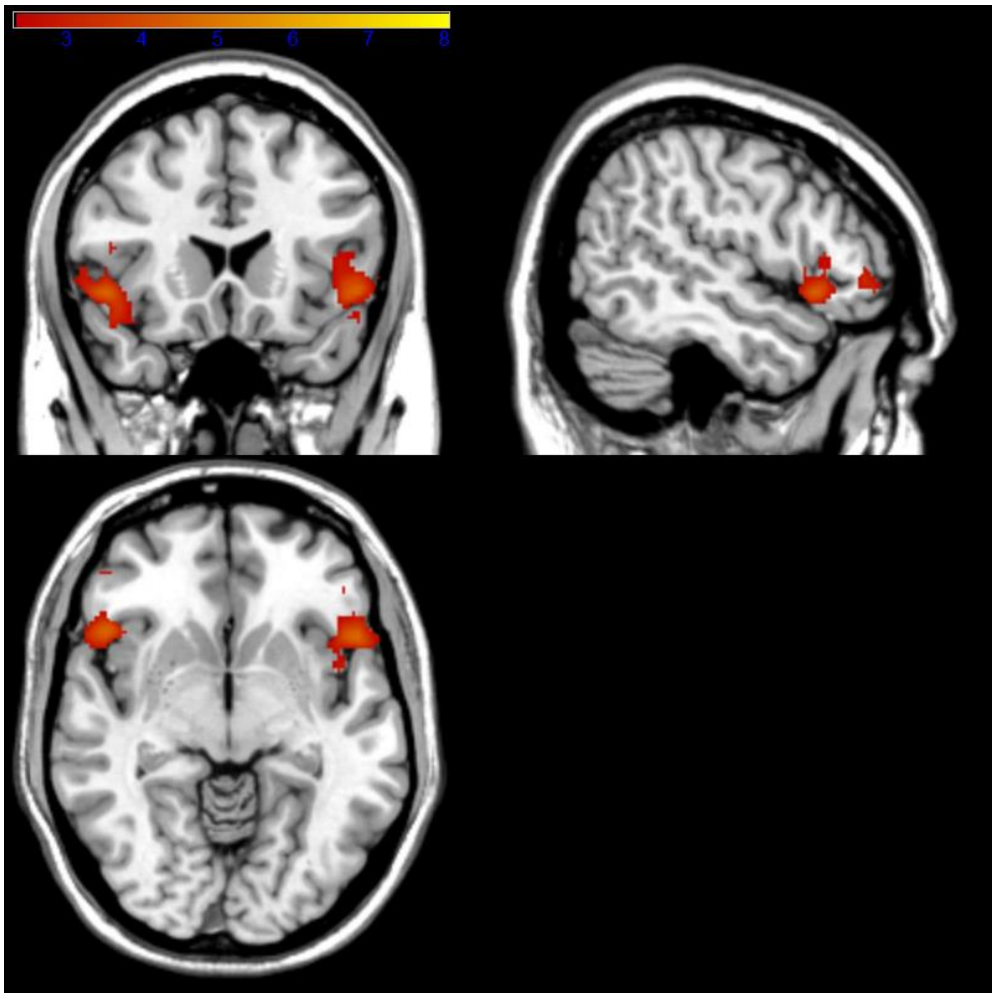

Figure S 4.4 Activations evoked by deciding on the ADD task, regardless of the emotional context (Choosing > Viewing Faces). Images are presented in the radiological convention. The colour bar represents Z scores ranging from 2.3 to 8. X = 50 Y = 20 Z = -6

Table S 4.5 Local maxima details and coordinates in MNI space for the cluster of voxels identified by the ADD Del>Imm regression with Negative Urgency. 'Voxels' refer to the number of voxels within each cluster. The Harvard-Oxford cortical and subcortical probabilistic atlases were used to identify each region.

Voxels	P	Z-MAX	MNI coordinates (mm)			Region	Side
		Z-MAX	Z-MAX X	Z-MAX Y	Z-MAX Z		
297	.038	3.38	16	-92	-4	Occipital Pole	R
		3.16	6	-92	16	Occipital Pole	R
		3.12	10	-94	20	Occipital Pole	R
		3.04	10	-84	-8	Lingual Gyrus	R
		3.04	22	-92	8	Occipital Pole	R
		3.01	20	-88	4	Occipital Pole	R

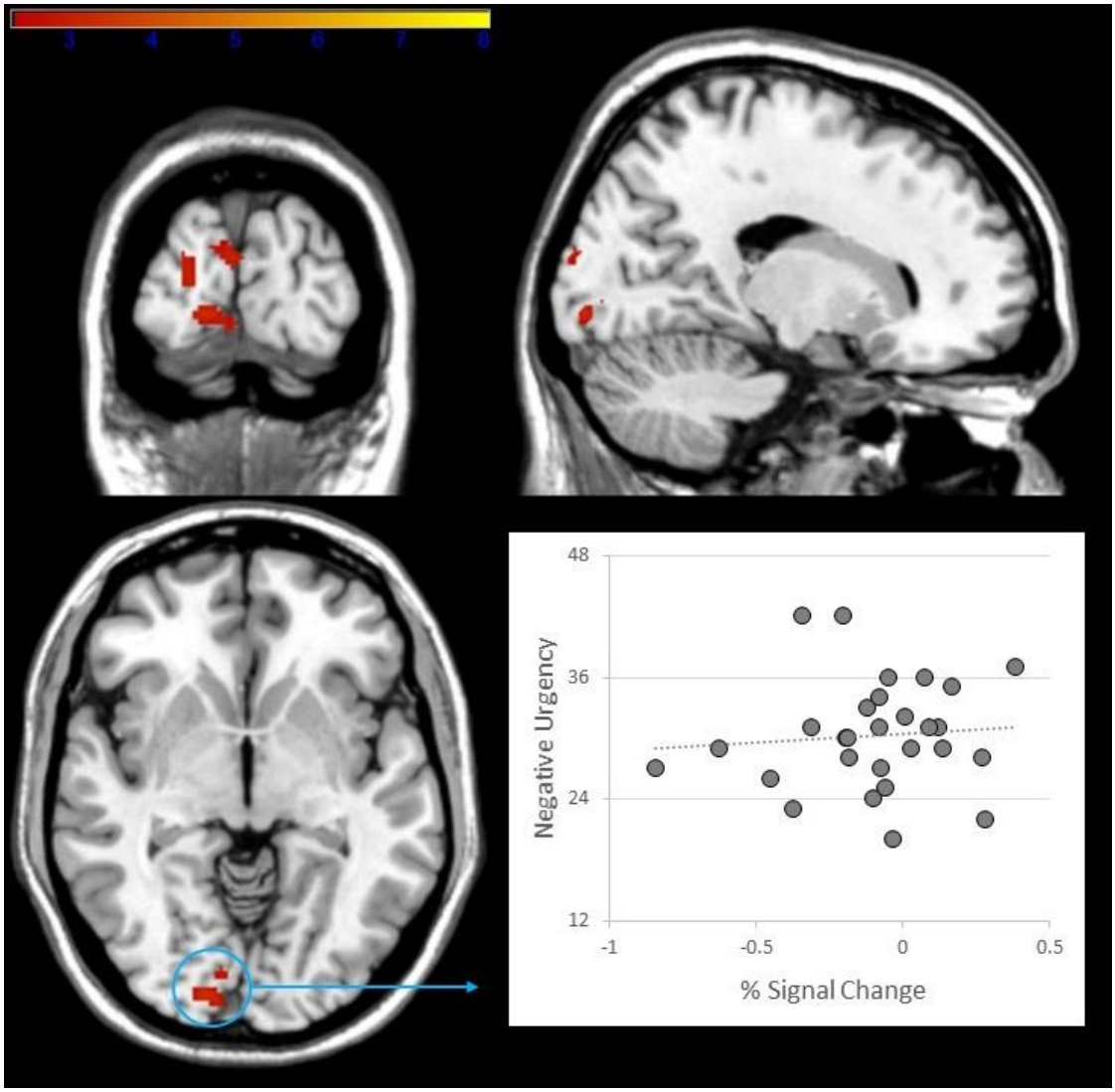

Figure S 4.5 Activations evoked by choosing a delayed vs immediate option on the ADD task, regardless of the emotional context (Del > Imm) associated with Negative Urgency. In the bottom right corner, the illustration of the correlation between the Negative Urgency score and the percentage signal change extracted from the region surrounded by the circle. Images are presented in the radiological convention. The colour bar represents Z scores ranging from 2.3 to 8. X = 16 Y = -92 Z = -4

4.7.2 Supplementary Discussion

ASST

We found evidence for excessive neural recruitment during successful inhibitory control in more impulsive individuals, as characterised by their BIS Total score and Negative Urgency score. Previously such increased activation has been interpreted as a compensatory mechanism (Chester *et al.*, 2016; Ding *et al.*, 2014). Specifically, in our study increased BIS Total score was associated with increased activity in the regions encompassing the right supramarginal gyrus, right superior, middle and inferior frontal gyri and paracingulate cortex during successful response inhibition. While the right middle frontal gyrus is implicated in general reorientation of attention (Japee *et al.*, 2015), the inferior frontal gyrus supports prioritised selection of salient actions. Correspondingly, this region is particularly recognised as key to successful response inhibition (Aron & Poldrack, 2006; Aron *et al.*, 2003; Deng *et al.*, 2017; Rubia *et al.*, 2001). The supramarginal areas are considered a part of the ventral attention network (Vossel *et al.*, 2014) vital for motor attention (Rushworth *et al.*, 1997). Similarly, enhanced activation during successful response inhibition was also observed in superior frontal/paracingulate gyrus, superior parietal lobule and frontal pole on the right side in individuals who reported higher Negative Urgency. Together, these results indicate altered functioning of the brain network supporting both inhibitory control and allocation of attentional resources in more impulsive individuals.

ADD

At the neural level, contemplating before making a decision (Choosing – passive face viewing contrast) evoked activation of the brain areas previously implicated in temporal decision-making, namely inferior frontal gyri, frontal orbital cortex, frontal pole, insular cortex and frontal opercular cortex (Claus *et al.*, 2011; Frost & McNaughton, 2017; Lim *et al.*, 2017; Luo *et al.*, 2009; Massar *et al.*, 2015; Sellitto *et al.*, 2016, 2010; Wang *et al.*, 2016). However, there was no main effect of decision type (delayed/immediate), contradicting previous findings (Claus *et al.*, 2011; Lim *et al.*, 2017; Luo *et al.*, 2009). Those discrepancies may be due to differences in sample characteristics between the past and present studies.

Regarding the relationship between personality traits and neural responses during intertemporal decisions, only association with Negative Urgency, and not BIS Total Score, was significant. Negative Urgency was associated with enhanced occipital pole activation during choosing a delayed versus immediate reward. This over-activation might reflect the fact that selecting a delayed reward may be more effortful for individuals showing elevated Negative Urgency levels. The involvement of occipital lobe in intertemporal decision-making is consistent with previous findings (Claus *et al.*, 2011; Lim *et al.*, 2017; Luo *et al.*, 2009) and

may be related to visually-directed attention. However, we believe that this is the first demonstration of enhanced occipital activation while choosing between delayed and immediate options with relation to Negative Urgency levels.

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CHAPTER 5.

STUDY 4.
THE IMPACT OF YOHIMBINE-INDUCED AROUSAL ON FACETS OF BEHAVIOURAL IMPULSIVITY

This paper is prepared for submission to the Psychopharmacology:

Herman, A. M., Critchley, H. D., & Duka, T. (2018). The impact of yohimbine-induced arousal on facets of behavioural impulsivity (in prep).

Contribution

I contributed to the study design and the interpretation of the results. I collected and analysed the data as well as prepared the initial manuscript.

5.1 Abstract

State-dependent changes in physiological arousal may be related to impulsive behaviours. To examine the relationship between arousal and impulsivity, we assessed the effects of yohimbine (an α_2 adrenergic receptor antagonist, which increases physiological arousal via noradrenaline release) on performance on standard laboratory-based impulsivity measures in healthy volunteers. Forty-three participants received a single dose of either yohimbine hydrochloride or placebo before completing a battery of impulsivity measures. Blood pressure and heart rate were monitored throughout the study. Yohimbine group showed higher blood pressure as well as better response inhibition in the Stop Signal Task relative to the placebo group. Additionally, individual changes in blood pressure were associated with performance on the Delay Discounting and Information Sampling tasks. Increased blood pressure following drug ingestion was associated with more far-sighted decisions in the Delay Discounting Task (lower temporal impulsivity) but decreased information gathering in the Information Sampling Task (increased reflection impulsivity). These results support the notion that impulsive behaviour depends on state physiological arousal; however, distinct facets of impulsivity are differentially affected by these changes.

Keywords: Yohimbine, Arousal, Noradrenaline, Blood Pressure, Stop Signal Task

5.2 Introduction

Impulsivity is often described as a tendency to act rapidly without considering the consequences of one's actions (Daruna & Barnes, 1993; Moeller, Barratt, Dougherty, Schmitz, & Swann, 2001). The importance of this phenomenon has long been recognised, both in everyday life, as it plays a vital role in the decision-making process, and in many neuropsychiatric conditions such as attention deficit and hyperactivity disorder (ADHD), manic episodes of bipolar disorder, Parkinson's disease, eating disorders, or substance abuse (American Psychiatric Association, 2013).

Impulsivity is a multidimensional construct that can be considered as a stable personality characteristic (trait) as well as a behaviour which varies depending on a situation (state impulsivity) (Herman, Critchley, & Duka, 2018a). The state-dependent changes in impulsivity may be related to current mood and/or arousal state (Herman et al., 2018a). Indeed, previous research has indicated that modulating one's state of physiological arousal causes changes in performance on impulsivity tasks. For example, acute moderate physical exercise decreases motor impulsivity (Chu, Alderman, Wei, & Chang, 2015). Furthermore, past studies suggested the role of individual differences in the relationship between state arousal and impulsivity. Some observed that individuals high in trait impulsivity have a low resting state of arousal (Fowles, 2000; Mathias & Stanford, 2003; Puttonen et al., 2008; Schmidt, Mussel, & Hewig, 2013). As every organism aims to reach an optimal internal state (i.e. one that feels best; Hebb, 1955), some hypothesise that these individuals behave impulsively in order to increase their arousal to the optimal level (Barratt, 1985; H. J. Eysenck & Eysenck, 1985; Zuckerman, 1969). Thus, trait impulsivity, associated with low resting state of arousal, might be an additional factor mediating the effects of arousal on behaviour. For example, impulsive individuals perform worse than low-impulsive subjects in the sustained attention task in the control (baseline) condition, but they obtain a greater benefit from caffeine than non-impulsive subjects (Smith, Rusted, Savory, Eaton-Williams, & Hall, 1991). As inattention is related to impulsive behaviours (de Wit, 2009), these results suggest that manipulation of the physiological state may influence state impulsivity, especially in highly impulsive individuals. This is further supported by clinical findings in ADHD patients, whereby treatment with stimulant drugs, which are known to increase arousal levels, leads to decreases in impulsive behaviour (Swanson, Baler, & Volkow, 2011). Similar observations were made in healthy populations. Schmidt et al., (2013) reported that the lower the participants' physiological arousal at rest, reflected in decreased heart rate, the faster the responses and the riskier the behaviour in a gambling game, indicating diminished impulse control. Interestingly, subjects tended to behave less risky in the gamble following physical exercise, compared to a resting condition.

State arousal can also be modulated pharmacologically with substances that act on the noradrenergic system. Past studies successfully used yohimbine hydrochloride, the α_2 receptor antagonist, which increases blood norepinephrine levels (Hedner et al., 1992) and causes an increase in physiological arousal (Goldberg, Hollister, & Robertson, 1983; Krystal et al., 1992; Swann et al., 2013). At higher doses, yohimbine can induce hypertension and changes in mood state, such as anxiety and nervousness (Cimolai & Cimolai, 2011); therefore, in many studies yohimbine is used as a pharmacological stressor (e.g. Mahoney, Barnes, Wiercigroch, & Olmstead, 2016; Moran-Santa Maria, McRae-Clark, Baker, Ramakrishnan, & Brady, 2014). Yohimbine is a fat-burning compound (Ostojic, 2006), sometimes used in body-building. It is also an aphrodisiac, which can aid erectile dysfunction (Guay, Spark, Jacobson, Murray, & Geisser, 2002).

Current research, mainly in rodents, indicates that yohimbine administration can induce acute changes in behavioural impulsivity. For example, a recent study showed that yohimbine acutely increased the preference for the large and delayed reinforcer over a smaller immediate one (decreased temporal impulsivity) (Schippers, Schetters, De Vries, & Pattij, 2016). On the other hand, some studies suggested that yohimbine might induce inflexibility in adjusting to changes in the relative value of different options (Montes, Stopper, & Floresco, 2015; Schwager, Haack, & Taha, 2014). It seems that the effects of yohimbine on behaviour might depend to some extent on individual differences. Schippers et al. (2016) reported that yohimbine affected motor response inhibition differently depending on the baseline performance: yohimbine improved response inhibition in highly impulsive rats but attenuated it in low-impulsive rats. Yohimbine has also been shown to induce dose-dependent increases in premature responding on the 5-Choice Serial Reaction Time Task (‘waiting’ motor impulsivity) in rats (Mahoney et al., 2016; Sun et al., 2010) and decreased attention; however, the effects did not depend on baseline impulsivity levels (Barlow, Dalley, & Pekcec, 2018). Similar findings have been reported in human participants, showing that yohimbine caused a dose-related increase in impulsive behaviour on the Immediate and Delayed Memory Task (IMT/DMT), which was correlated with the change in blood pressure (Swann et al., 2013; Swann, Birnbaum, Jagar, Dougherty, & Moeller, 2005). While understanding the relationship between bodily arousal and impulsive behaviours might yield valuable insights for clinical practice, a comprehensive study looking at how physiological arousal affects distinct measures of impulsivity is missing.

The aims of the current study were twofold; firstly, to determine whether a yohimbine-induced acute increase in arousal would be related to differences in behavioural impulsivity levels. We hypothesised that yohimbine administration would be associated with diminished behavioural impulsivity, particularly in more impulsive individuals (Barratt, 1985; H. J. Eysenck & Eysenck, 1985; Zuckerman, 1969). Alternatively, since noradrenergic

activation is vital for attention (Robbins, 1997), increasing noradrenergic activity may increase impulsive behaviour via its deleterious effects on the scope of attention. Secondly, we examined the alleged relationship between resting state arousal, expressed as heart rate and blood pressure, and trait impulsivity. In line with previous research (Fowles, 2000; Mathias & Stanford, 2003; Puttonen et al., 2008; Schmidt et al., 2013), we predicted that more impulsive individuals would show lower resting levels of arousal. We used two trait impulsivity measures to capture the wide range of impulsivity characteristics, including emotional impulsivity (positive and negative urgency).

