

**The role of emotions and physiological arousal in modulating impulsive
behaviour**

Aleksandra M. Herman^{a*}, Hugo D. Critchley^{bc}, Theodora Duka^{a*}

^a Behavioural and Clinical Neuroscience, School of Psychology, University of Sussex,
Brighton, United Kingdom

^b Sackler Centre for Consciousness Science, University of Sussex, Brighton, United
Kingdom

^c Brighton and Sussex Medical School, Brighton, United Kingdom

* To whom correspondence may be addressed (at address ^a above). Telephone: (AH)

01273872803, (TD) 01273678879; E-mail: a.herman@sussex.ac.uk, t.duka@sussex.ac.uk

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. 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 et al., 2004; Grau and Ortet, 1999), and predict increased food intake in normal-weight healthy women (Guerrieri et al., 2007a, 2007b).

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 and Västfjäll, 2012; Dolan, 2002; Sharot et al., 2004; Talarico and Rubin, 2007; Zadra and 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 growing body of literature shows the detrimental effects of inability to regulate one's emotions (Cisler et al., 2010; Wilcox et al., 2016) and a high prevalence of mood disorders in society (Kessler et al., 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.

2. 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 (Evdenden, 1999a, 1999b). There are, however, many definitions of this construct (Evdenden, 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 (Monterosso and 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 from an appropriate assessment of the consequences. Likewise, Eysenck (Eysenck and 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 a normal behaviour, and every person can be characterised on 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 (Eysenck and 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 - with high anxiety and high impulsivity levels. Gray 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.

3. 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 distinguish 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 dimensions 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 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 when 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 et al., 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 study (Otto et al., 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 et al., 2015).

In behavioural approach, 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 et al., 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 et al., 2015), which distinguished three independent subtypes. The '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). The 'motor'-impulsivity refers to the action execution stage and reflects an inability to inhibit a motor response when it is no longer

suitable. Finally, the ‘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 and 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.

4. 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 et al., 2006; Reynolds et al., 2006; Wingrove and 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.

4.1 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 and 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 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).