Participants' physiological arousal was modulated via oral administration of a single dose of yohimbine hydrochloride (α_2 receptor blocker). Participants (healthy volunteers) were randomly assigned to a control (placebo) or experimental (yohimbine) group and completed a battery of behavioural impulsivity tasks. Performance of these two groups was compared to see how an increase in arousal via noradrenergic mechanism influenced impulsive behaviour.

5.3 Materials and methods

5.3.1 Participants

The study design was approved by the BSMS Research Governance & Ethics Committee. 43 healthy volunteers (19 males) were randomly assigned to one of two experimental groups: placebo or yohimbine. Only volunteers who met strict inclusion criteria were recruited. These criteria involved: age between 18 and 40 years old, normal or corrected-to-normal vision, no lifetime history of any neurological or mental disorders, no current pharmacological treatment or psychological counselling, no drug use within five days prior the testing session or alcohol use 24h before testing session, weight above 55kg, systolic blood pressure (SYS BP) below 135mmHg and diastolic blood pressure (DIA BP) below 90 mmHg. Strict exclusion criteria involved a history of anxiety or panic attacks. Women who were not using a recommended means of birth control underwent a pregnancy test before participation in the study. All volunteers gave written informed consent to participate and received compensation for their time.

5.3.2 Materials

Questionnaires

Each participant completed a battery of questionnaires to assess current mood state, alcohol use, and impulsivity. The *Nuffield Hospitals Medical History Questionnaire* was used to record demographic details, past and present health status, use of medications and recreational drugs, and a number of cigarettes smoked per day.

The *Barratt Impulsiveness Scale* (BIS-11) (Patton, Stanford, & Barratt, 1995) and the *UPPS-P Questionnaire* (Cyders & Smith, 2007; Whiteside & Lynam, 2001), widely used questionnaires in impulsivity research, measured trait impulsivity. BIS provides an index of three impulsivity dimensions: motor, non-planning and in-attention. UPPS-P gives a measure of premeditation, perseverance, sensation seeking as well as tendencies to act impulsively while experiencing positive and negative emotions, positive and negative urgency, respectively.

Participants completed the *Rey Auditory Verbal Learning Test* (RAVLT, Rey, 1964), a measure of working memory capacity, to ensure that both experimental groups were matched on the basis of their cognitive abilities. Participants heard a list of 15 unrelated nouns with a presentation rate of one word per two seconds. Following a period of 2-min, while asked to count from 100 backwards out-loud to minimise mental repetition, participants were asked to recall as many words as they could remember. The number of correct recalls was the dependent variable.

Alcohol Use Questionnaire (AUQ, Mehrabian & Russell, 1978) provided an estimate of a number of alcohol units (1 unit = 8g of alcohol) consumed a week over the past six months.

Depression, Anxiety, Stress Scale (DASS; Henry & Crawford, 2005) consists of three 7-item self-report scales that measure the extent of depression, anxiety, and stress experienced over the past week. This scale was introduced to ensure group matching on negative mood ratings.

Drug Effects Questionnaire (DEQ; Morean et al., 2013) assesses two key aspects of subjective experience: the strength of substance effects and desirability of substance effects. It consists of five items, “Do you feel a drug effect right now?” (Feel); “Are you high right now?” (High); “Do you like any of the effects you are feeling right now?” (Like); “Do you dislike any of the effects you are feeling right now?” (Dislike); and “Would you like more of the drug you took, right now?” (More), rated on a 100-point visual analogue scale ranging from “not at all” to “extremely”.

Perceived Arousal Scale (Anderson, Deuser, & DeNeve, 1995) provides ratings of subjective arousal state. It consists of 24 adjectives indicating arousal (e.g. energetic) or a lack of arousal (e.g. sleepy) rated on a five-point scale from 1, "very slightly or not at all", to 5, "extremely". The scale has a high internal consistency (Cronbach $\alpha = .93$).

Positive Affect/Negative Affect Scale (PANAS) (Watson, Clark, & Tellegen, 1988) is a 20-item measure of self-reported positive (PA), and negative affect (NA) experienced at the present moment.

The State-Trait Anxiety Inventory (STAI; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983) was used to assess anxiety levels. It consists of two 20-item scales rated on a four-point scale.

Tasks

Affective Stop Signal Task (ASST) measured motor response inhibition in task-irrelevant emotional context. This modified version of the commonly used task was introduced as previous reports suggested that yohimbine might affect amygdala responses to fearful faces and change the perception of emotional faces (Schwabe, Höffken, Tegenthoff, & Wolf, 2013). Therefore, we used a paradigm with task-irrelevant emotional context (fearful faces).

The details on the ASST were published previously (Herman, Critchley, & Duka, 2018b; see Chapter 4). Briefly, instead of arrows, participants were presented with facial expressions from the FACES database (Ebner, Riediger, & Lindenberger, 2010) of males and females (50% each) displaying either fear or neutral expression (50% each). On the Go-trials (a facial expression surrounded by a white frame), participants were instructed to respond with an appropriate button-press to indicate whether the face displayed on the screen was male or female (implicit emotional context) as quickly as possible and to try and withhold their responses when the frame surrounding the picture changed colour (Stop-trials). The onset of the Stop Stimulus (the same picture surrounded by a yellow frame) was adjusted according to a staircase procedure depending on individual performance separately for each emotional condition, to obtain a probability of stopping 0.5 for each condition. Participants were informed that speed and accuracy on task are equally important and that they should not be delaying their responses to see whether the frame would turn yellow. The Stop-Signal Reaction Time (SSRT) was calculated separately for neutral (SSRT Neutral) and fearful (SSRT Fearful) trials.

Participants completed two runs of 160 trials with a rest break in-between. In total there were 120 Go Neutral, 120 Go Fearful, 40 Stop Neutral, and 40 Stop Fearful trials.

Probability Discounting task (PD; Madden, Petry, & Johnson, 2009) is a measure of risk-taking. It consists of a list of 30 choices between smaller certain rewards and uncertain

larger gains. The dependent variable is h parameter (ln-transformed to reduce skewness). Large h values indicate discounting of probabilistic rewards (risk aversion).

The Information Sampling Task (IST; Clark, Robbins, Ersche, & Sahakian, 2006) is a measure of reflection impulsivity. On each trial, a matrix of 5x5 grey squares was presented on a computer screen. The participant selected a square by clicking with the mouse over the square, to reveal one of two colours (e.g. red and blue) until they were confident which of the two colours was in the majority of the squares. There were two conditions of the task:

(i) IST fixed win condition (FW): the participant won 100 points if they made the right decision (regardless of how many boxes they have opened); otherwise, they lost 100 points. The participant completed 10 experimental trials.

(ii) IST reward conflict (RC): for every box opened, the participant lost 10 points from a bank of 250. If the participant chose correctly they won the remaining points from the bank; otherwise, they lost 100 points. Each participant completed 10 experimental trials.

The dependent variable for both conditions is P(correct) which reflects the certainty of being correct that a participant tolerates when they make a decision. P(correct) values of 1 indicate that the participant acquired full information before deciding, 0.5 indicates that the participant had only enough information to choose at chance.

The Monetary Choice Questionnaire (MCQ; Kirby, Petry, & Bickel, 1999) is a measure of temporal impulsivity. The participant was presented with 27 hypothetical choices between small, immediate rewards (SIR) and larger delayed rewards (LDR), for example, "would you prefer £54 today or £55 in 117 days?". The dependent variable was the proportion of LDR choices made.

5.3.3 Procedures

Before testing, all volunteers attended a standardised interview with a medical doctor (TD). The screening checked for exclusion criteria, history of medication and recreational drug use, contraceptive use, any current or chronic medical condition, current or lifetime history of any psychiatric or neurological disorder. 74 volunteers (48 females) entered initial screening, but 27 (36%) were excluded as they met one or more exclusion criteria and further four individuals (5%) withdrew from the study, yielding 43 individuals who participated.

Participants were instructed to refrain from caffeine-containing products on a day of testing and have a light breakfast in the morning before participating in the study. Following completion of RAVLT, alcohol use, personality and mood state (PANAS) questionnaires and BP measurement, participants were administered 20 mg Yohimbine (Yohimbine chlorhydrate, Arzneimittel GmbH) or placebo orally 45 min before the behavioural testing

began. Both the experimenters and the participants were blinded (double-blind experiment). Dosage and timing of drug administration were chosen according to previous studies using yohimbine, as this dosage was shown to evoke mild effects on the physiological arousal without causing mood-related side effects (anxiety and nervousness) (Plewnia, Bartels, Cohen, & Gerloff, 2001; Schwabe et al., 2013; Schwabe, Tegenthoff, Hoffken, & Wolf, 2010, 2012; Swann et al., 2013).

Within the first 45 minutes following tablets administration participants had time to relax and their heart rate (HR) and BP was monitored every 15 minutes. Subsequently, physiological measurements were taken every 30 minutes. All physiological measures were recorded while participants were sitting still. Approximately 20 min following the tablets administration, a light snack was served. Following 45 min rest period, testing commenced, during which participants completed behavioural impulsivity measures (ASST, IST, PD, and MCQ, in a randomised order) and further state-measure questionnaires (PANAS, Perceived Arousal Scale, and DEQ). Procedures are illustrated in Figure 5.1. After behavioural testing was completed, participants remained in the lab until their BP was <10 mmHg above baseline.

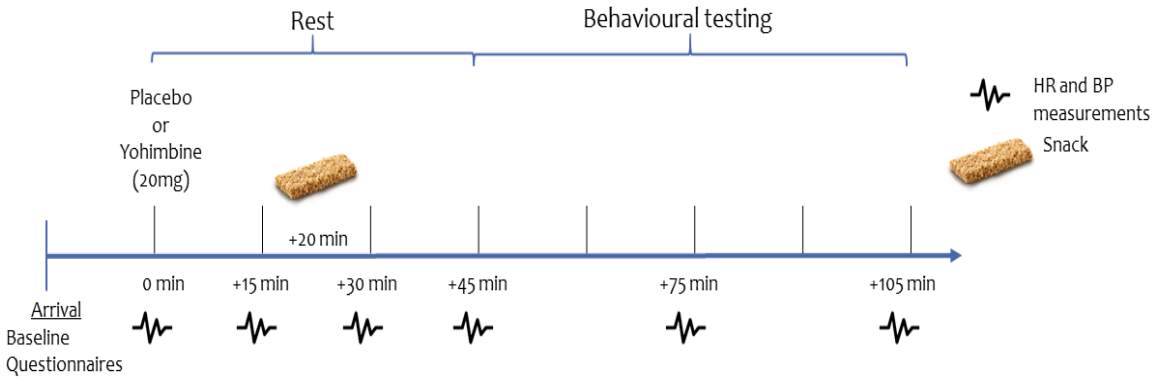

Figure 5.1 Procedures and timeline during the testing session.

5.3.4 Statistical analysis

An exploratory correlational analysis was undertaken to assess the relationship between the resting level of physiological arousal (HR, BP) and trait impulsivity measures. Differences between groups on demographic information and task performance (apart from the ASST) were compared using a series of independent samples *t*-tests or chi-square tests as appropriate. Response inhibition on the ASST was analysed with mixed-ANOVA with emotion condition (fearful and neutral) as a within-subject factor, and group (yohimbine or placebo) as a between-subject factor. Physiological measures were also analysed using

mixed-ANOVAs with time of measurement as a within-subject factor, and group (yohimbine or placebo) as a between-subject factor. Significant main or interaction effects were pursued with appropriate follow-up tests, including repeated-measures ANOVA. In case of violation of sphericity, multivariate ANOVAs were used (Maxwell & Delaney, 2004).

5.4 Results

5.4.1 Exclusions and missing data

One participant did not complete the study due to strong nausea and cardiovascular reaction to yohimbine. Therefore, the final sample consisted of 42 participants (23 females); 21 (12 females) received placebo and 21 (11 females) yohimbine. There were equal numbers of cigarettes smokers in each group (3 and 4 respectively, $X^2(1) = 0.17$, $p = .679$). Five participants did not complete RAVLT, data from MCQ were missing for two individuals, due to technical failure, all data from questionnaires administered after tablets ingestion (PANAS, Perceived Arousal Scale, and DEQ) were missing for one participant. Four participants were excluded from the ASST for failing to follow instructions not to wait for the stop signal, evidenced by long Go reaction times, and/or high Stop Accuracy values (> 2.5 standard deviations from the group mean).

The groups were well matched on demographics, mood state and personality variables; however, there were some group differences in sensation seeking (not significant after the Bonferroni correction for multiple comparisons, $p > .003$) (see Table 5.1). Therefore, to investigate the potential role of sensation seeking, each comparison was computed with and without including sensation seeking as a covariate.

5.4.2 Blinding

To establish whether the blinding procedure was successful, we compared the numbers of participants who correctly and incorrectly guessed their group allocation. Chi-square test was insignificant ($X^2(1) = 1.62$, $p = .204$), indicating that individuals in both the Placebo and Yohimbine groups were blind to the group allocation. Notably, 11 out of 21 participants in Yohimbine group thought they received placebo, while 15 out of 21 participants from the Placebo group thought they received placebo; therefore, the blinding procedure seemed to work better for the Yohimbine group (see Figure 5.2 for details).

Table 5.1 Group demographics, personality and mood state measures as well as group statistics.

		Placebo			Yohimbine						95% Confidence Interval	
Variable		**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	***t***	**df**	***p***	**Cohen's d**	**Lower**	**Upper**
Demographic information													
Age		21	21.29	3.27	21	23.19	5.41	-1.38	40	.175	-0.43	-4.69	0.88
Weight [kg]		21	70.99	10.72	21	68.96	8.15	0.69	40	.493	0.21	-3.90	7.97
Height [m]		21	1.76	0.10	21	1.73	0.09	0.84	40	.406	0.26	-0.04	0.08
BMI [kg/m²]		21	22.96	2.68	21	22.97	2.37	-0.02	40	.988	-0.01	-1.59	1.57
Alcohol Units per week		21	12.91	10.50	21	11.40	11.55	0.45	40	.659	0.14	-5.37	8.40
RAVLT		18	6.56	2.12	19	5.90	1.45	1.11	35	.274	0.37	-0.55	1.87
Trait impulsivity													
BIS Total		21	66.95	10.52	21	62.76	9.93	1.33	40	.192	0.41	-2.19	10.57
UPPS-P	Negative Urgency	21	28.91	6.58	21	25.19	5.40	2.00	40	.052	0.62	-0.04	7.47
	Premeditation	21	22.38	4.57	21	19.95	5.20	1.61	40	.116	0.50	-0.62	5.48
	Perseverance	21	21.05	4.93	21	18.81	5.22	1.43	40	.161	0.44	-0.93	5.41
	Sensation Seeking	21	40.24	5.21	21	34.57	7.53	2.83	40	.007	0.88	1.63	9.71
	Positive Urgency	21	30.43	10.19	21	26.52	7.31	1.43	40	.161	0.44	-1.63	9.44
Mood measures													
PANAS	NA Pre	21	11.71	2.43	21	12.86	2.46	-1.52	40	.138	-0.47	-2.67	0.38
	PA Pre	21	28.33	5.80	21	30.38	7.48	-0.99	40	.327	-0.31	-6.22	2.13
STAI	Trait Anxiety	21	39.10	7.08	21	39.71	7.46	-0.28	40	.784	-0.09	-5.15	3.92
	State Anxiety	21	34.91	7.88	21	32.71	7.81	0.91	40	.371	0.28	-2.70	7.08

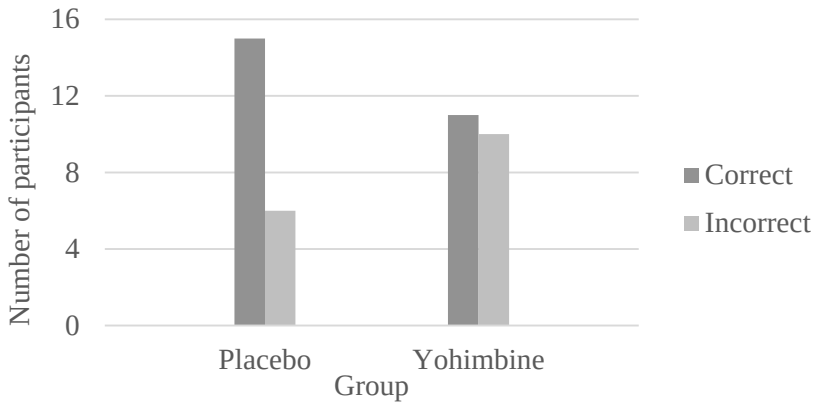

Figure 5.2 Deception - individuals' insights into group allocation.

5.4.3 Resting state arousal and trait impulsivity

Correlational analysis to examine the relationship between resting state measures of arousal (HR, DIA BP, SYS BP) and trait impulsivity measures (BIS and UPPS-P), showed no significant correlations (Table 5.2), indicating that trait impulsivity is not related to unusually low levels of arousal at rest.

Table 5.2 Person's correlations between trait impulsivity dimensions and measures of physiological arousal at baseline.

			Baseline BP SYS [mmHg]	Baseline BP DIA [mmHg]	Baseline HR [bmp]
BIS Total Score		Pearson's r	0.039	0.234	-0.146
		p-value	0.806	0.136	0.356
UPPS-P	**Premeditation**	Pearson's r	0.109	0.292	-0.102
		p-value	0.493	0.06	0.521
	Perseverance	Pearson's r	0.056	0.107	0.034
		p-value	0.723	0.5	0.829
	Sensation Seeking	Pearson's r	0.074	0.051	-0.245
		p-value	0.642	0.75	0.118
	Negative Urgency	Pearson's r	0.089	0.071	-0.059
		p-value	0.575	0.653	0.709
	Positive Urgency	Pearson's r	0.292	0.259	-0.182
		p-value	0.061	0.098	0.25

5.4.4 Yohimbine effects on affective state

Following drug ingestion, Yohimbine group reported increased levels of NA but did not differ from placebo in PA (Table 5.3). No group differences in self-perceived arousal or drug effects were found. The results did not change after including sensation seeking as a covariate.

Table 5.3 Descriptive statistics of the mood state measures and well as tasks performance group comparison following drug/placebo ingestion.

Variable		Placebo			Yohimbine						95% Confidence Interval	
		N	Mean	SD	N	Mean	SD	*t*	df	*p*	Cohen's d	Lower	Upper
State questionnaires													
DEQ	Feel	20	27.90	26.49	21	28.19	28.79	-0.03	39	.973	-0.01	-17.79	17.21
	High	20	20.15	22.76	21	15.43	24.30	0.64	39	.525	0.20	-10.17	19.61
	Dislike	20	21.85	27.46	21	22.29	24.01	-0.05	39	.957	-0.02	-16.71	15.84
	Like	20	34.60	21.23	21	39.52	27.37	-0.64	39	.525	-0.20	-20.45	10.60
	Want More	20	27.85	22.10	21	21.81	24.69	0.82	39	.415	0.26	-8.79	20.87
Perceived arousal		20	69.65	21.19	21	79.62	17.88	-1.63	39	.111	-0.51	-22.33	2.39
PANAS	PA Post	20	21.30	8.42	21	26.29	9.72	-1.75	39	.088	-0.55	-10.74	0.77
	NA Post	20	10.85	1.27	21	13.48	4.14	-2.72	39	.010	-0.85	-4.58	-0.67
Tasks performance													
IST	FW P(correct)	21	0.80	0.09	21	0.81	0.12	-0.29	40	.773	-0.09	-0.07	0.05
	RC P(correct)	21	0.73	0.06	21	0.72	0.10	0.60	40	.552	0.19	-0.04	0.07
MCQ	Proportion LDR	19	0.43	0.16	21	0.49	0.22	-1.02	38	.315	-0.32	-0.19	0.06
PD	ln h	21	2.83	3.79	21	2.21	1.64	0.68	40	.499	0.21	-1.21	2.44
ASST	SSRT Neutral	19	293.47	58.79	19	280.34	41.52						
	SSRT Fearful	19	313.94	67.96	19	279.90	38.15						

5.4.5 Yohimbine effects on physiological recordings

Systolic Blood Pressure

Mixed ANOVA revealed a trend for a time by group interaction ($F(5, 200) = 1.90$, $p = .096$, $\eta^2_p = .045$) and a significant main effect of time ($F(5, 200) = 4.81$, $p < .001$, $\eta^2_p = .107$), and no main effect of drug ($F(1, 40) = 1.19$, $p = .28$, $\eta^2_p = .029$). The SYS BP reached its peak 45 min following drug administration (see Fig 5.3A). Including SS as a covariate strengthened the interaction effect ($F(5, 195) = 2.62$, $p = .026$, $\eta^2_p = .063$), and the main effect of time was no longer significant $F(5, 195) = 0.712$, $p = .615$, $\eta^2_p = .018$). Post-hoc repeated measures ANOVA revealed that while the placebo group did not show significant changes in SYS BP over time, $F(5, 100) = 1.18$, $p = .326$, the yohimbine group did show changes over time, $F(5, 100) = 4.10$, $p = .002$.

Diastolic Blood Pressure

The Mauchy's Test of Sphericity was significant ($X(14) = 39.41$, $p < .001$); therefore, multivariate test was used. Wilks' Lambda test revealed time-group interaction ($F(5, 36) = 2.63$, $p = .040$, $\eta^2_p = .267$) and a main effect of time ($F(5, 36) = 7.77$, $p < .001$, $\eta^2_p = .519$). Post-hoc tests revealed that both groups showed DIA BP changes over time (placebo $F(5, 100) = 4.49$, $p = .001$; yohimbine $F(5, 100) = 4.66$, $p = .001$). The SYS BP reached its peak 30 min following drug administration (see Fig 5.3B). There was a trend for a main drug effect ($F(1, 40) = 3.04$, $p = .086$, $\eta^2_p = .071$), suggesting an overall higher DIA BP in the Yohimbine group regardless of the time of measurement.

After controlling for SS the interaction effect remained marginally significant ($F(5, 35) = 2.47$, $p = .051$, $\eta^2_p = .261$), the main effect of time was no longer significant ($F(5, 35) = 0.893$, $p = .496$, $\eta^2_p = .113$), and the main effect of drug remained unchanged ($F(1, 40) = 3.22$, $p = .080$, $\eta^2_p = .076$).

Heart Rate

There was a trend for a time by condition interaction ($F(5, 200) = 1.95$, $p = .088$, $\eta^2_p = .05$) and a main effect of time ($F(5, 195) = 5.24$, $p < .001$, $\eta^2_p = .12$), but not a main effect of drug ($F(1, 40) = 0.001$, $p = .975$, $\eta^2_p = .00$) (see Fig 5.3C).

After controlling for SS, there were no significant results (interaction term: $F(5, 195) = 1.43$, $p = .216$, $\eta^2_p = .04$; time: $F(5, 195) = 0.62$, $p = .687$, $\eta^2_p = .02$; drug: $F(1, 39) = 0.26$, $p = .611$, $\eta^2_p = .01$). Therefore, yohimbine did not affect the HR.

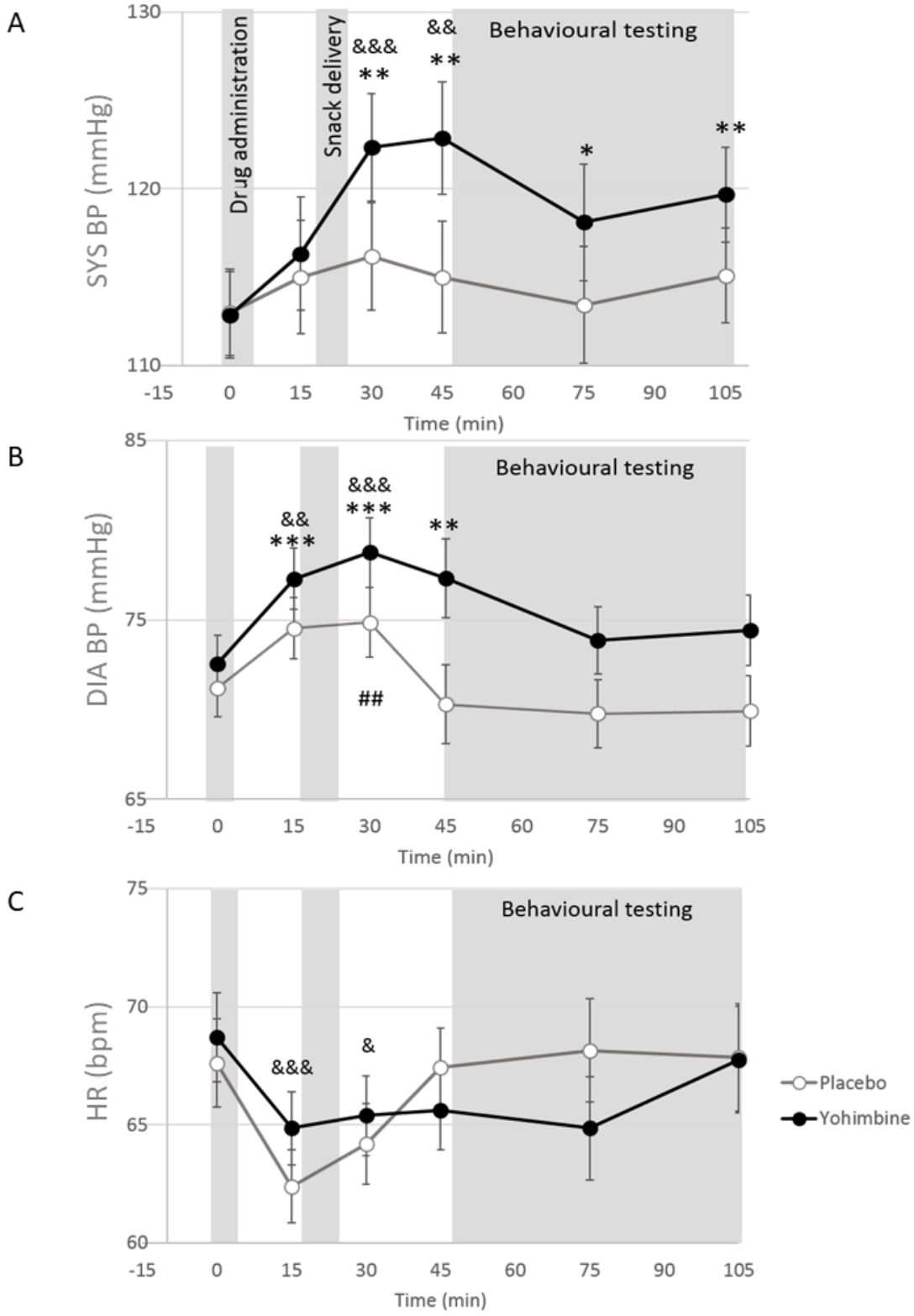

Figure 5.3 Measurements of (A) systolic blood pressure, (B) diastolic blood pressure and (C) heart rate of Yohimbine and Placebo groups across the session. Error bars represent standard error. Significant difference from baseline: *p < .05, **p < .01, ***p < .001 (yohimbine group); ##p < .01 (placebo group); &p < .05, &&p < .01, &&&p < .001 (main effect of time).

5.4.6 Performance on the tasks

ASST

A main effect of drug, $F(1, 35) = 4.30$, $p = .045$, $\eta^2_p = .11$), but not main effect of emotion or drug by emotion interaction effect (p's > .05) was found in the SSRT, indicating that under yohimbine participants had lower SSRT (i.e. they were better able to inhibit prepotent motor responses successfully). This effect, however, was only significant when controlling for individual differences in SS (Figure 5.4).

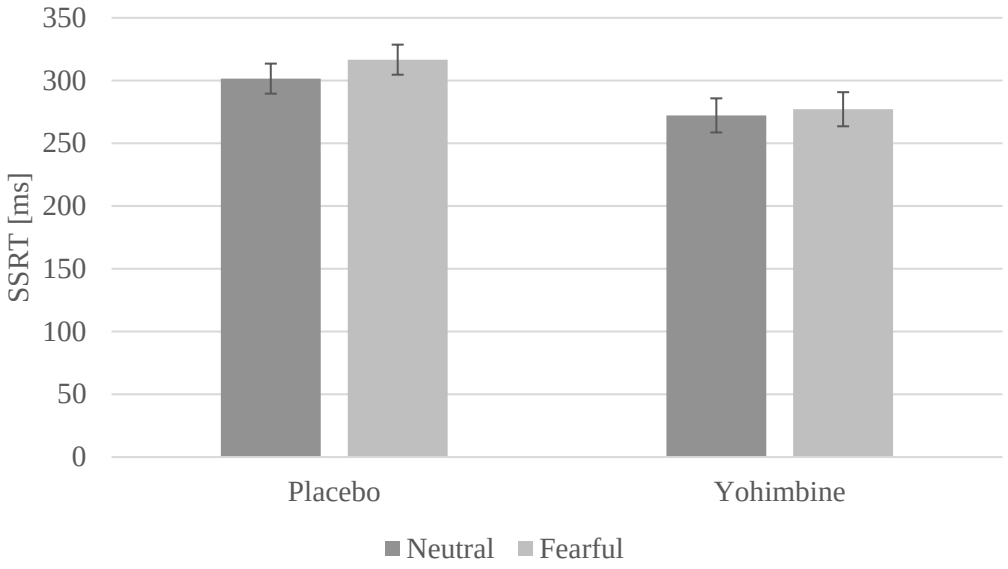

Figure 5.4 Group performance on the ASST. Results presented after controlling for Sensation Seeking.

MCQ, PD and IST

Independent samples *t*-test revealed that there were no group differences in performance on either MCQ, PD or IST, and controlling for SS had no effects on the results (Table 5.3). Therefore, yohimbine ingestion did not affect temporal impulsivity, or risk-taking, or reflection impulsivity.

Correlations

To further explore the relationship between individual changes in arousal and performance on the tasks, bivariate correlations coefficients were computed between post-drug ingestion changes in physiological parameters (BP and HR) and tasks dependent variables. For this analysis, for each participant we subtracted the baseline measurement from the average of post-tablets administration arousal measurements; therefore, change in arousal reflects increased state arousal following tablets ingestion relative to baseline level. Bonferroni correction for multiple comparisons was set to $p < .006$. The results indicated that increased DIA BP was associated with higher proportion of delayed versus immediate rewards selected in the MCQ

(Table 5.4, Figure 5.5A). Elevated DIA and SYS BP was also associated with less impulsive responding in the fearful context in the ASST, but this correlation did not survive the correction for multiple comparisons. In contrast, elevated DIA BP was associated with less information sampling in the IST RC condition (increased reflection impulsivity; Figure 5.5B). There were no other significant correlations (Table 5.4).

Table 5.4 Person correlations between changes in physiological parameters (delta = average post-drug measurement – pre-drug measurement) and performance on the impulsivity tasks.

		DIA BP Delta	SYS BP Delta	HR Delta
SSRT Neutral	Pearson's r	0.182	-0.177	0.039
	p-value	0.275	0.288	0.818
	N	38	38	38
SSRT Fearful	Pearson's r	-0.371 *	-0.335 *	0.021
	p-value	0.022	0.040	0.899
	N	38	38	38
IST FW P(correct)	Pearson's r	-0.091	0.065	0.174
	p-value	0.564	0.682	0.271
	N	42	42	42
IST RC P(correct)	Pearson's r	**-0.444 ****	-0.214	-0.141
	p-value	**0.003**	0.173	0.372
	N	**42**	42	42
MCQ Proportion LDR	Pearson's r	**0.496 ****	-0.036	0.006
	p-value	**0.001**	0.826	0.969
	N	**40**	40	40
PD ln h	Pearson's r	-0.098	0.056	0.112
	p-value	0.536	0.724	0.480
	N	42	42	42

* $p < .05$ (uncorrected), ** $p < .01$ (uncorrected), in bold are depicted correlations that survived the Bonferroni correction for multiple comparisons ($p < .006$)

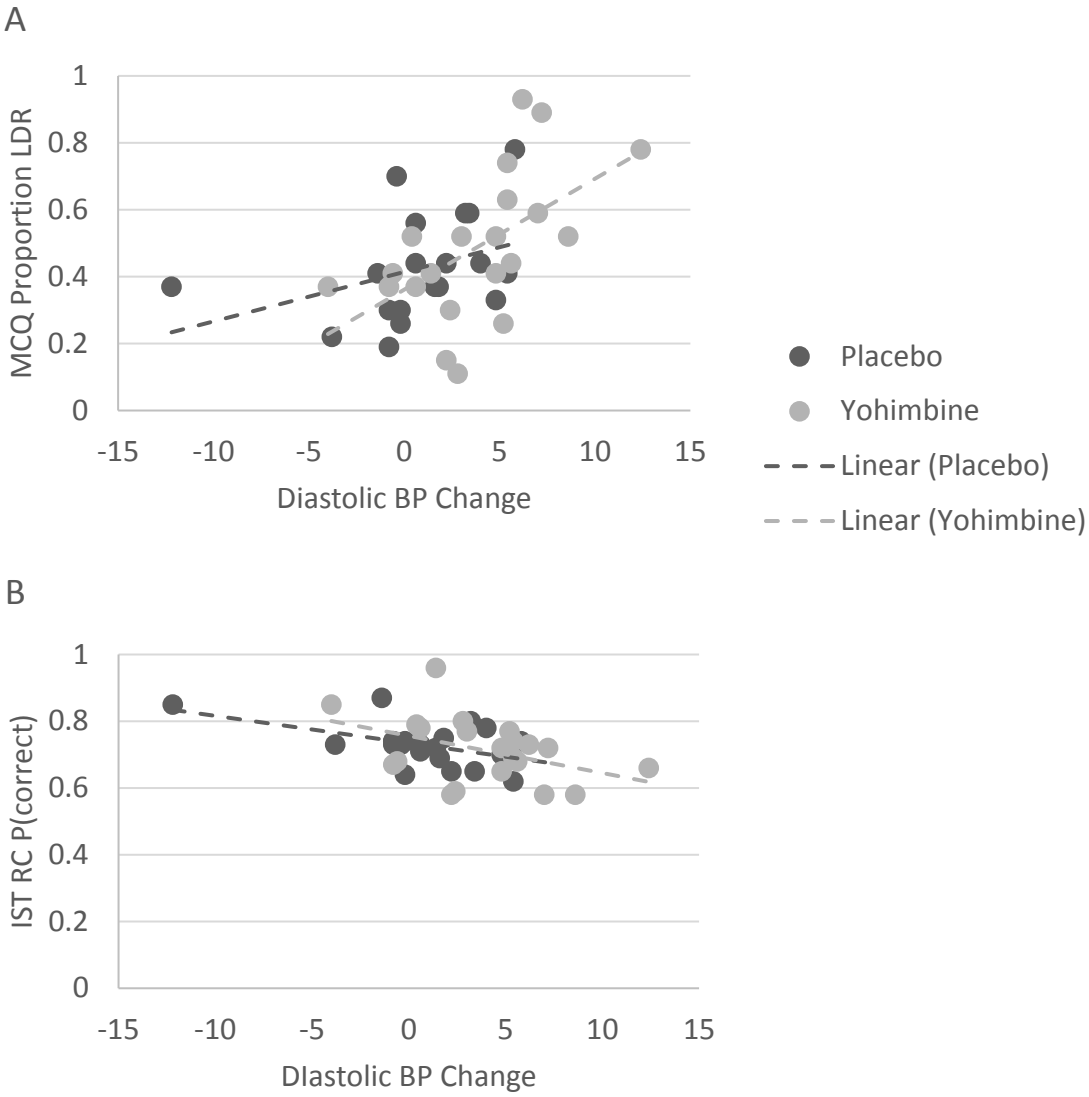

Figure 5.5 Scatterplots showing the relationship between the change in diastolic blood pressure and the proportion of larger delayed rewards (LDR) selected in the MCQ task (A) and the level of information gathering in the IST Reward Conflict condition (B). Different shades of grey depict the yohimbine and placebo groups.

5.5 Discussion

The current study examined the role of state arousal induced by administration of α_2-noradrenergic blocker, yohimbine, on distinct subtypes of behavioural impulsivity. We hypothesised that yohimbine-induced arousal would result in decreased impulsive behaviour.

In agreement with previous reports, yohimbine did not affect HR but caused an increase in BP, notably DIA BP (Krystal et al., 1992; Schwabe et al., 2010; Swann et al., 2013, 2005), proving to be a successful method of arousal induction.