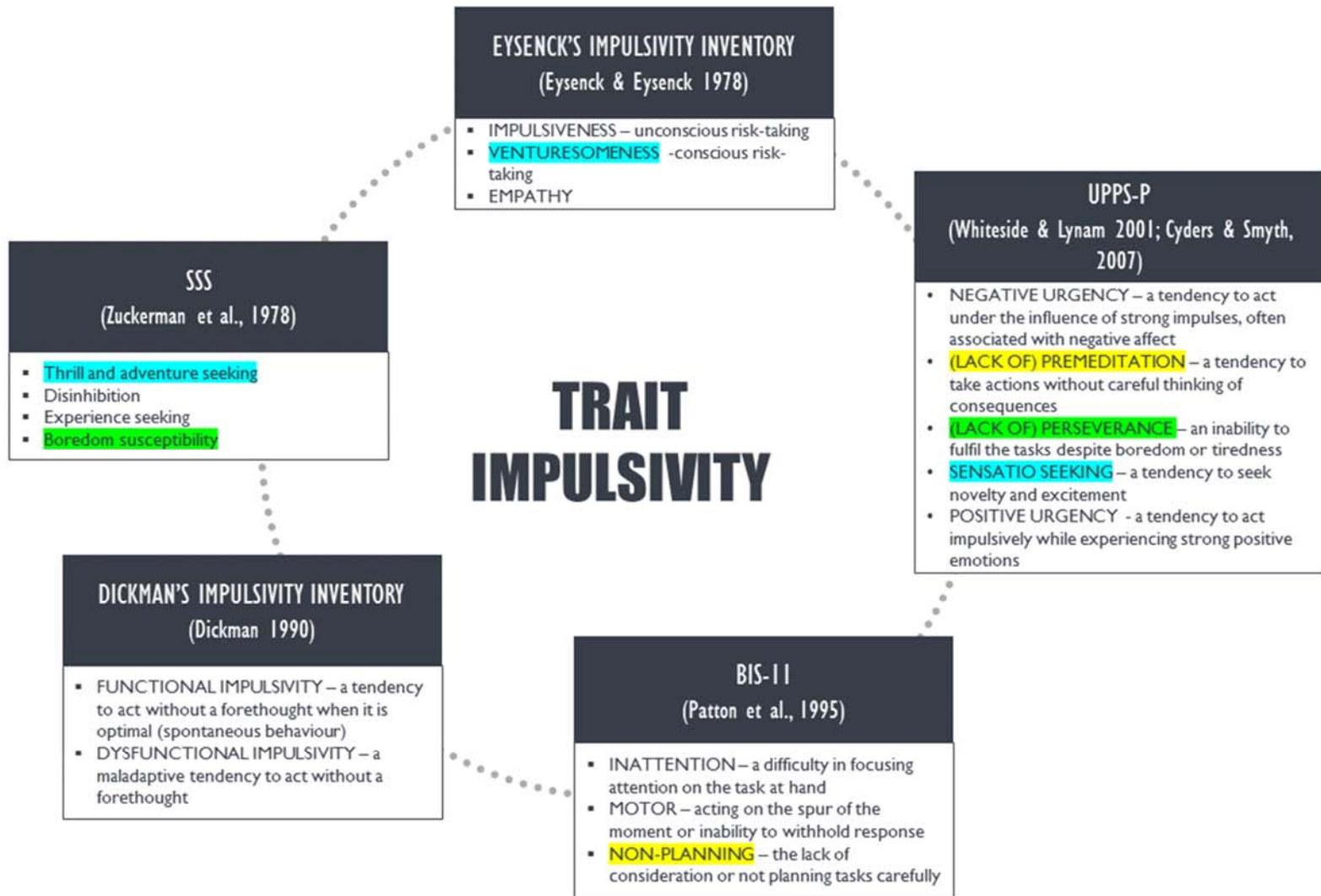


Figure 1 Selected views on impulsivity as a personality trait proposed by several researchers. Similar concepts are depicted in the same colour.

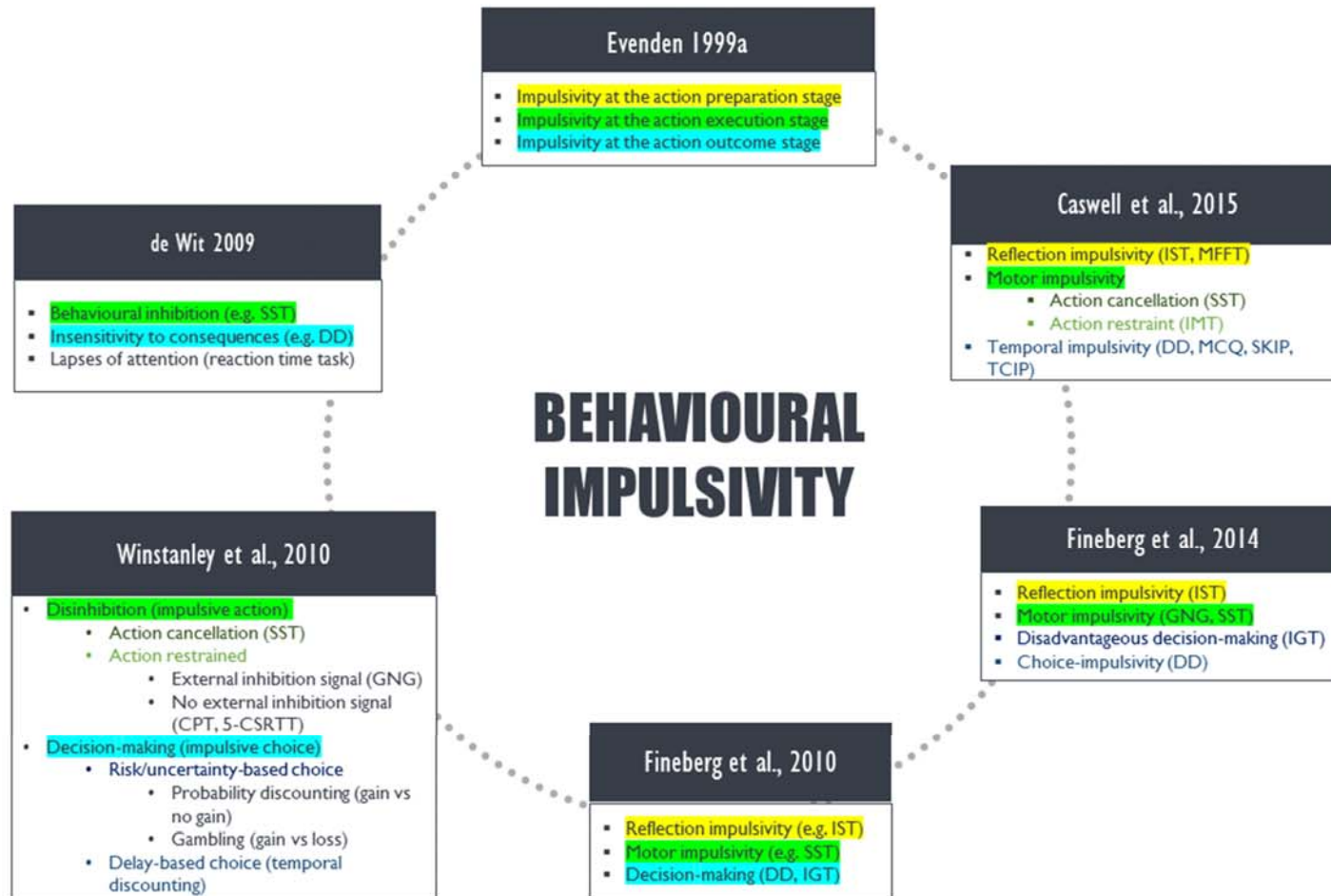


Figure 2 Selected views on behavioural impulsivity with examples of tasks used to assess particular impulsivity subtypes. Similar concepts are represented in the same colours. This figure was partly adapted from Winstanley et al., 2010.

4.2 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.

4.2.2 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 et al., 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 et al., 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 et al., 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 summarized in Figure 3.