The yohimbine group outperformed the placebo group at response inhibition in the ASST, as predicted. However, there were no group differences in performance in either risk-taking, or reflection, or temporal impulsivity tasks. Moreover, increased arousal, indexed by heightened DIA BP following drug administration, was associated with less impulsive behaviour in the ASST (motor impulsivity), albeit regardless of the emotional context, and MCQ (temporal impulsivity) tasks, but more impulsive behaviour on the IST RC task (increased reflection impulsivity). However, no association between trait impulsivity and resting state arousal was found; thus, the findings provide only partial support for our hypotheses.

5.5.1 Motor impulsivity

The yohimbine group showed lower motor impulsivity than placebo in the ASST, regardless of emotional context. This relationship, however, was only present when we controlled for individual differences in sensation seeking, indicating that personality characteristics might be a vital factor contributing to the role of arousal in inhibitory control. It seems relevant to note that in one study, sensation seeking correlated with performance on the Stop Signal Task (Muhlert, Boy, & Lawrence, 2015), suggesting that sensation seeking might play an important role in motor inhibition.

Overall, the findings of decreased motor impulsivity in the yohimbine group, which showed an increased level of arousal, and the correlational results of a trend for increased DIA and SYS BP following the drug administration vs baseline linked to better response inhibition, in the fearful context, support our hypothesis of reduced motor impulsivity in a state of heightened physiological arousal. These results also corroborate previous findings. For example, abrupt alerting cues (i.e., an irrelevant external signal that appears briefly), which temporarily increase arousal (i.e., phasic alertness), were found to improve the ability to stop an already initiated response (Weinbach, Kalanthroff, Avnit, & Henik, 2015). Similarly, response inhibition capacity seems to be affected by acute changes in cardiovascular arousal state within the cardiac cycle, such that participants are more likely to successfully inhibit motor responses during cardiac systole (increased state of physiological arousal) than diastole (lower state of cardiac arousal) (Rae et al., 2018). SSRT, an index of difficulty in motor response inhibition,

also decreases after acute exercise (Chu et al., 2015; Joyce, Graydon, McMorris, & Davranche, 2009). Moreover, atipamezole, another antagonist of α_2-adrenergic receptors, was also shown to decrease the SSRT in a rodent version of the SST (Bari & Robbins, 2013). Taking the previously reported data and our findings together, we conclude that a moderate increase in the level of arousal is related to a decrease in motor 'stopping' impulsivity.

However, there were no group differences in motor impulsivity in the neutral and fearful conditions in the ASST. This may suggest that putative yohimbine-induced changes in the processing of emotional faces (Schwabe et al., 2013), may not be interfering with response inhibition capacities. However, the previous report by Schwabe and colleagues (2013) suggested that there may be sex differences associated with the yohimbine-induced effect on emotional processing. Due to the small sample size in our study, we were unable to disentangle these effects reliably. Future studies should address this issue.

5.5.2 Temporal impulsivity

Although we did not observe any group differences in performance in any other tasks apart from ASST, we found associations between post-drug administration arousal change and impulsive decisions. Specifically, increased DIA BP following drug administration was associated with less impulsive choices in the MCQ task, suggesting that increased arousal at subject-level was associated with lower temporal impulsivity. Previous studies looking at the relationship between physiological arousal and delay discounting studied mainly stress reactivity with mixed findings. For example, Diller and colleagues (Diller, Patros, & Prentice, 2011) found that female participants with higher HR reactivity to acute stressor showed larger delay discounting (more temporal impulsivity), but this trend did not hold in males. Their results indicated that the stress reactivity of the autonomic nervous system might be related to impulsivity. Kimura *et al.*, (2013), on the other hand, did not find any significant association between HR or HR reactivity with delay discounting rates. Instead, stress increased the delay discounting only in a group of individuals who showed a cortisol increase, a marker of stress. A recent study (Lempert, Speer, Delgado, & Phelps, 2017) using within-subject design, reported that blunting arousal levels by propranolol administration, a β-adrenergic receptor antagonist, also did not affect temporal discounting rates. Together, these results indicate that the effects of arousal on delay discounting might not be straightforward and may mainly depend on individual changes in arousal level, which may affect biological changes in different ways.

5.5.3 Probability discounting

In contrast to temporal discounting, we found no association between the change in arousal and probability discounting. Indeed, a previous study looking at the role of

noradrenergic transmission in risky decisions in rodent models (Montes et al., 2015) found that yohimbine does not affect probabilistic discounting per se, but rather impairs the flexibility of response adjustments; when reward probabilities were initially large and then decreased (descending condition), yohimbine increased the number of risky choices in later blocks. The reverse was true for ascending condition (when the reward probabilities were initially small and then increased) - yohimbine resulted in reduced preference towards risky options. Since in our study the trials of different probabilities were intermixed (there was no ascending/descending condition), the 'pure' risk-taking was more likely to be tested. Lack of an effect of yohimbine in our task confirms the notion that noradrenergic activation may not be affecting risky decisions. Our data are in contrast to those by Schmidt et al., (2013), who reported that increased physiological arousal following physical exercise was associated with less risky behaviour in a gambling task compared to the resting condition. However, unlike in the current study, which asked hypothetical questions explicitly, Schmidt et al., (2013) employed a gambling game paradigm, in which the probabilities were not explicit, and participants were perceiving the probabilities from the outcomes of the gambles. Therefore, the type of risk task (implicit or explicit) could be differentially affected by arousal level.

5.5.4 Reflection impulsivity

To our knowledge, this is the first investigation of the role of physiological arousal mediated by noradrenergic mechanisms in reflection impulsivity. Our results suggest that the DIA BP reactivity was negatively correlated with the degree of information sampling in the IST reward conflict condition. The results provide an indication that individuals showing a greater increase in DIA BP also gathered less information before deciding in the task. Importantly, this relationship was only present in reward conflict condition, in which the potential gains decrease as participants sample more data (information sampling/reward trade-off), and not in the fixed win condition, in which gathering as much information as possible is the most advantageous. Therefore, state arousal may affect reflection impulsivity in more challenging, more ambiguous circumstances.

5.5.5 Conclusions

In conclusion, our findings indicate that yohimbine-induced arousal is associated with decreased motor impulsivity, suggesting that yohimbine treatment might prove to be a means of reducing 'stopping' impulsivity. Moreover, increased arousal, at the individuals' level, is associated with decreased temporal but increased reflection impulsivity. Probability discounting, a measure of risk-taking, was not related to arousal level. These results further support the notion that distinct subtypes of impulsivity are differentially affected by modulators.

Additionally, we did not find any support for the under-arousal hypothesis of impulsivity (Barratt, 1985; H. J. Eysenck & Eysenck, 1985; Zuckerman, 1969), as we did not observe any relationship between resting measures of arousal and trait impulsivity.

These data highlight the importance of state of physiological arousal in behavioural impulsivity.

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CHAPTER 6.

STUDY 5.
INTEROCEPTIVE ACCURACY PREDICTS NON-PLANNING TRAIT IMPULSIVITY

This article has been submitted to Psychophysiology:

Herman, A. M., Rae, C. L, Critchley, H. D, & Duka, T. Interoceptive accuracy predicts non-planning trait impulsivity. *Psychopharmacology* (under review).

Contribution

I contributed to the study design and the interpretation of the results. I collected and analysed the data as well as prepared the initial manuscript.

6.1 Abstract

Influential theories concerning personality argue that many impulsive individuals show physiological under-arousal at rest. This interoceptive state is proposed to be egodystonic, motivating impulsive maladaptive actions to enhance arousal. However, there is little empirical research on this matter. The current study tested the relationship between physiological markers of arousal, measures of interoceptive (in)sensitivity and trait impulsivity. Experiment 1 investigated whether individuals with high trait impulsivity show decreased resting measures of arousal (indexed from heart rate, heart rate variability, and sympathetic electrodermal activity). Experiment 2 assessed whether trait impulsivity is linked to interoceptive abilities. Overall, our results do not provide any compelling support for the under-arousal theory of impulsivity. However, impaired interoceptive (cardiac discrimination) accuracy predicted the degree of Barratt Non-Planning impulsivity; such that individuals with a better ability to distinguish between internal (bodily) and external signals manifest lower levels of Non-Planning trait impulsivity. These findings open an avenue for potential novel interventions aimed at improving planning abilities via better interoceptive discrimination.

Keywords: Interoception, Barratt Impulsiveness Scale, Heart Rate Variability, Skin Conductance, Heart Rate.

6.2 Introduction

The concept of an optimal level of arousal was first proposed by Hebb (1955), who suggested that each individual has an optimal level of arousal which 'feels best' and is linked to their capacity for highest level of performance. The theory also poses that individuals engage in activities that aim to maintain that optimal arousal state. By extension, individuals with a chronically low resting level of arousal will experience dysphoria unless they engage in behaviours to increase stimulation and evoke greater arousal towards their optimal level. The optimal level of arousal theory led to the development of personality theories based on this concept. According to these theories, impulsive individuals are under-stimulated at rest, have high sensitivity to signals of reward, and seek external means to evoke behavioural activation in order to raise arousal to the optimal level and mitigate the unpleasant psychological experience of an under-aroused state (Barratt, 1985; Eysenck & Eysenck, 1978; Zuckerman, 1969).

In support, some studies report diminished resting physiological arousal in individuals displaying impulsive behaviours. Heuristically, physiological arousal is associated with action-ready states, facilitated by sympathetic activation. Sympathetic activation is apparent as increased heart rate and blood pressure (through baroreflex suppression, and associated withdrawal of parasympathetic cardiovascular tone). Other autonomic measures, such as electrodermal activity also index centrally-driven peripheral arousal states. Thus, there is evidence linking lower resting heart rate with behavioural (delay discounting) and trait impulsivity (Fung, Crone, Bode, & Murawski, 2017; Mathias & Stanford, 2003), aggression (Mawson, 2009), and criminal behaviour (Choy, Raine, Venables, & Farrington, 2017; Latvala, Kuja-Halkola, Almqvist, Larsson, & Lichtenstein, 2015). Additionally, indices of sympathetic arousal are elevated during risk-taking behaviours such as gambling (Diskin & Hodgins, 2003; Meyer et al., 2000; Schmidt, Mussel, & Hewig, 2013). These findings support the assumption that participants with low physiological arousal may seek stimulation to approach their optimal arousal level.

One physiological marker, more related to self-control, is heart-rate variability (HRV) (Segerstrom & Nes, 2007; Thayer, Hansen, Saus-Rose, & Johnsen, 2009; Zahn et al., 2016). HRV refers to the beat-to-beat variation in heart rate and is dominated by parasympathetic (cardiorespiratory vagal) influences on the heart (Appelhans & Luecken, 2006). HRV is considered to be an indicator of resting state and of psychophysiological flexibility, enabling the autonomous nervous system to adjust cardiac activity according to situational demands (Appelhans & Luecken, 2006; McCraty & Shaffer, 2015). Indeed, research has linked heightened HRV with behavioural, emotional and cognitive self-control capacities. HRV is therefore sometimes regarded as a biomarker for self-regulation (Holzman & Bridgett, 2017;

Reynard, Gevirtz, Berlow, Brown, & Boutelle, 2011; Segerstrom & Nes, 2007; Thayer et al., 2009; Zahn et al., 2016).

Interoceptive ability is another factor associated with adaptive behaviour: Interoception refers to the communication and central processing of internal bodily signals, including the ability to perceive accurately changes in bodily arousal, which can guide actions and decisions (Craig, 2009; Damasio, 1996; Paulus, Stewart, & Haase, 2013). Therefore, if the arousal theories of impulsivity are correct, impulsive individuals might be more sensitive to low states of, or subtle reductions in, bodily arousal state (i.e. reflected in increased interoceptive abilities) and engage in impulsive or risky actions as a maladaptive way of regulating their arousal levels. Alternatively good interoceptive abilities may be advantageous, particularly when potential risk is involved (Kandasamy et al., 2016; Werner, Jung, Duschek, & Schandry, 2009), while insensitivity to arousal signals may be present in highly impulsive individuals, who consequently may pursue excessive ill-considered behaviours to engender normative experiences of physiological arousal in compensation for blunted perception of bodily signals.

Therefore, the current experiments aimed to clarify the relationship between physiological markers of arousal, interoceptive abilities, and trait impulsivity. Experiment 1 tested the hypothesis that trait impulsivity is associated with decreased measures of resting arousal, including heart rate and sympathetic electrodermal activity as well as decreased HRV, indexing arousal related shifts in the balance between sympathetic and parasympathetic influences on the heart. Experiment 2 assessed whether trait impulsivity is linked to altered interoceptive abilities.

6.3 Experiment 1

Experiment 1 tested whether impulsive individuals are characterised by a low resting state level of physiological arousal, employing complementary measures of autonomic arousal, namely heart rate (HR), tonic electrodermal activity (i.e. skin conductance level; SCL) and HRV. We also used two distinct self-report scales to assess trait impulsivity, quantifying distinct aspects of impulsive personality.

6.3.1 Methods 1

Participants

31 participants (14 males) from the University of Sussex and Brighton & Sussex Medical School community were recruited to take part in the study. All participants were right-handed, free from psychiatric or neurological disorders and had normal or corrected to

normal hearing and vision. Participants gave written informed consent. The study was approved by the Brighton & Sussex Medical School Research Governance & Ethics Committee.

Questionnaires

Self-reported trait impulsivity was measured using the Barratt Impulsivity Scale (Patton, Stanford, & Barratt, 1995), which consists of a 30-item checklist. The 30 items can be subdivided into scales measuring attention, motor and non-planning impulsivity. Another self-report measure of impulsivity, the UPPS-P Impulsive Behavior Scale (Cyders et al., 2007; Whiteside & Lynam, 2001) is a 59-item checklist measuring five different facets of impulsivity, including emotional impulsivity: negative urgency, (lack of) perseverance, (lack of) premeditation, sensation seeking and positive urgency.

Physiological recording

Cardiac measures were obtained using electrocardiography (ECG). Three Ag/AgCl monitoring electrodes were attached with foam tape (3M Healthcare, Neuss, Germany), two on the participant's left and right upper chest. A ground electrode was also located above the left hipbone at the superior ilium. Electrodes were connected to an ECG Electrode Adapter (1902-11, Cambridge Electronic Design). The signal was amplified (1902 Quad System, Cambridge Electronic Design) and relayed to Spike2 recording software via an analogue-to-digital recorder (1401, Cambridge Electronic Design). The ECG signal was sampled at 1000Hz and heart rate and heartrate variability measures were computed from these time-series data.

For sympathetic skin conductance level (SCL) recordings, two Ag/AgCl electrodes were filled with an isotonic recording electrode gel and attached with 2.5cm wide Transpore Surgical Tape to the palmer surface of the middle phalanx of the index and middle fingers of the participants' left hand. Electrodes were connected to a proprietary skin conductance module (2502, Cambridge Electronic Design). The signal was relayed to the Spike2 recording software via an analogue-to-digital recorder (1401, Cambridge Electronic Design). To minimize movement and increase comfort, the participant's left arm was rested on a pillow.

Procedures

Each participant was asked to rest quietly with eyes open for at least 5 minutes before physiological recording commenced. This established a resting arousal level. Next, the participant continued to rest, with gaze fixated on a cross that was displayed on the screen in front of them for 2.5 minutes while ECG and SCL were recorded. Resting HR, HRV and

tonic SCL measures were derived from the recordings taken during this 2.5 minute period, in order to characterise the overall degree of arousal, which decreases with physiological relaxation states such as rest and sleep (Malmo, 1959).

Data analyses

Each participant's ECG waveform was thresholded to isolate each R-wave peak, and the inter-beat intervals were calculated using in-house scripts written with Spike2 (CED). Inter-beat intervals were entered to the HRVAS toolbox (Ramshur, 2010) in Matlab (R2012a, Mathworks). Heart rate variability was indexed as the root mean square of the successive differences (RMSSD). The HRVAS output also gave each participant's heart rate in beats per minute (bpm). The skin conductance data were analysed with a Matlab toolbox: Ledalab Version 3.4.3 (http://www.ledalab.de/), using continuous decomposition analysis (CDA) (Benedek & Kaernbach, 2010), to quantify tonic (CDA.tonic) skin conductance activity (SCL).

Pearson's correlations, *r*, two-tailed, were used to confirm the relationship between trait impulsivity and arousal level. Bonferroni correction for multiple comparisons, set to $p \leq .002$, was introduced for key correlations of interest, between nine measures of trait impulsivity (BIS and UPPS-P scores) and three autonomic measures of arousal (HR, HRV, SCL). For completeness, the full correlation matrix is included in Table 6.1.

We also undertook a median split of participants, to investigate whether individuals distinguished by high and low trait impulsivity (reflected in BIS Total score) differed in resting arousal measures. Highly impulsive individuals were those with the BIS score of 67 and above (N = 16, mean = 75.5, SD = 5.63), while low impulsive individuals scored 66 or below (N = 15, mean = 57.73, SD = 7.94). Independent *t*-tests compared arousal measures between the two groups. The statistical analysis was conducted in JASP version 0.8.6.0 (JASP Team, 2018).

6.3.2 Results 1

Group demographics and descriptive statistics are presented in Table 6.2. The correlational analysis showed that resting-state level of arousal indexed by HR or SCL was not related to any of the trait impulsivity measures (Table 6.1). HRV, indexed by the RMSSD, was positively correlated with Positive Urgency. The effect size was moderately strong; however, this effect did not survive the correction for multiple comparisons ($p > .002$). Subscales of BIS strongly correlated with each other as well as measures of UPPS-P scale. An exception was Sensation Seeking which, on the other hand, did not correlate significantly with other impulsivity measures.

Moreover, we found no significant differences in any of the arousal measures between high and low impulsive individuals (see Table 6.3 for details). The difference in SCL approached significance; however, the relationship tended in the direction opposite to expected under the optimal arousal level theory, that is impulsive group showed higher resting skin conductance level (tonic sympathetic state) than less impulsive group.

Table 6.1 Bivariate correlation coefficients. Relationships of interest are surrounded by a frame.

		1	2	3	4	5	6	7	8	9	10	11	12	13
1. RMSSD	*r*	—												
	p	—												
2. HR (bpm)	*r*	-.626 ***	—											
	p	< .001	—											
3. SCL (µS)	*r*	-.297	.255	—										
	p	.105	.166	—										
4. BIS Total	*r*	.124	.021	.106	—									
	p	.506	.910	.569	—									
5. BIS Attention	*r*	.171	.010	-.100	.870 ***	—								
	p	.357	.957	.593	< .001	—								
6. BIS Motor	*r*	.104	-.074	.159	.888 ***	.687 ***	—							
	p	.579	.692	.392	< .001	< .001	—							
7. BIS Planning	*r*	.048	.125	.212	.836 ***	.576 ***	.601 ***	—						
	p	.800	.503	.253	< .001	< .001	< .001	—						
8. Negative Urgency	*r*	.149	-.072	-.060	.601 ***	.549 **	.568 ***	.438 *	—					
	p	.424	.701	.748	< .001	.001	< .001	.014	—					
9. Sensation Seeking	*r*	-.079	.049	-.035	.132	.131	.331	-.133	-.154	—				
	p	.673	.793	.850	.477	.481	.069	.476	.409	—				
10. Positive Urgency	*r*	.409 *	-.140	-.065	.683 ***	.636 ***	.731 ***	.396 *	.713 ***	.284	—			
	p	.022	.454	.727	< .001	< .001	< .001	.027	< .001	.122	—			
11. Perseverance	*r*	.166	.080	.071	.651 ***	.555 **	.432 *	.712 ***	.354	.006	.324	—		
	p	.372	.669	.705	< .001	.001	.015	< .001	.051	.975	.076	—		
12. Premeditation	*r*	.020	.038	.129	.644 ***	.451 *	.616 ***	.601 ***	.338	.273	.470 **	.567 ***	—	
	p	.916	.837	.489	< .001	.011	< .001	< .001	.063	.138	.008	< .001	—	
13. Age	*r*	.132	-.268	-.108	-.184	-.305	-.118	-.056	.008	-.251	-.155	-.173	-.131	—
	p	.480	.144	.565	.322	.095	.526	.763	.968	.173	.405	.352	.483	—
14. Sex (1=male, 2=female)	*r*	.023	.139	-.091	.138	.127	.207	.018	.076	.276	.230	-.150	.154	-.275
	p	.902	.456	.627	.460	.497	.265	.922	.686	.132	.214	.420	.408	.135

* p < .05, ** p < .01, *** p < .001

Table 6.2 Descriptive statistics.

Variable		Mean	SD	Minimum	Maximum
Age		22.45	2.80	18	29
BIS	BIS Attention	17.87	4.26	11	28
	BIS Motor	24.16	4.55	17	36
	BIS Planning	24.87	4.26	17	31
	BIS Total	66.90	11.30	48	95
BPQ	Body awareness	67.52	22.18	32	109
UPPS-P	Negative Urgency	28.74	7.31	14	41
	Perseverance	19.39	4.64	11	27
	Positive Urgency	28.32	9.62	14	48
	Premeditation	22.19	5.43	12	38
	Sensation Seeking	34.81	6.51	19	48
Resting arousal	HR (bmp)	74.99	10.40	55.20	101.80
	HRV	44.56	24.69	7.30	103.90
	SCL (μS)	3.50	0.26	3.15	4.14

Table 6.3 Comparison between High impulsive and Low impulsive individuals (group allocation based on Barratt Impulsiveness Scale sample median split).

Independent Samples t-Test

	Low impulsive		High impulsive					Cohen's d	95% CI	
	Mean	SD	Mean	SD	t	df	p		Lower	Upper
RMSSD	42.21	24.84	46.76	25.16	0.51	29	0.617	0.18	-22.92	13.84
HR (bpm)	74.03	9.62	75.89	11.31	0.49	29	0.627	0.18	-9.6	5.88
SCL (μS)	3.41	0.23	3.59	0.27	1.95	29	0.061	0.7	-0.36	0.01

6.3.3 Discussion 1

Experiment 1 did not confirm the relationship between high trait impulsivity and diminished resting state of arousal, indexed by either cardiac or skin conductance measures. This contradicts previous findings on delay discounting task and BIS questionnaire (e.g. Fung, Crone, Bode, & Murawski, 2017; Mathias & Stanford, 2003). However, most past studies investigated male participants only (e.g. Mathias & Stanford, 2003), highlighting the possibility that sex differences may be an important factor to test for in further research. Moreover, high trait impulsivity in our experiment was not associated with diminished HRV, considered by some to be a physiological biomarker of self-regulation capacities (Holzman & Bridgett, 2017; Reynard et al., 2011; Segerstrom & Nes, 2007; Thayer et al., 2009; Zahn et al., 2016). On the contrary, elevated positive urgency, i.e. a tendency to act

impulsively while experiencing strong positive emotions (Cyders & Smith, 2007), was linked to higher HRV, indicating a better cardiac adjustment to circumstances in more impulsive individuals (although this relationship did not survive the correction for multiple comparisons). Therefore, our results do not provide evidence for the link between HRV and of trait impulsivity.

As expected, subscales of BIS strongly correlated with each other, and measures of UPPS-P scale (apart from Sensation Seeking). Thus, all of these dimensions of trait impulsivity strongly relate and are likely elements of an overall construct. These results also indicate that despite emotional impulsivity components (i.e. negative and positive urgency) present in the UPPS-P scale, both scales, BIS and UPPS-P, are similar to each other with regards to the strong degree of inter-relation amongst their subscale dimensions. However, as an outlier to this general rule, Sensation Seeking did not correlate significantly with other impulsivity measures, suggesting that this element reflects a separate construct of impulsivity, probably related to a greater extent to risk-taking rather than impulsive tendencies *per se*. Importantly, despite reported links between cardiac arousal and risk-taking in the literature (e.g. Schmidt et al., 2013), we failed to confirm any relationship between Sensation Seeking and any of the physiological measures of arousal.

6.4 Experiment 2

Experiment 2 tested the hypothesis that trait impulsivity is associated with altered interoception. According to arousal theories of personality, some individuals may act impulsively to increase arousal to an optimal level. Therefore, we hypothesised that impulsive individuals may be more sensitive to subtle changes in their (low) arousal level and correspondingly show intact or even heightened interoceptive abilities. However, since in Experiment 1 we did not find any evidence of any association between trait impulsivity and resting arousal levels, we hypothesised that the alternative may be more plausible: Since physiological cues can guide our actions and decisions, impulsive individuals could exhibit impulsive behaviours as a result of blunted sensory or psychological sensitivity to changes within their bodies, evidenced by diminished interoceptive performance.

In Experiment 1, we found a strong association between measures of impulsivity assessed with BIS and UPPS-P subscales. Therefore, for efficiency, we employed only the BIS scale in Experiment 2.

6.4.1 Methods 2

Participants

Sixty volunteers (16 males) were recruited from staff and students of the University of Sussex to take part in the study. Each participant provided written informed consent, with all procedures approved by the local Cross-School Research Ethics Committee.

Tasks and Questionnaires

BIS as described above was used to assess trait impulsivity. Subjectively perceived sensitivity to bodily sensations was measured using the Awareness subscale of the Body Perception Questionnaire (Cabrera et al., 2017), consisting of 45 questions on awareness of bodily feelings, such as respiratory sensation or stomach and gut pains in daily life.

Interoceptive performance was assessed using both the heartbeat (HB) tracking and discrimination tasks. These tasks have distinct psychophysiological properties; hence their combination enhances inferential power.

In **HB tracking task** (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015; Schandry, 1981) participants were instructed to count silently, without manually checking, heartbeats they feel in the body during variable time periods. These ratings were compared against the actual number of heartbeats, as recorded objectively and non-invasively by a clinical-grade pulse oximeter (Nonin Inc.) fitted with a soft (i.e. not spring-loaded) cuff, placed over the participant's index or middle finger of their non-dominant hand. There were six trials with a variable time-windows of 25, 30, 35, 40, 45 and 50 s, presented in a randomised order. For each trial, an accuracy score equalled [1 − (|nBeatsReal− nBeatsReported|)/((nBeatsReal + nBeatsReported)/2)] x 100. Resulting values were averaged over the 6 trials, yielding an overall accuracy score for each participant (Hart, McGowan, Minati, & Critchley, 2013).

In **HB discrimination task** (Garfinkel et al., 2015), participants judged whether trials, consisting of a series of ten auditory tones (presented at 440 Hz and lasting 100 ms) were synchronous with their heartbeat (binary yes/no answers). On synchronous trials, the ten notes occurred at the rising edge of finger pulse pressure wave; on asynchronous trials, they followed 300 ms later. Approximately half the tones were thus presented 'on the heartbeat' and half were delayed (Wiens & Palmer, 2001). The order of these synchronous and delayed trials was fully randomised for each participant. In both conditions, the tones were presented at the same rate. Participants could therefore not use the tempo of tones or other knowledge about their heart rate to guide responses: phase synchrony of tones and heartbeats served as the only informative cue. Since the discrimination task delivered external feedback that could be used to infer heart rate, these tasks were performed after the heartbeat counting

task. There were 20 trials in total. The HB discrimination accuracy reflected the percentage of correct answers.

Confidence ratings

At the end of each trial, in both the tracking and discrimination tasks, participants immediately rated their confidence in their answer using a continuous visual analogue scale ranging from "Total guess" (i.e. 0) to "Complete confidence" (i.e. 100). The mean confidence ratings reflected the interoceptive sensibility of self-reported heartbeat perception (Garfinkel et al., 2015).

Interoceptive insight refers to the metacognitive measure of one's performance, that is the extent to which confidence predicts task accuracy (Garfinkel et al., 2015; Khalsa et al., 2018). Insight score for the HB tracking task was assessed by calculating the within-participant Pearson correlation, *r*, between confidence and accuracy scores. Due to binary (yes/no) responses on the HB discrimination task, interoceptive insight for this measure was quantified using receiver operating characteristic (ROC) curve analysis (Green & Swets, 1966).

Statistical analysis

The relationship between self-reported impulsivity and the measures of interoception were first explored with correlational analyses (a series of Pearson's two-tailed correlations). Next, we investigated whether interoception predicted trait impulsivity using multiple regressions. A series of three linear regressions applied the three subscales of trait impulsivity (attention, motor, non-planning) as dependent variables, and the demographic variables (age and sex), baseline HR and dimensions of interoception as independent variables. The statistical analysis was conducted in JASP version 0.8.6.0 (JASP Team, 2018).

6.4.2 Results 2

Due to equipment failure, digitized Body Perception Questionnaire data were missing for one participant, and one other participant did not complete the heartbeat discrimination task. Descriptive statistics are presented in Table 6.4**.**

Correlational analysis (Table 6.5) revealed that heart rate was negatively correlated with both heartbeat tracking and heartbeat discrimination accuracy, indicating that individuals with lower heart rate performed with greater accuracy on these interoceptive tasks. However, similarly to results from Experiment 1, no significant correlations between HR and measures of BIS were found. There were also no significant associations between measures of impulsivity and interoception (see Table 6.5 for details).

Multiple regressions analysis indicated that the regression model for the prediction of BIS Planning score was significant ($F(10, 47) = 2.55$, $p = .015$, $R = .593$, $R^2 = .352$). Specifically, heartbeat discrimination accuracy, heart rate and age added statistically significantly to the prediction (see Table 6.6 for details). In contrast, neither BIS Attention ($F(10, 47) = 0.39$, $p = .946$; no significant coefficients), nor BIS Motor ($F(10, 47) = 0.85$, $p = .588$; no significant coefficients) were related to any dimensions of interoception.

Table 6.4 Sample demographics and descriptive statistics. Bpm – beats per minute

Variable	**N**	**Minimum**	**Maximum**	**Mean**	**SD**
Age	60	18	37	22.33	3.75
BIS Attention	60	10	25	17.73	3.42
BIS Motor	60	16	36	24.23	4.28
BIS Planning	60	12	38	29.1	5.83
BIS Total	60	43	90	71.07	10.98
BPQ Body Awareness Score	59	36	100	65.98	15.46
HB Tracking Accuracy	60	-8	98	58.63	26.11
HB Tracking Insight	60	-0.9	0.95	0.22	0.49
HB Tracking Confidence	60	4	90	39.68	21.13
HB Discrimination Accuracy	59	10	95	49.11	14.92
HB Discrimination Insight	59	0.12	0.95	0.53	0.15
HB Discrimination Confidence	59	4	88	49.2	18.32
HR (bpm)	60	51.3	100	75.34	10.15

Table 6.5 Bivariate correlations

		1	2	3	4	5	6	7	8	9	10	11	12	13
1. Age	*R*	—												
	p	—												
2. Sex (1=male, 2=female)	*R*	0.176	—											
	p	0.180	—											
3. BIS Attention	*R*	-0.001	-0.014	—										
	p	0.995	0.915	—										
4. BIS Motor	*R*	0.029	-0.082	0.508 ***	—									
	p	0.827	0.532	< .001	—									
5. BIS Planning	*R*	-0.298 *	0.076	0.460 ***	0.469 ***	—								
	p	0.021	0.566	< .001	< .001	—								
6. BIS Total	*R*	-0.147	0.004	0.754 ***	0.797 ***	0.857 ***	—							
	p	0.263	0.978	< .001	< .001	< .001	—							
7. Body awareness	*R*	-0.083	0.285 *	0.113	0.141	0.060	0.122	—						
	p	0.533	0.029	0.393	0.288	0.649	0.357	—						
8. HB Tracking Accuracy	*R*	0.118	-0.137	0.106	-0.077	0.115	0.064	0.024	—					
	p	0.370	0.298	0.421	0.560	0.382	0.626	0.857	—					
9. HB Tracking Confidence	*R*	-0.081	-0.149	-0.010	-0.114	-0.100	-0.100	-0.055	0.266 *	—				
	p	0.537	0.255	0.942	0.387	0.446	0.445	0.677	0.040	—				
10. HB Tracking Insight	*R*	-0.126	-0.202	0.060	0.043	0.139	0.109	0.015	0.132	0.177	—			
	p	0.336	0.121	0.649	0.747	0.290	0.407	0.913	0.314	0.177	—			
11. HB Discrimination Accuracy	*R*	-0.161	0.029	0.006	-0.218	-0.225	-0.201	-0.080	0.098	0.002	-0.011	—		
	p	0.224	0.825	0.964	0.097	0.086	0.127	0.549	0.462	0.989	0.936	—		
12. HB Discrimination Confidence	*R*	-0.148	-0.172	-0.051	-0.048	-0.101	-0.087	-0.018	0.118	0.652 ***	0.224	-0.138	—	
	p	0.262	0.194	0.703	0.719	0.448	0.511	0.891	0.374	< .001	0.089	0.296	—	
13. HB Discrimination Insight	*R*	-0.054	-0.050	-0.029	0.003	-0.098	-0.060	0.115	0.118	0.184	0.144	0.428 ***	-0.060	—
	p	0.684	0.705	0.828	0.984	0.459	0.654	0.390	0.374	0.163	0.276	< .001	0.653	—
14. HR (bpm)	*R*	-0.119	0.199	-0.158	-0.049	-0.101	-0.122	0.198	-0.257 *	0.067	-0.018	-0.381 **	0.198	-0.362 **
	p	0.364	0.127	0.229	0.711	0.441	0.353	0.133	0.048	0.609	0.890	0.003	0.132	0.005

* p < .05, ** p < .01, *** p < .001

Table 6.6 Predictors of BIS Non-Planning impulsivity. Significant variables are depicted in **bold**.

Predictors	Unstandardized	Standard Error	Standardized	t	p	95% CI	
						Lower	Upper
(Intercept)	64.28	10.13		6.35	< .001	43.92	84.68
Age	**-0.75**	**0.2**	**-0.48**	**-3.7**	**< .001**	**-1.15**	**-0.34**
Sex	3.33	1.72	0.26	1.93	0.059	-0.14	6.8
Body awareness	-0.01	0.05	-0.03	-0.2	0.821	-0.11	0.09
HB tracking	0.04	0.03	0.2	1.47	0.147	-0.02	0.1
HB tracking Confidence	-0.02	0.05	-0.06	-0.4	0.717	-0.11	0.08
HB Tracking Insight	1.9	1.52	0.15	1.25	0.219	-1.16	4.97
HB discrimination	**-0.17**	**0.06**	**-0.44**	**-3.1**	**0.003**	**-0.28**	**-0.06**
HB Discrimination Confidence	-0.05	0.05	-0.14	-0.9	0.396	-0.15	0.06
HB Discrimination Insight	-3.18	5.74	-0.08	-0.6	0.582	-14.76	8.3
HR (bpm)	**-0.18**	**0.08**	**-0.32**	**-2.2**	**0.035**	**-0.35**	**-0.01**

6.4.3 Discussion 2

Overall, the results support – to a degree - the hypothesis that trait impulsivity is associated with impaired interoceptive processing. Specifically, we observed that greater BIS Non-Planning impulsivity is predicted by lower HB discrimination ability, while there was no evidence that other impulsivity subscales (i.e. Motor and Attentional impulsivity) were related to interoception.

BIS Non-planning impulsivity reflects a lack of future orientation (Patton et al., 1995). In the realm of heartbeat detection performance, both tasks seek to quantify individual differences in the strength of one cardioceptive channel of interoception from the degree to which it can be differentially and declaratively sensed (Khalsa et al., 2018). Interoceptive abilities positively correlate with both insula grey matter volume and with insula activity during the heartbeat discrimination task (e.g. Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004). The right anterior insular cortex may, therefore, integrate internal and external information (Critchley et al., 2004; Hassanpour et al., 2016). The insula may be specifically involved in conscious awareness of body states that constitute the necessary substrate for the emotional-self though time (Craig, 2009; Hassanpour et al., 2016).

Insula function is also associated with self-reported impulsivity. For example, relative to low impulsive individuals, those with high impulsivity show increased activity across several structures, including the insula, when performing a risky decisions task (Lee et al., 2008). Moreover, activation of the right anterior insula and middle frontal cortex during Stop as compared to Go trials of the Stop Signal Task, an index of pre-potent response inhibition,

negatively correlates with motor and non-planning impulsivity scores (Farr, Hu, Zhang, & Li, 2012). Furthermore, response inhibition on the stop signal task is improved during momentary states of cardiovascular arousal when the heart contracts (Rae et al., 2018), suggesting a critical role for insula function in impulsivity.

It is plausible that the relationship between enhanced interoceptive discrimination abilities and non-planning impulsivity reflect interactions amongst critical neural substrates broadly underpinning motivational behaviour, and embodied prediction. Future studies should address this hypothesis using neuroimaging techniques.