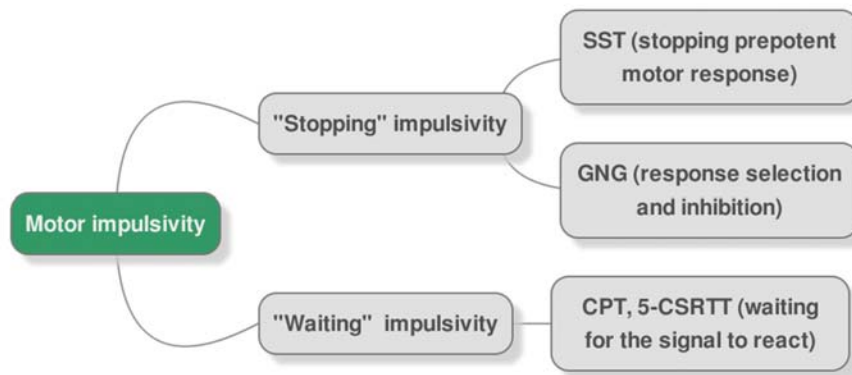


Figure 3 Motor impulsivity according to Robinson et al., 2009 and Dalley et al., 2011.

4.2.3 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 decision 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 et al., 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 the 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 and 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 reflective.

4.2.4 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 the 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, the 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 real rewards are (Baker et al., 2003; Bickel et al., 2009; Johnson and Bickel, 2002; Lagorio and Madden, 2005; Lawyer et al., 2011). Some evidence, however, suggests that real rewards are related to decreased temporal impulsivity compared with hypothetical gratification (Hinvest and 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) (Bechara et al., 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 (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.

5. 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.

5.1 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 et al., 2017; Nikolaou et al., 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 et al., 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).

5.2 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 et al., 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).

5.3 Impulsive decision-making

Three distinct brain networks were proposed to be involved in temporal discounting (Peters and 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 and McNaughton, 2017; Sellitto et al., 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 the gambling tasks depends on them (Clark et al., 2008, 2003; Fukui et al., 2005; MacPherson et al., 2009; Rao et al., 2008; Zeeb and 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 and 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 and Winstanley, 2011). Therefore, temporal discounting and risk-taking share underlying neural circuitry, providing an evidence that they may be grouped into a single impulsivity subtype.

5.4 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 et al., 2014; Phillips and Swartz, 2014), regions implicated in impulsive actions and decision-making.

6. 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 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 et al., 2011; Murphy et al., 2003; Phan et al., 2004, 2002; Xie et al., 2011; Zeeb and 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 with 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 et al., 2014).

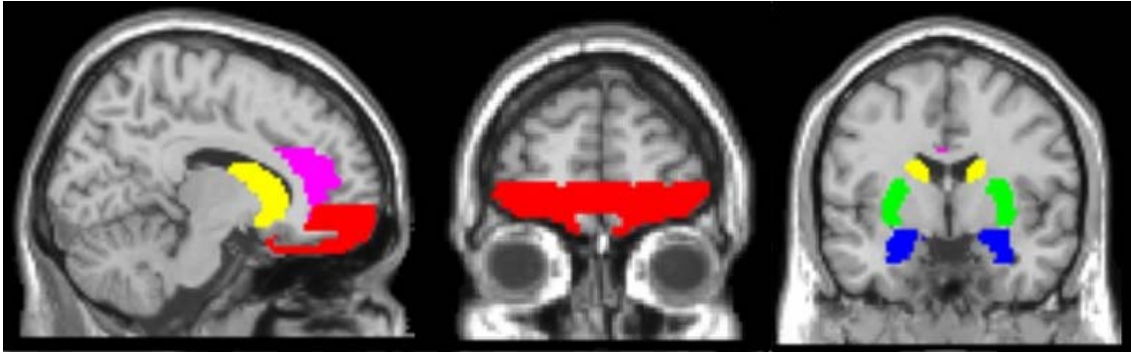


Figure 4 Brain regions implicated in both emotional experience and impulsive behaviour. Orbitofrontal cortex – red, amygdala – blue, anterior cingulate cortex – violet, caudate nucleus (basal ganglia) – yellow, putamen (basal ganglia) - green.

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 and 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.

7. 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.

7.1 Risk-taking

The influence of the affective state on risk-taking and decision-making 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 averse (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 and 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 et al., 2013; Starcke et al., 2008). However, the impact of stress on risky choice may depend on subjects' gender (Lighthall et al., 2009; van den Bos et al., 2009). For male participants, acute cortisol administration and a stress challenge were found to increase risky behaviours in males, but decreased it among females (Lighthall et al., 2009; Putman et al., 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.

7.2 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 et al., 1976). These findings were also replicated in adult populations. Several studies showed that negative emotions, either naturally occurring (Koff and Lucas, 2011) or experimentally induced in participants by a presentation of aversive images (Augustine and 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 et al., 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 et al., 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 the 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. Taken 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.

7.3 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 and Tibboel, 2010; Kalanthroff et al., 2013; Lindström and Bohlin, 2012; Pessoa et al., 2013; Rebetez et al., 2015; Verbruggen and 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 none 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 et al., 2007; Smallwood et al., 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 the 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.

7.4 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.

7.5 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 on decision-making; therefore, how exactly emotions shape other impulsivity subtypes (motor, reflection) yet need to be confirmed.

8. 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 and 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 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 and Stanford, 2003; Puttonen et al., 2008; Schmidt et al., 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 et al., 2014; Muñoz and Anastassiou-Hadjicharalambous, 2011). However, it is worth noting that some research focused on male participants only (Mathias and 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 et al., 2009, 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 et al., 2016). Blunted autonomic reactivity to stress has also

been reported in impulsive adolescents and adults (Allen et al., 2009; Stankovic et al., 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 et al., 2008; Ginty et al., 2012; Koo-Loeb et al., 1998; Lovallo et al., 2000; Paris et al., 2010; Pesonen et al., 2011), these lowered physiological responses in impulsive subjects may reflect blunted autonomic reactivity to challenge in impulsive individuals may be maladaptive and result in health problems.

Neuroimaging studies start to unveil the neural mechanisms linking arousal regulation and impulse control. Brown and colleagues (Brown et al., 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 the activity in the ventral amygdala, anterior cingulate gyrus, 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 (Zhang et al., 2014). The PFC is also known to be critical for successful response inhibition (Horn et al., 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 (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 (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 et al., 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).

9. Concluding remarks

Term ‘impulsivity’ refers to both a stable personality trait and a range of behaviours that are susceptible to modulation. Trait impulsivity is typically assessed with 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): the reflection impulsivity occurs at the action preparation stage, the 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 conceptualizations of impulsivity, sometimes grouped together with temporal impulsivity in a single construct of impulsive-choice (Fineberg et al., 2014, 2010; 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 (summarized in Figure 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 the 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 (Barratt, 1985; Eysenck and 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 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.

Acknowledgements

The work was supported by Sussex Neuroscience.

References:

- Abrantes, A.M., Strong, D.R., Lejuez, C.W., Kahler, C.W., Carpenter, L.L., Price, L.H., Niaura, R., Brown, R.A., 2008. The role of negative affect in risk for early lapse among low distress tolerance smokers. *Addict. Behav.* 33, 1394–1401. doi:10.1016/j.addbeh.2008.06.018
- Ainslie, G., 1975. Specious reward: a behavioral theory of impulsiveness and impulse control. *Psychol. Bull.* 82, 463–496. doi:10.1037/h0076860
- Allen, M.T., Hogan, A.M., Laird, L.K., 2009. The relationships of impulsivity and cardiovascular responses: The role of gender and task type. *Int. J. Psychophysiol.* 73, 369–376. doi:10.1016/j.ijpsycho.2009.05.014
- Allen, M.T., Matthews, K. a, Kenyon, K.L., 2000. The relationships of resting baroreflex sensitivity, heart rate variability and measures of impulse control in children and adolescents. *Int. J. Psychophysiol.* 37, 185–194.
- American Psychiatric Association, 2013. *Diagnostic and Statistical Manual of Mental Disorders*, 5th ed, American Psychiatric Publishing. Washington, DC. doi:10.1176/appi.books.9780890425596.744053
- Aron, A.R., 2007. The neural basis of inhibition in cognitive control. *Neuroscientist* 13, 214–228. doi:10.1177/1073858407299288
- Aron, A.R., Durston, S., Eagle, D.M., Logan, G.D., Stinear, C.M., Stuphorn, V., 2007. Converging evidence for a fronto-basal-ganglia network for inhibitory control of action and cognition. *J Neurosci.* 27, 11860–11864. doi:10.1523/JNEUROSCI.3644-07.2007
- Aron, A.R., Fletcher, P.C., Bullmore, E.T., Sahakian, B.J., Robbins, T.W., 2003. Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nat. Neurosci.*

- 6, 115–116. doi:10.1038/nm1003
- Asutay, E., Västfjäll, D., 2012. Perception of loudness is influenced by emotion. *PLoS One* 7, 2–6. doi:10.1371/journal.pone.0038660
- Augustine, A., Larsen, R.J., 2011. Affect regulation and temporal discounting: interactions between primed, state, and trait affect. *Emotion* 11, 403–412. doi:10.1037/a0021777
- Ayduk, O., Mendoza-Denton, R., Mischel, W., Downey, G., Peake, P.K., Rodriguez, M., 2000. Regulating the interpersonal self: strategic self-regulation for coping with rejection sensitivity. *J. Pers. Soc. Psychol.* 79, 776–792. doi:10.1037/0022-3514.79.5.776
- Baker, F., Johnson, M.W., Bickel, W.K., 2003. Delay discounting in current and never-before cigarette smokers: similarities and differences across commodity, sign, and magnitude. *J. Abnorm. Psychol.* 112, 382–392. doi:10.1037/0021-843X.112.3.382
- Banca, P., Lange, I., Worbe, Y., Howell, N. a., Irvine, M., Harrison, N. a., Moutoussis, M., Voon, V., 2016. Reflection impulsivity in binge drinking: behavioural and volumetric correlates. *Addict Biol.* 21, 504–15. doi:10.1111/adb.12227
- Barratt, E.S., 1985. Impulsiveness subtraits: Arousal and information processing, in: *Motivation, Emotion, and Personality*. pp. 137–146.
- Barratt, E.S., 1959. Anxiety and Impulsiveness Related to Psychomotor Efficiency. *Percept. Mot. Skills* 9, 191–198. doi:10.2466/pms.1959.9.3.191
- Bechara, A., Damasio, A.R., Damasio, H., Anderson, S.W., 1994. Insensitivity to future consequences following damage to human prefrontal cortex. *Cognition* 50, 7–15. doi:10.1016/0010-0277(94)90018-3
- Bechara, A., Damasio, H., Damasio, A.R., 2000. Emotion, decision making and the