6.5 General discussion

The theory suggests that impulsive individuals may engage in rash actions as a maladaptive means of regulating their arousal level (Barratt, 1985; Eysenck & Eysenck, 1978; Zuckerman, 1969), but empirical evidence is limited. The current study investigated the relationship between trait impulsivity, resting-state arousal level and interoceptive dimensions. Contrary to the optimal arousal level theory, we did not find evidence in more impulsive individuals for decreased resting-state arousal, expressed by lower skin conductance level and heart rate, or heart rate variability. We did, however, observe a relationship between self-reported impulsivity and interoception: increased accuracy on the heartbeat discrimination task, alongside age, heart rate, and, marginally, sex, was predictive of BIS Non-planning impulsivity subscale. These results add to the growing body of evidence suggesting that enhanced interoceptive abilities guide adaptive behaviour and better decision-making (Craig, 2009; Damasio, Tranel, & Damasio, 1991; Dunn et al., 2010; Kandasamy et al., 2016; Werner et al., 2009). However, equally importantly, the other two subscales of impulsivity, i.e. inattention or motor impulsivity, were not predicted by any of the impulsivity dimensions, suggesting specificity of the observed effect to the Non-Planning dimension.

Neither Experiment 1 nor 2 revealed a relationship between physiological markers and impulsivity, in contrast to previous reports (Allen, Hogan, & Laird, 2009; Allen, Matthews, & Kenyon, 2000; Fung et al., 2017; Mathias & Stanford, 2003). However, previous research has often found a relationship between physiological arousal and impulsivity in males only (Allen et al., 2009, 2000; Mathias & Stanford, 2003). It is plausible that sex differences might be a contributing factor: indeed, in our data, sex reached trend as a predictor of Non-Planning impulsivity. Another possibility is that the relationship between resting state arousal and impulsivity only occurs at the very high (maladaptive) impulsivity levels, which could not be captured with our sample of highly functioning individuals (university students).

Instead, our results indicate that increased interoceptive accuracy is predictive of decreased BIS Non-Planning impulsivity, but not significantly of other subtypes of trait

impulsivity subtypes. Importantly, in the current study, we were able to differentiate between distinct dimensions of interoception (Garfinkel et al., 2015; Khalsa et al., 2017) and their contribution to impulsive tendencies. Better performance on the heartbeat discrimination task requires correct differentiation between internal bodily signals (heartbeats) and external cues (tones). Therefore, the ability to correctly differentiate between internal and external signals predicts better planning tendencies (lower Non-Planning impulsivity score). Unsurprisingly, age was also a predictor of Non-Planning impulsivity. This finding agrees with the past literature indicating that self-reported impulsivity decreases with age (Churchwell & Yurgelun-Todd, 2013; Steinberg et al., 2008).

These results provide some initial evidence for a future avenue of research, which may include interoceptive training (e.g. biofeedback techniques) as a means of improving self-control capacities and enhanced decision-making in everyday situations. Specifically, since Non-Planning impulsivity is known to play a vital role in binge drinking and alcohol use and abuse (Caswell, Celio, Morgan, & Duka, 2015; Hamilton, Sinha, & Potenza, 2012; Jakubczyk et al., 2013), if replicated, these finding bear a great potential for novel therapeutic interventions, which could aid alcohol abuse prevention and treatment.

Importantly, none of the other dimensions of interoception (sensibility, accuracy on the heartbeat tracking task, subjective confidence ratings, nor metacognitive insight) were predictive of trait impulsivity. These findings signify the distinction between interoceptive dimensions. Similarly, the fact that better interoceptive abilities predicted only Non-Planning impulsivity, indicated that subtypes of trait impulsivity are not equivalent.

In conclusion, our data do not support the hypothesis that impulsivity is associated with under-arousal at rest in a normative sample of males and females. Instead, we report that improved ability to discriminate between internal bodily sensations and external cues might be a mitigating factor for Non-planning impulsivity. These findings also open a new avenue for potential novel interventions which could improve planning abilities by enhancing interoceptive accuracy.

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CHAPTER 7.

GENERAL DISCUSSION

Fragments of the discussion come from the manuscript submitted to the Neuroscience and Biobehavoural Reviews:

Herman, A. M. & Duka, T. Facets of impulsivity and alcohol use: What role do emotions play? *Neuroscience and Biobehavioural Reviews* (in press).

7.1 Review of general aims and summary of findings

7.1.1 Aims

The studies described in this thesis stemmed from the idea that behavioural impulsivity is not as stable as trait impulsivity but instead undergoes momentary changes depending on the circumstances (de Wit, 2009) and, therefore, can be modulated. Those state-depended changes could 'tip-over' self-control resources leading to impulsive actions and, further, to negative consequences, ranging from having one pint too many in a pub to a potentially life-devastating decision to take a dose of heroin. A better understanding of how and to what extent changes in emotional and physiological states may affect impulsivity aspects, might help identify risky states as well as develop coping strategies for susceptible individuals.

The aim of this thesis was threefold. The **first** aim was to clarify the influence of emotions on different dimensions of impulsive behaviours (study 1 and 3), also considering the role individual differences may play in this relationship (study 2 and 3). The distinct dimensions of impulsive behaviours studied were: (1) motor impulsivity, subdivided into motor 'stopping impulsivity'- an inability to inhibit an inappropriate motor response and motor 'waiting impulsivity' - difficulty awaiting correct signal to respond, (2) reflection impulsivity (fast decisions without sufficient information gathering and evaluation) and (3) choice impulsivity, further divided into temporal impulsivity (difficulty in delaying gratification) and risk-taking. The **second** aim was to look at neural correlates underpinning the impact of emotions on distinct subtypes of impulsivity (study 3). Finally, the **third** aim was to establish the relationship between impulsivity (behavioural and trait) and physiological arousal (studies 4 and 5). To address these aims, we conducted a set of experiments using a variety of methods including behavioural testing, physiological recordings, psychopharmacology and neuroimaging. Such a variety of approaches used allowed for a comprehensive understanding of the issues in question.

7.1.2 Summary of findings

The **study 1** used mood manipulations in a laboratory setting to establish how emotional states (specifically self-reported emotional valence, activity, and stress) affect distinct subtypes of impulsivity dimensions. The results indicated that induced affective states across the different mood induction groups did not affect behavioural impulsivity level; instead, *subjective changes in mood state* were associated with performance on impulsivity tasks. In particular, elevated state of tension (increased subjective stress ratings) was associated with more impulsive performance in the reflection impulsivity task. Increased activity (subjective ratings of arousal level) was associated with lower level of delay discounting (decreased temporal impulsivity).

The results regarding motor impulsivity, both 'stopping' and 'waiting' subtypes, were less conclusive but implied that increased subjective stress ratings might lead to more difficulty in response inhibition, while higher self-perceived activity (vs tiredness) might lead to decreased waiting impulsivity. These results not only show an important role of the perceived emotional state in impulsive behaviours but also highlight the increasingly recognised distinction between impulsivity dimensions by revealing that the dimensions of behavioural impulsivity are differentially affected by subjective mood state. Furthermore, these findings suggest that an ability to successfully regulate one's emotions might be an important mechanism for behavioural self-control.

Study 2 followed upon results from study 1 but instead looked at naturally occurring mood states in a large group of individuals sampled from the general population using an online study approach. The results indicated that impulsive personality trait was the best predictor of both reflection and temporal impulsivities, while probability discounting was best predicted by reward sensitivity, suggesting a separation between measures of impulsivity and risk-taking. Although mood state was not a predictor of any facets of impulsivity studied, correlations were found between affective state ratings and both trait and behavioural measures. Specifically, increased negative emotion ratings were associated with elevated impulsivity (trait, temporal and reflection), while higher ratings of positive emotions were associated with higher levels of sensation seeking, further supporting the differentiation between measures of impulsivity and risk-taking.

In **study 3** we investigated the role of emotional context in impulsive behaviours. Specifically, we examined whether task-irrelevant emotional context affected impulsive actions and decisions and investigated neural mechanisms underpinning these processes with functional magnetic resonance imaging (fMRI). Following on our results from study 2, the role of trait impulsivity as a potential modulator of this relationship was evaluated. The emotional context did not affect impulsive performance at the behavioural level. However, individuals with higher trait impulsivity presented compensatory neural activations in brain regions associated with working memory, attention and somatomotor processing while executing motor inhibition successfully. This compensatory effect was further potentiated under fearful compared to neutral contexts. These findings suggest that in emotional circumstances, compensatory neural resources need to be recruited more in impulsive individuals to achieve the same level of motor inhibitory control. Presumably, depending on the intensity of the emotional circumstances such a compensatory mechanism may fail, leading to impulsive behaviours. In contrast, temporal discounting was not affected by emotional context at the behavioural or neural level; however, increased emotional impulsivity trait (Negative Urgency) was associated with enhanced activation in visual attention areas when choosing delayed options over immediate ones.

The subsequent experiments examined the relationship between physiological arousal and behavioural as well as trait impulsivity. In **study 4** increased state of physiological arousal was induced via oral administration of pharmacological stressor, yohimbine hydrochloride, which induces noradrenergic activation. Participants under yohimbine showed lower 'stopping' impulsivity than those under placebo, indicating that increased level of physiological arousal improved an ability to inhibit pre-potent responses. Yohimbine did not affect other facets (either risk-taking or temporal, or reflection impulsivity); however, subject-specific changes in arousal level were associated with behavioural impulsivity. Specifically, the more the increase in diastolic blood pressure post-administration, the lower the temporal and 'stopping' impulsivity scores. On the contrary, higher diastolic blood pressure (an index of enhanced arousal) was associated with higher reflection impulsivity. Together, these findings point to the role of individual changes in state arousal in modulating behavioural impulsivity.

We did not find any support in our data for the under-arousal theory of impulsivity (Barratt, 1985; H. J. Eysenck & Eysenck, 1985; Zuckerman, 1969) stating that highly impulsive individuals would show low resting state level of arousal, for whom impulsive actions serve as maladaptive ways of elevating arousal level to the optimal one.

Finally, in **study 5** we challenged again the putative under-arousal hypothesis of impulsivity using cardiovascular indexes of arousal as well as skin conductance level. Once more, we did not find any relationship between trait impulsivity and resting arousal level. Therefore, in a subsequent experiment we set out to investigate whether instead of the maladaptively low resting level of arousal, more impulsive individuals would show an altered perception of internal bodily signals (i.e. interoception). The results indicated that poor interoceptive accuracy, specifically difficulty in discriminating between internal and external cues, was a predictor of non-planning impulsivity. Therefore, impulsive individuals, particularly those showing lack of planning-tendencies, present impaired sensitivity to bodily cues. Since an ability to correctly read bodily sensations is vital for maintaining homeostasis, poor interoceptive discrimination may result in maladaptive decisions and, further, impulsivity.

7.2 Discussion of each addressed aim

7.2.1 Clarification of the role of emotional states in different dimensions of impulsive behaviours

The role of emotional states in impulsive behaviours was long suspected. Some previous studies were devoted to understanding how affective states might impact impulsive performance (reviewed in Chapter 1). However, those previous experiments predominantly focused on choice impulsivity (temporal impulsivity and risk-taking). Moreover, various measures of both

temporal impulsivity and risk-taking have been adopted (for example, some studies used hypothetical risk-taking, others - real potential risk), hindering a broad comparison across studies. With an increased understanding that impulsivity is a heterogeneous construct with distinct underlying neural mechanisms, a comprehensive approach comparing the role of emotional states across a variety of impulsivity dimensions was lacking. Therefore, **the current research not only allows us to establish the role of emotional states in impulsive behaviours and decisions but also shows the extent to which distinct impulsivity facets are differentially affected by emotional states** (for a summary see Table 7.1), further supporting the notion of impulsivity as a multidimensional concept with distinct modulators.

Table 7.1 Summary of findings regarding the role of emotional and physiological states in impulsive behaviour.

Impulsivity dimension	**Change in internal bodily state**	
	Subjective emotional state (study 1)	**Physiological arousal (study 4)**
Temporal	↓ with ↑ activity ratings	↓ with ↑ arousal
Reflection	↓ with ↑ relaxation ratings	↑ with ↑ arousal
Motor 'stopping'	↑ with ↑ tension (stress) ratings	↓ with ↑ arousal
Motor 'waiting'	↓ with ↑ activity ratings	-------
In-attention	↑ with sadness ratings	-------

↑ - an increase; ↓ - a decrease; --- - relationship not tested, in grey – tentative relationships

Previously, researchers reported that inducing negative affective state (but not stress state) results in enhanced **temporal impulsivity** (more short-sighted decisions) (e.g. Guan, Cheng, Fan, & Li, 2015; Lerner, Li, & Weber, 2013), while the opposite was true for positive affective state (e.g. Liu, Feng, Chen, & Li, 2013; Weafer, Baggott, & de Wit, 2013). Results regarding the role of stress state on temporal discounting are mixed, but some suggestions on the role of individual sensitivity to stress and cortisol responses have been made (e.g. Kimura et al., 2013; Lempert, Porcelli, Delgado, & Tricomi, 2012).

In study 1 we did not confirm the role of emotional experience valence (positive/negative mood state) or stress state on temporal discounting; instead, we observed a role of self-perceived activity level. In study 2, however, we found correlational evidence for increased delay discounting tendencies with elevated negative emotion reports. Moreover, a task-irrelevant fearful context in study 3 did not affect performance on the delay discounting task. We also found evidence that trait impulsivity is a predictor of delay discounting tendencies. Therefore, our findings only partly corroborate previous reports regarding the influence of negative emotional state on temporal discounting and instead indicate the role of self-perceived differences in activity (which are more linked to arousal level).

Possibly, our findings do not fully replicate previous results because past studies mainly focused on the valence of emotional experience (i.e. positive vs negative, happy vs sad), while in our first study we used a measure of mood-state rating which differentiates the emotional

valence from arousal (tired vs active) and stress state (tension vs relaxation). Indeed, in a previous study when self-reported arousal was also assessed, higher ratings of arousal were associated with decreased temporal impulsivity (Weafer et al., 2013). Together, these results highlight the role of different aspects of emotional experience in temporal impulsivity. Moreover, our findings raise a possibility that the distinction between subjective measures of emotional valence and arousal could additionally explain the variability of the results concerning the role of stress on delay discounting.

To our knowledge, there is very little information about the role of affective states in **reflection impulsivity**. Initial investigations have suggested that positive emotional states might increase reflection impulsivity via enhanced efficiency of the decision-making process (Isen & Means, 1983; Isen, Rosenzweig, & Young, 1991; Messer, 1970). Our results from study 1 indicate that increased reports of tension (subjective stress ratings), were associated with less information gathering in the Information Sampling Task (higher reflection impulsivity). Interestingly, this relationship was mainly present in the more challenging version of the task, reward conflict condition, which involves a trade-off between information gathering and possible reward. In study 2, we found a very weak relationship in the same direction between negative emotional state and reflection impulsivity, which did not survive the correction for multiple comparisons. Taking these results together, it seems that some aspects of reflection impulsivity might be dependent on subjective stress ratings, but the valence of the experience or the perceived activity (self-reported arousal state) might not play such a significant role.

Past studies looking at the role of emotional states on **motor 'stopping' impulsivity** yielded highly inconsistent results with some studies reporting no effect of mood state on response inhibition, some reporting enhanced or diminished response inhibition following a stress induction (Chepenik, Cornew, & Farah, 2007; Patterson et al., 2016; Scholz et al., 2009; Smallwood, Fitzgerald, Miles, & Phillips, 2009; Weafer et al., 2013). The lack of agreement in previous literature might derive from distinct measures of 'stopping' impulsivity employed. To overcome this problem, in our studies, we only used a Stop Signal Task (or an emotional version), which is a well-validated measure of cancellation of action that has already been initiated. In study 1 we found tentative evidence for a positive relationship between response inhibition failure and the changes in subjective stress ratings, but no relationship between either activity or valence of emotional experience and "stopping impulsivity" was found. Accordingly, in study 3, task-irrelevant fearful context did not affect response inhibition, and the behavioural performance was not related to trait impulsivity level. Therefore, contributing to the past research, our results indicate that emotional experiences may modulate pre-potent response inhibition measured with the Stop Signal Task to a little extent.

'Waiting' impulsivity is another sub-dimension of motor impulsivity. It reflects the difficulty in waiting for an appropriate signal to occur to initiate an action. It can be measured

with the 5-CSRTT, which only relatively recently has been translated from rodent to human versions. We believe that we were the first to investigate whether emotional states modulate 'waiting' impulsivity. Our initial results from study 1 give some tentative evidence for the role of self-perceived activity (vs tiredness) in decreasing waiting impulsivity. These initial results need further replication but may provide a new avenue of research, since waiting impulsivity is implicated to play a substantial role as a vulnerability factor for developing alcohol misuse (Sanchez-Roige, Stephens, & Duka, 2016).

Inattention is also considered a part of impulsivity construct. Previous research on the role of mood state on attention indicates that positive emotional states broaden the scope of attention, while negative states – narrow it (Fredrickson & Branigan, 2005; Gasper & Clore, 2002; Rowe, Hirsh, & Anderson, 2007). In agreement, high happiness state compared to low happiness state is associated with lower search times on the visual search task when the number of distractors is high (Maekawa, Anderson, De Brecht, & Yamagishi, 2018). Moreover, it has been suggested increased negative mood state might lead to attentional lapses (Smallwood et al., 2009). Our data lend some tentative support to that claim, as in our study sadness induction was related to the highest number of errors of omission on the 5-CSRTT. Additionally, in agreement with previous reports (Littman & Takács, 2017; Stockdale, Morrison, Kmiecik, Garbarino, & Silton, 2015), in **study 3**, we did find that response accuracy on the ASST was affected by task-irrelevant emotional context. Specifically, in the context of fear, accuracy was diminished, further suggesting that emotional processes might disrupt attention to some extent. It is important to point out in the context of this task, however, that the underlying processes might not reflect inattention, but rather selection of the most crucial environmental stimuli. When subjects are presented with the threat cues, it is highly adaptive, and more important, to correctly identify and interpret those cues, rather than who is showing them (male or female).

Overall, our findings corroborate the literature in that negative emotional states, in this case sadness, might lead to increased inattention. Moreover, in agreement with previous reports, we demonstrated that task-irrelevant emotional cues might be related to distractibility. The significance of these findings for daily life is probably best exemplified by the potentially deleterious effects of mood state (or emotional cues) on driving behaviour (Chan & Singhal, 2015; Hu, Xie, & Li, 2013).