- orbitofrontal cortex. *Cereb Cortex*. 10, 295–307. doi:10.1093/cercor/10.3.295
- Bekker, M.H.J., Van De Meerendonk, C., Mollerus, J., 2004. Effects of negative mood induction and impulsivity on self-perceived emotional eating. *Int. J. Eat. Disord*. 36, 461–469. doi:10.1002/eat.20041
- Bennett, C., Blissett, J., Carroll, D., Ginty, A.T., 2014. Rated and measured impulsivity in children is associated with diminished cardiac reactions to acute psychological stress. *Biol. Psychol*. 102, 68–72. doi:10.1016/j.biopsycho.2014.07.009
- Bibbey, A., Ginty, A.T., Brindle, R.C., Phillips, A.C., Carroll, D., 2016. Blunted cardiac stress reactors exhibit relatively high levels of behavioural impulsivity. *Physiol. Behav*. 159, 40–44. doi:10.1016/j.physbeh.2016.03.011
- Bickel, W.K., Pitcock, J. a, Yi, R., Angtuaco, E.J.C., 2009. Congruence of BOLD response across intertemporal choice conditions: fictive and real money gains and losses. *J Neurosci*. 29, 8839–8846. doi:10.1523/JNEUROSCI.5319-08.2009
- Boehler, C.N., Appelbaum, L.G., Krebs, R.M., Hopf, J.M., Woldorff, M.G., 2010. Pinning down response inhibition in the brain — Conjunction analyses of the Stop-signal task. *Neuroimage* 52, 1621–1632. doi:10.1016/j.neuroimage.2010.04.276
- Boisseau, C.L., Thompson-Brenner, H., Caldwell-Harris, C., Pratt, E., Farchione, T., Harrison Barlow, D., 2012. Behavioral and cognitive impulsivity in obsessive-compulsive disorder and eating disorders. *Psychiatry Res*. 200, 1062–1066. doi:10.1016/j.psychres.2012.06.010
- Broos, N., Schmaal, L., Wiskerke, J., Kosteljik, L., Lam, T., Stoop, N., Weierink, L., Ham, J., de Geus, E.J.C., Schoffemeer, A.N.M., van den Brink, W., Veltman, D.J., de Vries, T.J., Pattij, T., Goudriaan, A.E., 2012. The relationship between impulsive choice and

impulsive action: A cross-species translational study. *PLoS One* 7, 1–9.

doi:10.1371/journal.pone.0036781

Brown, S.M., Manuck, S.B., Flory, J.D., Hariri, A.R., 2006. Neural basis of individual differences in impulsivity: contributions of corticolimbic circuits for behavioral arousal and control. *Emotion* 6, 239–245. doi:10.1037/1528-3542.6.2.239

Brunner, D., Hen, R., 1997. Insights into the neurobiology of impulsive behavior from serotonin receptor knockout mice. *Ann N Y Acad Sci.* 836, 81–105. doi:10.1111/j.1749-6632.1997.tb52356.x

Cackowski, S., Reitz, A.-C., Ende, G., Kleindienst, N., Bohus, M., Schmahl, C., Krause-Utz, A., 2014. Impact of stress on different components of impulsivity in borderline personality disorder. *Psychol. Med.* 44, 3329–3340. doi:10.1017/S0033291714000427

Cairns, E., Cammock, T., 1978. Development of a more reliable version of the Matching Familiar Figures Test. *Dev. Psychol.* 14, 555–560. doi:10.1037//0012-1649.14.5.555

Carli, M., Robbins, T.W., Evenden, J.L., Everitt, B.J., 1983. Effects of lesions to ascending noradrenergic neurones on performance of a 5-choice serial reaction task in rats; implications for theories of dorsal noradrenergic bundle function based on selective attention and arousal. *Behav Brain Res.* 9, 361–380. doi:10.1016/0166-4328(83)90138-9

Carroll, D., Phillips, A.C., Der, G., 2008. Body mass index, abdominal adiposity, obesity, and cardiovascular reactions to psychological stress in a large community sample. *Psychosom. Med.* 70, 653–660. doi:10.1097/PSY.0b013e31817b9382

Caswell, A.J., Bond, R., Duka, T., Morgan, M.J., 2015. Further evidence of the heterogeneous nature of impulsivity. *Pers. Individ. Dif.* 76, 68–74. doi:10.1016/j.paid.2014.11.059