Findings in study 1 depended on experimental manipulations of individuals' mood state in the laboratory. This process poses many challenges as the setting is quite artificial. Another factor to consider is that individuals may respond differently to various stimuli (differences in sensitivity to mood induction) (e.g. Bibbey, Carroll, Roseboom, Phillips, & de Rooij, 2013; Lynar, Cvejic, Schubert, & Vollmer-Conna, 2017; Mardaga, Laloyaux, & Hansenne, 2006). Additionally, lab-based studies depend on university populations, mainly psychology students, who may be more aware of manipulations (demand characteristics). Drawing conclusions based

solely on a university population also raises questions regarding the generalisability of the findings. Therefore, to overcome these limitations, we also conducted a large-scale online study (study 2) which assessed impulsive decision-making in a more representative sample with participants in their naturally occurring mood state. The results revealed a separation of temporal and reflection impulsivities, which mapped onto the domain of impulsivity trait (including emotional impulsivities – positive and negative urgency), from probability discounting, which seemed to be more aligned with risk-taking and sensation seeking aspects of personality. The separation between these two dimensions was further enhanced by the fact that impulsivity measures increased with enhanced self-reports of negative emotions, while measures of risk-taking were more related to the positive affective state. Therefore, when naturally occurring mood states are considered, enhanced negative states may be associated with people behaving impulsively (seeking immediate gratifications, making rushed decisions), while when experiencing positive states, people may show increased risky actions (gambling, extreme sports). Indeed, our findings corroborate the literature showing increased trait impulsivity in patients suffering from mood disorders including depression (Ngo, Street, & Hulse, 2011; Swann, Steinberg, Lijffijt, & Moeller, 2008), and enhanced sensation seeking associated with higher positive affect (Sperry, Lynam, Walsh, Horton, & Kwapil, 2016).

Overall, our results regarding the role of emotional state on impulsive actions and decisions, further support the notion that impulsivity is a highly heterogeneous concept (Caswell, Bond, Duka, & Morgan, 2015; Evenden, 1999; Whiteside & Lynam, 2001), and that distinct subtypes of impulsivity are sensitive to different aspects of emotional experience (valence, activity, or stress). Specifically, we demonstrate here that some subtypes of impulsivity are more affected by emotional states than others. Importantly, the data from study 1 indicate that not the mood state, induced (sad or anxious or positive) by certain manipulations, is related to impulsive behaviours, but rather the relative changes **in affective state at the individual level**. Specifically, motor impulsivity, both 'stopping' and 'waiting' subtypes, seem not to be highly modulated by the changes in affective state, while reflection and temporal impulsivities are. We had very little evidence to make strong claims about the role of emotional processes in inattention; however, our studies give tentative support to the notion that negative emotions might result in higher inattention. These findings bear important implications for future researchers in impulsivity area. Subjective state of the participants is often disregarded in research while our results show that this may influence the results, particularly in studies using within-subject designs, in which participants' mood state is likely to shift between testing. Importantly, since the results indicated the relationship between impulsive actions and decisions and changes in affective state at an individual level, we would like to suggest that promoting emotional regulation strategies might be an effective way of managing impulsive behaviours.

7.2.2 The neural correlates behind the impact of emotions on distinct subtypes of impulsive behaviours

In study 3 we investigated the neural correlates behind the impact of emotions on action inhibition ('stopping' impulsivity) and inter-temporal decision-making (temporal impulsivity). Examining neural mechanisms underlying emotion-impulsivity interaction is crucial for improving our understanding of those suffering from high impulsivity levels as well as mood/anxiety disorders, which may lead to improvement in the therapeutic options. For this study, instead of looking at the effects of mood state, we investigated the role of task-irrelevant emotional context. Several factors motivated the use of emotional context: mood induction in the experimental setting is challenging enough and conducting it in the fMRI scanner is related to additional confounding factors, such as participants' anxiety (or excitement) related to the scanning procedures, scanner noise and environment. Moreover, since not mood state per se, but rather individual changes in mood state reports were associated with behavioural impulsivity in study 1, individual differences in how those mood states are encoded in the neural activity might have been too big to decipher group-level differences in the fMRI analysis. Therefore, we developed tasks which measure self-control abilities in task-irrelevant emotional context. These tasks simulate real-life situations when decisions/actions need to be taken in emotional situations, for example, when we witness someone in distress.

We recognise the fact that individuals differ dramatically in how they respond to different situations; however, the role of individual differences in the context of self-control in emotional situations received little attention. Therefore, we also investigated the role of differences in trait impulsivity levels, predicting that more impulsive individuals would be affected by emotional context to a greater extent.

Similar studies, investigating the role of task-irrelevant emotional context on motor impulsivity yielded inconsistent results both at the behavioural and neural levels (Brown et al., 2012; Chester et al., 2016; Patterson et al., 2016; Sagaspe, Schwartz, & Vuilleumier, 2011). The reproducibility of the findings is partly hindered by a variety of methodologies employed. Therefore, in the current study, we used a paradigm resembling the one used previously (Nikolaou, Critchley, & Duka, 2013; Sagaspe et al., 2011). Although no effects of fearful context on response inhibition was found at the behavioural level (as reported by others e.g. Brown et al., 2012; Sagaspe et al., 2011), at the neural level we observed that individuals showing high levels of trait impulsivity, indexed by high BIS score (but not Negative Urgency), presented compensatory activation in several brain regions while executing response inhibition successfully in the fearful vs neutral context. This enhanced activation in more impulsive individuals agrees with previous reports (Chester et al., 2016) and was present in the superior parietal lobule, lateral occipital cortex and postcentral gyrus, regions involved in working

memory, somatosensory and visual-attentional processes. The compensatory activation indicates that in emotional (fearful) circumstances more impulsive individuals need to engage extra neural resources in order to achieve the same level of inhibitory control as less impulsive individuals. These results also imply that in a highly emotional context (more than fearful facial expressions), **more impulsive individuals may not be able to compensate sufficiently, which could result in impulsive actions.**

Importantly, a group of regions within the Somatomotor resting-state network showed decreased functional connectivity patterns in more impulsive individual, suggesting that this network might generally be altered in highly impulsive subjects predisposing them for acting on impulse. Specifically, higher trait impulsivity was associated with the decreased coupling of the lateral occipital cortex and the Somatomotor Network. Indeed, the inter-subject variability in response inhibition efficiency has been associated with the Somatomotor network activity (Zhang, Tsai, et al., 2015). The lateral occipital cortex is usually associated with visual perception and multisensory integration (Beauchamp, 2005; Grill-Spector, Kourtzi, & Kanwisher, 2001); however, it has also been implicated in impulsivity (Davis et al., 2013) and disorders commonly associated with impulsivity, such as ADHD (Castellanos & Proal, 2013). Therefore, this 'decoupling' of somatomotor and visual areas may reflect itself in a less effective integration of perceptual information, visual and somatosensory, in behavioural control manifesting itself in impulsive behaviours.

Our finding from the Affective Stop Signal Task (ASST) and resting state analysis bear vital implications for future research: Since the ASST taxes overlapping brain networks which show decreased functional integration at rest, training individuals on the ASST may results in better functional integration of sensory and motor regions, resulting in improved inhibitory-control capacities in vulnerable individuals.

To our knowledge, this was the first study looking at the neural levels of temporal impulsivity in task-independent emotional context. Behaviourally, past research reported negative emotional context is associated with increased temporal impulsivity (Augustine & Larsen, 2011; Guan et al., 2015). In our study fearful context did not affect the temporal impulsivity at the behavioural or neural levels, and trait impulsivity did not play a role here either. These inconsistencies with the past research might derive from differences in stimuli used as emotional context: Past studies employed images of anxiety-provoking scenes, while our study used fearful faces only. Possibly these images were not sufficiently threatening to affect delay discounting; therefore, future studies should use more negative or arousing images to assess the neural correlates of emotionally-induced temporal impulsivity.

7.2.3 Establishing the relationship between impulsivity and physiological arousal

Moving away from the role of emotions, the final two studies investigated the relationship between physiological arousal and impulsivity dimensions. The reasons for that were two-fold. Firstly, changes in physiological arousal are a vital component of emotional experience; however, there is very little research trying to decipher whether the component of arousal or emotional experience valence are equally important as modulators/drivers of impulsive actions and decisions. Secondly, in early days of impulsivity research, it was suspected that impulsivity might be an effect of maladaptive coping strategy to regulate one's arousal level (Barratt, 1985; H. J. Eysenck & Eysenck, 1985; Zuckerman, 1969). These suggestions derived from the optimal arousal hypothesis, which posits that for every individual there is an optimal level of arousal which not only feels best, but is also associated with the highest level of performance (Hebb, 1955). Thus, individuals should repeatedly engage in activities which can bring them closer to the optimal arousal level. Theories of impulsivity suspected that impulsive individuals are characterised by a too low resting level of arousal and engaging in impulsive behaviours may serve as a maladaptive way of optimising their activity level. Some experimental and cross-sectional studies provided support for this hypothesis linking lower resting heart rate with elevated behavioural (delay discounting) and trait impulsivity (Fung, Crone, Bode, & Murawski, 2017; Mathias & Stanford, 2003), although the evidence is not substantial. Therefore, we aimed to examine the relationship between resting state physiological arousal and impulsivity in a normative sample. In addition, we wanted to see whether pharmacologically modulating physiological arousal would result in changes in behavioural impulsivity level. We suspected that impulsive individuals might benefit from the initial increase in arousal which would result in less impulsive performance on behavioural tasks (as impulsive subjects would not have to additionally 'activate' themselves by acting impulsively).

Firstly, our results from studies 4 and 5, did not provide any evidence for the under-arousal hypothesis of impulsivity although we employed various measures to assess arousal level including heart rate, skin conductance and blood pressure. Therefore, we conclude that within a healthy population of young adults, **trait impulsivity is not associated with low resting-state arousal level.** Of course, it is possible that low resting level of arousal is associated with impulsive behaviours only in individuals at a pathological end of the impulsivity spectrum, and that our samples, which consisted of relatively highly functioning young adults (university students), did not include these individuals. Indeed, past research reported that low resting arousal is associated, or even predicts, impulse-related behaviours, such as criminal offences, later in life. For example, previous large scales studies found that low resting HR in

young men was associated with increased likelihood of antisocial behaviour later in life (Choy, Raine, Venables, & Farrington, 2017; Latvala, Kuja-Halkola, Almqvist, Larsson, & Lichtenstein, 2015). Moreover, some experimental studies found an association between resting state arousal and impulsivity, but in males only (Allen, Matthews, & Kenyon, 2000; Mathias & Stanford, 2003). Due to small sample sizes, and low proportions of male subjects recruited, we were unable to investigate potential sex differences in that matter. Therefore, there might be certain sex differences which may determine the associations between resting arousal level and impulsivity which need to be explored in the future.

Secondly, we wanted to examine whether increasing one's level of arousal via pharmacological manipulations, will be reflected in diminished impulsive performance. We chose α_2 noradrenergic blocker, yohimbine hydrochloride, which is known to increase arousal level and has little effect on mood state at low doses (Plewnia, Bartels, Cohen, & Gerloff, 2001; Schwabe, Höffken, Tegenthoff, & Wolf, 2013; Schwabe, Tegenthoff, Hoffken, & Wolf, 2010, 2012; Swann et al., 2013). Our results demonstrate that yohimbine-induced **arousal mainly affects motor 'stopping' impulsivity, improving an ability to inhibit pre-potent responses.** This is consistent with a growing body of evidence showing that increasing physiological arousal via physical exercise, cues, cardiac timing results in better response inhibition (Chu, Alderman, Wei, & Chang, 2015; Joyce, Graydon, McMorris, & Davranche, 2009; Rae et al., 2018; Weinbach, Kalanthroff, Avnit, & Henik, 2015). Noteworthy, in our study, the effect of yohimbine-induced arousal on response inhibition was only present when correcting for between-group differences in sensation seeking, indicating that potentially personality aspects could have a role. Additionally, a correlational analysis showed that individuals who had a greater increase in diastolic BP following drug-ingestion, showed lower motor impulsivity, confirming that this effect on impulsivity is related specifically to changes in arousal and not to other mechanisms. The summary of the influence of physiological arousal on dimensions of impulsivity is presented in Table 7.1.

Similarly, individuals who presented a larger increase in blood pressure, also showed a decreased level of temporal impulsivity. These findings are consistent with our observations from study 1 of increased subjective change in activity being associated with less steep discounting of delayed rewards. Together, these results highlight the importance of relative change in subjective as well as objective measures of arousal for temporal impulsivity.

Interestingly, the opposite pattern was visible for reflection impulsivity, whereby increased arousal was associated with more impulsive performance (although the correlation did not survive correction for multiple comparisons). Specifically, this pattern was only observed for a more challenging condition of the task (reward conflict), which involves a conflict between information gathering and potential reward. The simple condition (fixed-win), in which the reward depended solely on accuracy, was not associated with changes in arousal level.

Interestingly, in study 1 we also observed an association between change in (subjective) tension state and reflection impulsivity in the reward conflict condition. Thus, increased activation might hinder reflective performance in circumstances where a trade-off between information gathering and rewards occurs. Additionally, the simple version of the task (fixed-win condition) might not be challenging enough to show changes in different circumstances. We believe this is the first demonstration of the role of arousal in reflection impulsivity.

Together, these results indicate that impulsivity level might be more associated with **state arousal and not with the resting level of arousal.** Since the changes in the state arousal level seem to play a role in behavioural impulsivity, it is reasonable to assume that also an ability to perceive those changes correctly might be important. Therefore, the last experiment examined whether an ability to accurately perceive subtle bodily sensations (interoception; Craig, 2009; Khalsa et al., 2017) is relevant to impulsivity. It has long been recognised that bodily cues guide our actions to help maintain homeostasis (Berntson, Cacioppo, & Quigley, 1993) and that lack of those signals, or the inability to perceive them, may lead to many negative consequences (Bechara, Damasio, Tranel, & Damasio, 1997; Damasio, Tranel, & Damasio, 1991). However, the relevance to impulsive actions has been unexplored. Due to the multifaceted nature of impulsivity, we decided to investigate the relationship between different dimensions of interoceptive abilities and trait impulsivity indexed by BIS total score.

Our results indeed indicated that interoceptive abilities, specifically an ability to accurately distinguish bodily signals from external cues (interoceptive discrimination), were predictive of BIS Non-planning subscale but not of either motor or attention subscale. This finding indicates that 1) even distinct subtypes of trait impulsivity have distinct predictors, 2) interoceptive abilities may indeed prevent maladaptive behaviours. Heartbeat discrimination belongs to an interoceptive accuracy subgroup of interoception, and refers to an ability to accurately sense one's own internal state (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015; Khalsa et al., 2018). Interoceptive accuracy is different from other forms of interoception, such as interoceptive sensibility, which reflects subjective perception of being attuned to bodily sensations (assessed via self-report questionnaires), and metacognitive interoception (insight), which reflects conscious awareness of bodily signals (alignment of accuracy and subjective axis) (Garfinkel et al., 2015; Khalsa et al., 2018). Moreover, heartbeat discrimination depends on perceptual discrimination between internal bodily cues and external stimuli, a process that is far more difficult than an ability to simply provide an estimate of one's heart rate without any external distractions (i.e. heartbeat counting). Additionally, heartbeat tracking task is increasingly criticised for potentially confounding factors of time estimation instead of heartbeat counting, knowledge of one's heart rate and underreporting of heartbeats (Ring & Brener, 1996, 2018; Zamariola, Maurage, Luminet, & Corneille, 2018). Noteworthy, out of all interoceptive

dimensions which were considered in our study, only heartbeat discrimination showed predictive value for impulsivity.

The fact that interoceptive accuracy is related to non-planning impulsivity is a novel finding. Previous studies looking at interoceptive abilities and behaviour mainly focused on risk-taking (Kandasamy et al., 2016; Werner, Jung, Duschek, & Schandry, 2009), concluding that better interoceptive accuracy might guide advantageous (less risky) decision-making. Our own findings from study 2 suggested that higher temporal discounting (increased temporal impulsivity) might be related to enhanced interoceptive sensibility, indicating that better interoceptive abilities might be associated with poorer self-control and less advantageous behaviour. However, it is important to note that this study considered self-reported interoception only and no objective measures of interoception were collected. Similarly to impulsivity, people's subjective ratings (interoceptive sensibility) are rarely aligned with objective performance (interoceptive accuracy) (Garfinkel et al., 2015). Accordingly, heightened interoceptive sensibility was recently linked to poorer response inhibition, but no relationship with accuracy measures was found (Rae et al., 2018). Instead, these results might indicate that misinterpretation of bodily signals may lead to incorrect adaptation to current bodily needs (c.f. subsection "Significance and Future Directions").

7.3 Refining and clarifying the model of factors determining the role of internal states in behavioural impulsivity

In Chapter 1, based on the past research reviewed, we proposed a model to account for how impulsive actions and decisions are affected by our current affective and physiological state. Through this model we suggested that **internal states impact on behaviour through dependence on a set of factors** (summarised in Figure 7.1):

(1) the subtype of impulsivity in question,

(2) individual differences,

(3) the baseline (resting state) level of arousal.

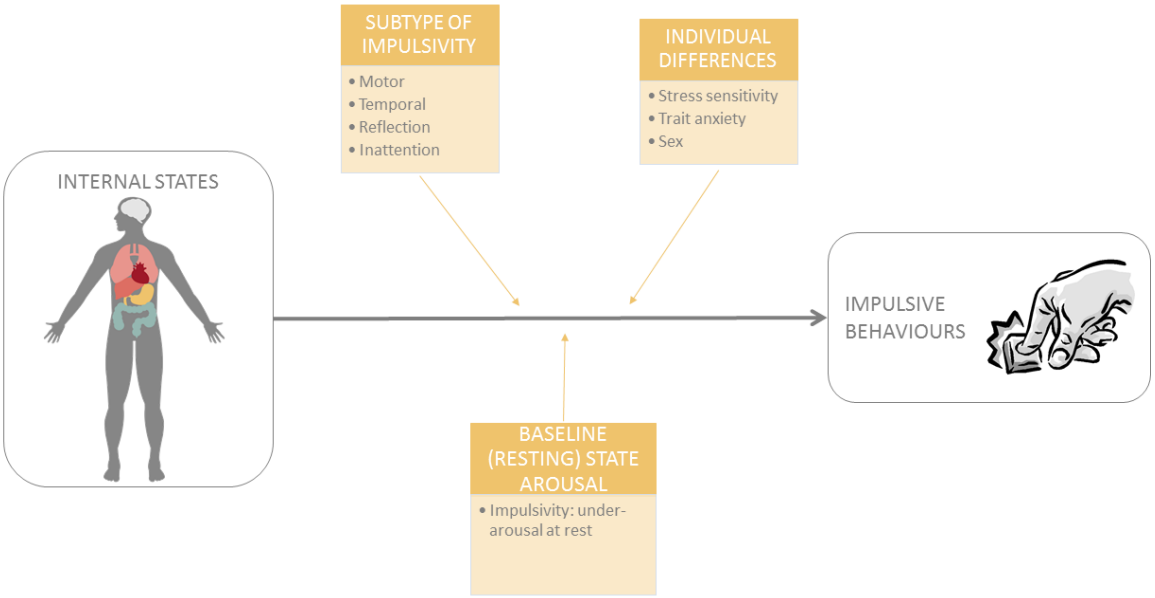

Figure 7.1 Dimensions of impulsivity and their modulators – the initial model based on the literature review (Chapter 1).

In this thesis, we conducted a set of experiments which verified but also refined this model. Below, I am going to address how our findings relate to each factor in this model, providing evidence to confirm or update it.

Regarding the impact of internal states on distinct subtypes of impulsivity in question (1), our results from studies 1 and 4, confirm that **distinct facets of impulsivity** are differentially affected by internal bodily state, specifically the **individual's change** in that state. Furthermore, we have established that specific subtypes of impulsivity are more affected by the changes in subjective affective state (for example reflection impulsivity), while others are more dependent on the changes in physiological arousal (motor 'stopping' impulsivity). This clarification should not be underestimated as it highlights the importance of individual experience and suggests that various individuals may be affected to a different degree by situational circumstances. It also justifies the use of individual treatment approaches which address personal needs.

Our initial model also predicted **that individual differences** such as gender, trait anxiety or stress sensitivity might mediate the influence of the internal bodily state on behavioural impulsivity (2). In this thesis we investigated the role of **trait impulsivity**, using a standard questionnaire approach, in behavioural impulsivity in different states/contexts. In study 2 we observed that trait impulsivity is one of the predictors of temporal and reflection impulsivity, while reward sensitivity predicts probability discounting. We also found that these traits were associated with mood state measures. In study 3, we further observed that higher trait impulsivity was associated with more effortful (compensatory brain activation) response inhibition in the fearful vs neutral contexts; however, no relationship between personality traits and performance on the task was found at the behavioural level. Therefore, we suggest that

individuals presenting high trait impulsivity levels might show self-control deficits in states of intense emotional experience/arousal when they are no longer able to engage compensatory mechanisms successfully.

In contrast, we found no evidence for the role of trait impulsivity in impulsive choice (temporal impulsivity), at either behavioural or neural level, in emotional context. However, the resting-state functional analysis revealed that trait impulsivity is associated with a functional decoupling within the Somatomotor network encompassing regions implicated by the task-related analysis, providing stronger evidence for a neural mechanism underlying self-control deficits. Together, these findings suggest that (a) trait impulsivity might reflect a baseline level of behavioural self-control and not behavioural control under response demanding conditions; (b) the relationship between trait impulsivity and behavioural impulsivity in emotional circumstances may be different for motor and temporal impulsivity. Specifically, more impulsive individuals (trait) need to exert more neural resources to inhibit pre-potent motor responses successfully, particularly in the context of fear, while such a relationship may not exist for temporal impulsivity. Thus, we propose that individual differences in trait impulsivity should be added as a factor in our revised model.

The last feature in our initial model of factors through which internal states might affect impulsive behaviours is the **resting state arousal level** (3). Namely, according to the under-arousal hypothesis of impulsivity, disadvantageously low resting level of arousal could predispose individuals to display impulsive actions as a means of regulating unpleasant internal state (Barratt, 1985; H. J. Eysenck & Eysenck, 1985; Zuckerman, 1969). Despite using various measures of baseline arousal level in studies 4 and 5, we were unable to find any evidence for under-arousal at rest of individuals showing high impulsivity level. Instead, our results suggest that an ability to accurately discriminate between internal and external cues (a dimension of interoception) is predictive of lower non-planning impulsivity. Given the role of interoception in emotional awareness, decision-making and cognition (Dunn et al., 2010; Garfinkel & Critchley, 2013; Seth, 2013), we suggest that **interoceptive abilities** might be another factor which determines how internal states affect impulsivity. This should be further confirmed in future research using different behavioural paradigms, but our initial results are promising and fit well into a growing body of existing literature showing that bodily cues guide our behaviours and that inability to perceive those cues may lead to negative consequences (Bechara et al., 1997; Damasio, 1996; Kandasamy et al., 2016; Katkin, Wiens, & Ohman, 2001; Werner et al., 2009).

A revised model of factors which affect the influence of bodily states on impulsive behaviours is illustrated in Figure 7.2.

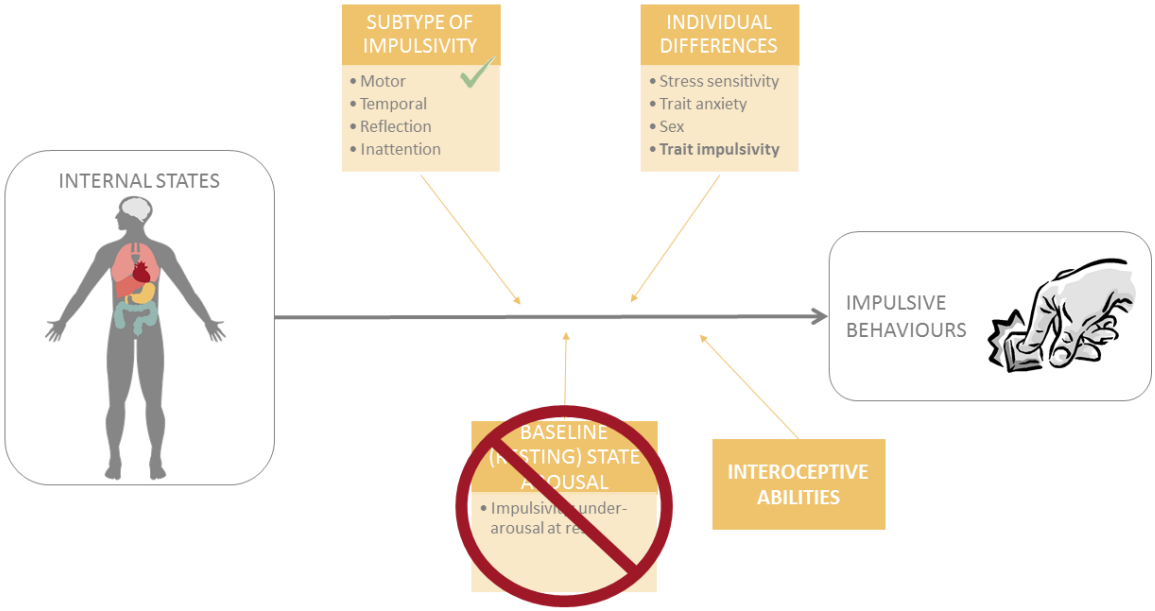

Figure 7.2 Dimensions of impulsivity and their modulators – model revised.

7.4 Limitations

There were some methodological limitations to these studies which should be briefly discussed. In all experiments, apart from study 2, only volunteers from the University community were tested. Therefore, all individuals represented certain educational level and cognitive abilities, as well as a shared environment. These factors reduce the generalisability of the findings. Study 2 was designed to account from some of those problem by recruiting individuals via various means to acquire a more representative sample.

One potential limitation regards mood induction procedure in study 1, which included simultaneous presentation of affective pictures and congruent musical excerpts and an additional cognitive stressor for anxiety induction. It is vital to note that individual sensitivity to those images and interpretation of these scenes might differ significantly (Lynar et al., 2017; Mardaga et al., 2006; Park et al., 2013; Vuoskoski & Eerola, 2011). Those individual differences may have accounted to some extent for the fact that we did not see significant group differences in impulsive performance, although mood manipulation evoked expected effects on the mood state ratings. Therefore, using another induction technique, possibly tailored for an individual, may have yielded different results.

In study 3, the emotional context was evoked via presentation of facial expressions depicting fear or neutral appearance only. No other emotional context (anger, sadness, disgust, content) were examined, therefore, it is difficult to establish whether the findings are specific for the context of fear only, or whether they are more generalizable across negative valence dimension or maybe the effect is due to heightened arousal only. Future studies should elaborate on that also using different stimuli to evoke specific contexts.

The relationship between resting state arousal and impulsivity was examined in relatively small groups of males and females, which did not allow a reliable comparison between sexes. This aspect appeared several times in the literature (e.g. Allen, Hogan, & Laird, 2009; Zhang et al., 2015) and might be an important avenue for future exploration. Indeed, the role of sex differences in impulsivity and their manifestation gains increasing attention (Mansouri, Fehring, Gaillard, Jaberzadeh, & Parkington, 2016; Silverman, 2003; Weafer & de Wit, 2014). Examining sex differences in the context of impulsivity might be of value in clinical practice and prevention efforts since males tend to engage more in certain impulsivity-related behaviours, which has been linked to the resting arousal levels (Choy et al., 2017).

Finally, the findings are based on studies which use laboratory-based tasks or questionnaires to assess impulsivity level. These very useful forms of testing provide much-needed models of behaviour, show good consistency and validity, and are related (predictive) to many real-life behaviours associated with negative consequences. However, more ecologically valid approaches should also be used to translate mood-based impulsivity into real-life scenarios.

7.5 Significance and Future Directions

The current studies make an appealing argument that individual differences matter when it comes to impulsive behaviours. This was demonstrated at many different levels including individual differences in mood state change, trait impulsivity level, individual differences in arousal change following pharmacological challenge as well as individual ability to accurately sense internal bodily state (interoception).

Impulsive behaviour is a core of many pathologies, including drug addiction (American Psychiatric Association, 2013). By providing evidence for the role of internal bodily states in momentary impulsivity levels, our research also offers a platform for further research into how state-dependent changes in distinct domains of impulsivity contribute to drug use initiation and relapse

Here I am going to demonstrate how our finding may contribute to the understanding of the role of internal bodily states and behavioural impulsivity in addictive behaviours, using alcohol use and misuse as an example.

Alcohol dependency is a chronic relapsing disorder characterised by compulsive drinking, which denotes harmful use of alcohol despite its negative consequences. Recently published statistics on alcohol use in the United Kingdom (National Statistics, 2017) states that 57% of those aged 16 or above drink alcohol; 15% of responders report heavy drinking (i.e. consumption of over eight units of alcohol for men and over six units for women at one occasion) in the previous week. Adolescents are also using alcohol – 38% of those aged 11-15

had already drunk alcohol. Moreover, 4% of adolescents report regular drinking (at least once a week). Alarmingly, nearly half (49%) of pupils who had drunk alcohol in the last month had been drunk; 63% of whom did it deliberately. Shockingly, there has been a 10% increase in alcohol-related deaths in the UK between 2005 and 2015. In the United States, alcohol is the third leading preventable cause of death, after tobacco and poor diet and physical activity (Mokdad, Marks, Stroup, & Gerberding, 2004). Alcohol use, therefore, is a major public concern.

The importance of impulsivity in development of alcohol use, continuation and escalation of drinking leading to alcohol dependency has long been acknowledged (Dick et al., 2010; Lejuez et al., 2010; Potenza and de Wit, 2010). Moreover, the role of momentary 'state' increases in impulsive behaviour which may drive drinking episodes (de Wit, 2009) is increasingly recognised. Theory and evidence suggest that people drink alcohol to enhance positive or manage negative emotional states, and reduce tension (Conger, 1956; Cooper, Frone, Russell, & Mudar, 1995; Dvorak, Pearson, Sargent, Stevenson, & Mfon, 2016; Peacock, Cash, Bruno, & Ferguson, 2015; Simons, Dvorak, Batien, & Wray, 2010; Simons, Gaher, Oliver, Bush, & Palmer, 2005; Swendsen et al., 2000; Zack, Toneatto, & MacLeod, 2002). For example, recent findings indicate that a faster escalation in the volume of use among adolescence was predicted by lower levels of positive affect, suggesting that youth may escalate their drinking to boost positive affect (Lopez-Vergara, Spillane, Merrill, & Jackson, 2016). Moreover, experience of stress, which is associated with increased physiological arousal and negative affect, is considered a major trigger in alcohol relapse. Indeed, stressful events increase the urge to drink and chances of relapse in treated alcoholics (Sinha, 2012; Sinha et al., 2009). Alcohol consumption is then used as a means of managing physiological and emotional states, in accordance with the negative reinforcement theory of addiction. Indeed, data from social drinkers suggests that alcohol consumption reduces the effects of stressful emotional stimuli on mood (Van Tilburg & Vingerhoets, 2002) and that alcohol drinking is related to a subsequent decrease in nervousness (Swendsen et al., 2000) supporting the self-medication hypothesis of alcohol use. Importantly, repeated alcohol exposure leads to a negative emotional state enhancing the stress response, resulting in a vicious cycle of alcohol abuse (Garland, Boettiger, & Howard, 2011; Koob & Le Moal, 2008).

Research suggests that indulging in impulsive drinking to regulate one's mood state may be a strategy used particularly often by individuals presenting high trait or behavioural impulsivity levels (Anthenien, Lembo, & Neighbors, 2017; Cyders et al., 2010; Dinc & Cooper, 2015; Fox, Bergquist, Gu, & Sinha, 2010; Simons et al., 2010). For example, in a recent study, negative mood state predicted drinks on drinking nights, but only for those with poor response inhibition (Dvorak et al., 2016).

Together, the results summarised above suggest that individuals may engage in drinking alcohol to manage emotional states, particularly if they are associated with high arousal. Moreover, it seems that using alcohol as a coping strategy is most frequent in highly impulsive individuals.

Findings presented in this thesis suggest that behavioural impulsivity level is associated with changes in one's emotional (study 1) and physiological states (study 4). We propose that better emotion regulation capacities alongside with more accurate detection and interpretation of internal bodily states could be helpful in preventing unwanted consequences of fluctuations in emotional states. Moreover, an exciting new finding regards the association between accurate discrimination of internal from external signals (interoceptive sensitivity, study 5) and opens a novel avenue of interesting research which may lead to fresh therapeutic opportunities. Together with findings from study 4, in which we demonstrated an association between state-related changes in arousal at the individual level and behavioural impulsivity, our findings suggest that accurate perception of internal bodily state might be an adaptive mechanism guiding our actions. When this mechanism does not work correctly, negative consequences might occur. Indeed, in a broader sense, non-planning impulsivity is widely recognised to be associated with binge drinking, alcohol use and abuse (Caswell, Celio, Morgan, & Duka, 2015; Hamilton, Sinha, & Potenza, 2012; Jakubczyk et al., 2013).

Poor ability to correctly identify bodily state may result in a confusion of bodily sensations such as signals of hunger, arousal, proprioception, tiredness or temperature with affective states (i.e. misinterpret anger as heat, pain or hunger etc.; R. Brewer, Cook, & Bird, 2016). This, of course, may lead to various negative consequences such as inappropriate actions due to misperceived sensations and ineffective management of arousal due to an inability to interpret it. Indeed, it has been suggested that interoceptive ability is vital for higher-order-cognition, and that atypical interoception may predispose to psychopathology, risky behaviour, as well as poor emotional functioning or resilience to stressful situations (Haase et al., 2016; Murphy, Brewer, Catmur, & Bird, 2017).

Allostasis refers to the process of maintaining homeostasis through an adaptive change of the organism's internal environment to meet perceived and anticipated demands (Sterling & Eyer, 1988). In other words, allostasis is a prediction of the body's energy needs and preparation to satisfy those requirements before they arise (Sterling, 2012). Importantly, interoception is thought to be a key element of allostasis (Barrett, Quigley, & Hamilton, 2016; Gu & FitzGerald, 2014): Only when we are able to detect our current bodily needs, we can adjust our behaviour accordingly (Gu & FitzGerald, 2014). Further, it is possible that enhancing one's ability to recognise bodily states at an early stage accurately may serve to maintain energy-balance via better planning abilities. For example, training individuals on heartbeat discrimination task might lead to better accuracy on the task which potentially could extend into a better general

perception of bodily cues in daily life. This improved interoceptive accuracy could also lead to more adaptive behavioural strategies for dealing with those sensations and decreased impulsivity.

Since alcohol is sometimes used to manage unwanted bodily sensations, better interoceptive interferences may allow earlier sensation of heightened arousal or unpleasant states. Earlier detection of those cues could lead to adaptive behaviour adjustments (allostasis) according to the circumstances, for example via relaxation techniques, instead of alcohol use. Similarly, thanks to improved emotion regulation and interoceptive abilities individuals may not need to use maladaptive coping strategies, such as alcohol use, to manage unwanted emotions and enhanced arousal.

Moreover, our findings also offer an explanation of why impulsive individuals may be more prone to impulsive behaviours, such as alcohol drinking, in emotional circumstances. In study 3 we have demonstrated that higher trait impulsivity is associated with enhanced activation in several brain regions including the right supramarginal gyrus, right superior, middle and inferior frontal gyri and paracingulate cortex during successful inhibitory control. Furthermore, these effects were increased in the fearful vs neutral context, suggesting that impulsive individuals need to engage more neural resources to implement inhibitory control successfully in the emotional context, relative to neutral one. Thus, when an impulsive person is experiencing an intense emotional state, they may not be able to engage compensatory mechanisms in place to a satisfactory degree and indulge in impulsive action, such as alcohol use. Further, we observed overlap in networks involved in successful inhibitory control in the emotional context and showing decreased functional connectivity at rest in more impulsive individuals (within the Somatomotor network). Therefore, since the Affective Stop Signal Task seems to target just the right neural substrates, training individuals on the task may strengthen the connectivity between affected brain regions and result in better inhibitory capacities. Future studies should assess the validity of this approach.

7.6 Concluding remarks

Collectively, the findings presented in this thesis demonstrate the significance of bodily states (the relative changes in emotional and physiological states) in impulsive behaviours and provided some initial evidence for the importance of individual sensitivity to those bodily states in the context of trait impulsivity, especially non-planning component. Importantly, these observations were made across distinct impulsivity dimensions, showing that various states affect separate 'impulsivities' to a different degree, providing further evidence for a heterogeneous nature of impulsivity concept. Using neuroimaging techniques, we identified neural correlates which may be responsible for decreased self-control capacities in the

emotional context in impulsive individuals. These neural substrates, in turn, may be used as targets in future research and therapeutic practice. Since in our experiments we studied 'healthy volunteers' (not any specific clinical population), our findings are relevant to impulse-related problems prevention. Firstly, increasing awareness of these processes may encourage people to stay more attuned to changes in their bodily state and effectively regulate their emotion. This, in turn, may inspire adaptive ways to adjust behaviour according to current bodily needs, which may help reduce impulsivity levels and minimise the associated negative consequences. Secondly, our findings may lead to development of novel training or therapeutic opportunities which may involve interoceptive training to develop a better sensitivity to internal bodily changes or training impulsive individuals on affective impulsivity tasks (e.g. ASST), which engage the Somatomotor neural network.

7.7 References

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