- Chepenik, L.G., Cornew, L.A., Farah, M.J., 2007. The influence of sad mood on cognition. *Emotion* 7, 802–811. doi:10.1037/1528-3542.7.4.802
- Cisler, J.M., Olatunji, B.O., Feldner, M.T., Forsyth, J.P., 2010. Emotion regulation and the anxiety disorders: An integrative review. *J. Psychopathol. Behav. Assess.* doi:10.1007/s10862-009-9161-1
- Clark, L., Bechara, A., Damasio, H., Aitken, M., Sahakian, B., Robbins, T., 2008. Differential effects of insular and ventromedial prefrontal cortex lesions on risky decision-making. *Brain* 131, 1311–22. doi:10.1093/brain/awn066
- Clark, L., Manes, F., Antoun, N., Sahakian, B.J., Robbins, T.W., 2003. The contributions of lesion laterality and lesion volume to decision-making impairment following frontal lobe damage. *Neuropsychologia* 41, 1474–1483. doi:10.1016/S0028-3932(03)00081-2
- Clark, L., Robbins, T.W., Ersche, K.D., Sahakian, B.J., 2006. Reflection Impulsivity in Current and Former Substance Users. *Biol Psychiatry* 60, 515–522. doi:10.1016/j.biopsych.2005.11.007
- Congdon, E., Canli, T., 2008. A Neurogenetic Approach to Impulsivity. *J. Pers.* 76, 1447–1483. doi:10.1016/j.biotechadv.2011.08.021.Secreted
- Cooper, M.L., Frone, M.R., Russell, M., Mudar, P., 1995. Drinking to regulate positive and negative emotions: a motivational model of alcohol use. *J. Pers. Soc. Psychol.* 69, 990–1005. doi:10.1037/0022-3514.69.5.990
- Critchley, H.D., Mathias, C.J., Josephs, O., O’Doherty, J., Zanini, S., Dewar, B.K., Cipolotti, L., Shallice, T., Dolan, R.J., 2003. Human cingulate cortex and autonomic control: Converging neuroimaging and clinical evidence. *Brain* 126, 2139–2152. doi:10.1093/brain/awg216

- Cyders, M. A., Smith, G.T., 2008. Emotion-based Dispositions to Rash Action: Positive and Negative Urgency. *Psychological Bull.* 134, 807–828. doi:10.1037/a0013341.Emotion-based
- Cyders, M. A., Smith, G.T., 2007. Mood-based rash action and its components: Positive and negative urgency. *Pers. Individ. Dif.* 43, 839–850. doi:10.1016/j.paid.2007.02.008
- D’Alberto, N., Funnell, M., Potter, A., Garavan, H., 2017. A split-brain case study on the hemispheric lateralization of inhibitory control. *Neuropsychologia* 99, 24–29. doi:10.1016/j.neuropsychologia.2017.02.017
- Dalley, J.W., Everitt, B.J., Robbins, T.W., 2011. Impulsivity, Compulsivity, and Top-Down Cognitive Control. *Neuron* 69, 680–694. doi:10.1016/j.neuron.2011.01.020
- Daruna, J.H., Barnes, P.A., 1993. A neurodevelopmental view of impulsivity., in: McCown, W.G., Johnson, J.L., Shure, M.B. (Eds.), *The Impulsive Client: Theory, Research and Treatment*. American Psychological Association, Washington, DC, pp. 23–37. doi:10.1016/j.cpr.2006.01.001
- De Houwer, J., Tibboel, H., 2010. Stop what you are not doing! Emotional pictures interfere with the task not to respond. *Psychon. Bull. Rev.* 17, 699–703. doi:10.3758/PBR.17.5.699
- de Wit, H., 2009. Impulsivity as a determinant and consequence of drug use: A review of underlying processes. *Addict Biol.* 14, 22–31. doi:10.1111/j.1369-1600.2008.00129.x
- Decker, J.H., Figner, B., Steinglass, J.E., 2015. On weight and waiting: Delay discounting in anorexia nervosa pretreatment and posttreatment. *Biol. Psychiatry* 78, 606–614. doi:10.1016/j.biopsych.2014.12.016
- Dickman, S., Meyer, D., 1988. Impulsivity and speed-accuracy tradeoffs in information

- processing. *J Pers Soc Psychol.* 54, 274–90.
- Dickman, S.J., 1990. Functional and dysfunctional impulsivity: personality and cognitive correlates. *J. Pers. Soc. Psychol.* 58, 95–102. doi:10.1037/0022-3514.58.1.95
- Dolan, R.J., 2002. Emotion, Cognition, and Behavior. *Science* 298, 1191–94.
- Dougherty, D.M., Marsh, D.M., Mathias, C.W., 2002. Immediate and delayed memory tasks: a computerized behavioral measure of memory, attention, and impulsivity. *Behav Res Meth Instrum Comput* 34, 391–398. doi:10.3758/BF03195467
- Dougherty, D.M., Mathias, C.W., Marsh, D.M., Jagar, A.A., 2005. Laboratory behavioral measures of impulsivity. *Behav Res Methods* 37, 82–90. doi:10.3758/BF03206401
- Eagle, D.M., Bari, A., Robbins, T.W., 2008. The neuropsychopharmacology of action inhibition: Cross-species translation of the stop-signal and go/no-go tasks. *Psychopharmacology (Berl)*. 199, 439–456. doi:10.1007/s00213-008-1127-6
- Evenden, J.L., 1999a. Impulsivity: a discussion of clinical and experimental findings. *J Psychopharmacol.* 13, 180–192. doi:10.1177/026988119901300211
- Evenden, J.L., 1999b. Varieties of impulsivity. *Psychopharmacology (Berl)*. 146, 348–361. doi:10.1007/PL00005481
- Eysenck, H.J., Eysenck, M.W., 1985. *Personality and Individual Differences: A Natural Science Approach*, 1st ed, *Personality and Individual Differences: A Natural Science Approach*. Plenum Press, New York. doi:10.1016/j.paid.2009.08.015
- Eysenck, S., Eysenck, H., 1978. Impulsiveness and venturesomeness: their position in a dimensional system of personality description. *Psychol. Rep.* 1247–1255.
- Fineberg, N.A., Chamberlain, S.R., Goudriaan, A.E., Stein, D.J., Vanderschuren, L.J.M.J.,

- Gillan, C.M., Shekar, S., Gorwood, P. a. P.M., Valerie Voon, S.M.-Z., Denys, D., Sahakian, B.J., Moeller, F.G., Robbins, T.W., Potenza, M.N., 2014. New developments in human neurocognition: clinical, genetic, and brain imaging correlates of impulsivity and compulsivity. *CNS Spectr.* 19, 69–89. doi:10.1017/S1092852913000801
- Fineberg, N.A., Potenza, M.N., Chamberlain, S.R., Berlin, H.A., Menzies, L., Bechara, A., Sahakian, B.J., Robbins, T.W., Bullmore, E.T., Hollander, E., 2010. Probing compulsive and impulsive behaviors, from animal models to endophenotypes: a narrative review. *Neuropharmacology* 35, 591–604. doi:10.1038/npp.2009.185
- Fowles, D.C., 2000. Electrodermal hyporeactivity and antisocial behavior: does anxiety mediate the relationship? *J. Affect. Disord.* 61, 177–189. doi:10.1016/S0165-0327(00)00336-0
- Frost, R., McNaughton, N., 2017. The Neural Basis of Delay Discounting: A Review and Preliminary Model. *Neurosci. Biobehav. Rev.* 79, 48–65. doi:https://doi.org/10.1016/j.neubiorev.2017.04.022
- Fukui, H., Murai, T., Fukuyama, H., Hayashi, T., Hanakawa, T., 2005. Functional activity related to risk anticipation during performance of the Iowa gambling task. *Neuroimage* 24, 253–259. doi:10.1016/j.neuroimage.2004.08.028
- Gigerenzer, G., Todd, P.M., ABC Research Group, 1999. Simple heuristics that make us smart. Oxford University Press. doi:10.1007/s13398-014-0173-7.2
- Ginty, A.T., Phillips, A.C., Higgs, S., Heaney, J.L.J., Carroll, D., 2012. Disordered eating behaviour is associated with blunted cortisol and cardiovascular reactions to acute psychological stress. *Psychoneuroendocrinology* 37, 715–724. doi:10.1016/j.psyneuen.2011.09.004

- Granö, N., Virtanen, M., Vahtera, J., Elovainio, M., Kivimäki, M., 2004. Impulsivity as a predictor of smoking and alcohol consumption. *Pers. Individ. Dif.* 37, 1693–1700. doi:10.1016/j.paid.2004.03.004
- Grau, E., Ortet, G., 1999. Personality traits and alcohol consumption in a sample of non-alcoholic women. *Pers. Individ. Dif.* 27, 1057–1066. doi:10.1016/S0191-8869(99)00047-1
- Gray, J.A., 1981. A critique of Eysenck's theory of personality., in: Eysenck, H.J. (Ed.), *A Model for Personality*. Springer, Berlin, pp. 246–276. doi:10.1017/S0140525X00061872
- Gray, J.A., 1972. The psychophysiological basis of introversion-extraversion: A modification of Eysenck's theory, in: Nebylitsyn, V.D., Gray, J.A. (Eds.), *Biological Bases of Individual Behavior*. Academic, New York, pp. 182–205. doi:10.1016/0005-7967(70)90069-0
- Guan, S., Cheng, L., Fan, Y., Li, X., 2015. Myopic decisions under negative emotions correlate with altered time perception. *Front. Psychol.* 6, 1–10. doi:10.3389/fpsyg.2015.00468
- Guerrieri, R., Nederkoorn, C., Jansen, A., 2007a. How impulsiveness and variety influence food intake in a sample of healthy women. *Appetite* 48, 119–122. doi:10.1016/j.appet.2006.06.004
- Guerrieri, R., Nederkoorn, C., Stankiewicz, K., Alberts, H., Geschwind, N., Martijn, C., Jansen, A., 2007b. The influence of trait and induced state impulsivity on food intake in normal-weight healthy women. *Appetite* 49, 66–73. doi:10.1016/j.appet.2006.11.008
- Haushofer, J., Cornelisse, S., Seinstra, M., Fehr, E., Joëls, M., Kalenscher, T., 2013. No Effects of Psychosocial Stress on Intertemporal Choice. *PLoS One* 8, e78597.

doi:10.1371/journal.pone.0078597

Hebb, D.O., 1955. Drives and the C. N. S. (conceptual nervous system). *Psychol. Rev.* 62, 243–254. doi:10.1037/h0041823

Hinvest, N.S., Anderson, I.M., 2010. The effects of real versus hypothetical reward on delay and probability discounting. *Q. J. Exp. Psychol. (Hove)*. 63, 1072–1084. doi:10.1080/17470210903276350

Hinvest, N.S., Elliott, R., McKie, S., Anderson, I.M., 2011. Neural correlates of choice behavior related to impulsivity and venturesomeness. *Neuropsychologia* 49, 2311–2320. doi:10.1016/j.neuropsychologia.2011.02.023

Hogg, B.Y.J., Evans, P.L.C., Adrian, H., 1975. Stimulus generalization following extra-dimensional training in educationally subnormal (severely) children. *Br J Psychol.* 66, 211–24.

Holt, D.D., Green, L., Myerson, J., 2003. Is discounting impulsive?: Evidence from temporal and probability discounting in gambling and non-gambling college students. *Behav Process.* 64, 355–367. doi:10.1016/S0376-6357(03)00141-4

Horn, N.R., Dolan, M., Elliott, R., Deakin, J.F.W., Woodruff, P.W.R., 2003. Response inhibition and impulsivity: an fMRI study. *Neuropsychologia* 41, 1959–1966. doi:10.1016/S0028-3932(03)00077-0

Hornak, J., Bramham, J., Rolls, E.T., Morris, R.G., O'Doherty, J., Bullock, P.R., Polkey, C.E., 2003. Changes in emotion after circumscribed surgical lesions of the orbitofrontal and cingulate cortices. *Brain* 126, 1691–712. doi:10.1093/brain/awg168

Isen, A.M., Geva, N., 1987. The influence of positive affect on acceptable level of risk: The person with a large canoe has a large worry. *Organ. Behav. Hum. Decis. Process.* 39,

145–154. doi:10.1016/0749-5978(87)90034-3

Isen, A.M., Means, B., 1983. The Influence of Positive Affect on Decision-Making Strategy.

Soc. Cogn. 2, 18–31. doi:http://dx.doi.org/10.1521/soco.1983.2.1.18

Isen, A.M., Patrick, R., 1983. The effect of positive feelings on risk taking: When the chips are down. *Organ. Behav. Hum. Perform.* 31, 194–202. doi:10.1016/0030-

5073(83)90120-4

Isen, A.M., Rosenzweig, A.S., Young, M.J., 1991. The Influence of Positive Affect on

Clinical Problem solving. *Med. Decis. Mak.* 11, 221–227.

doi:10.1177/0272989X9101100313

Jentsch, J.D., Taylor, J.R., 1999. Impulsivity resulting from frontostriatal dysfunction in drug abuse: Implications for the control of behavior by reward-related stimuli.

Psychopharmacology (Berl). 146, 373–390. doi:10.1007/PL00005483

Johnson, M.W., Bickel, W.K., 2002. Within-subject comparison of real and hypothetical money rewards in delay discounting. *J Exp Anal Behav* 77, 129–146.

doi:10.1901/jeab.2002.77-129

Kagan, J., 1965a. Individual differences in the resolution of response uncertainty. *J. Pers.*

Soc. Psychol. 2, 154–160. doi:10.1037/h0022199

Kagan, J., 1965b. Reflection-impulsivity and reading ability in primary grade children. *Child*

Dev. 36, 609–628. doi:10.2307/1126908

Kagan, J., Rosman, B.L., Day, D., Albert, J., Phillips, W., 1964. Information processing in

the child: Significance of analytic and reflective attitudes. *Psychol. Monogr. Gen. Appl.*

doi:10.1037/h0093830

Kalanthroff, E., Cohen, N., Henik, A., 2013. Stop feeling: inhibition of emotional

interference following stop-signal trials. *Front. Hum. Neurosci.* 7, 78.

doi:10.3389/fnhum.2013.00078

Kalkhoven, C., Sennef, C., Peeters, A., van den Bos, R., 2014. Risk-taking and pathological gambling behavior in Huntington's disease. *Front. Behav. Neurosci.* 8, 103.

doi:10.3389/fnbeh.2014.00103

Kessler, R.C., Chiu, W.T., Demler, O., Walters, E.E., 2005. Prevalence, severity, and comorbidity of twelve-month DSM-IV disorders in the National Comorbidity Survey Replication (NCS-R). *Arch. Gen. Psychiatry* 62, 617–627.

doi:10.1001/archpsyc.62.6.617

Kim, S., Lee, D., 2011. Prefrontal cortex and impulsive decision making. *Biol Psychiatry*.

doi:10.1016/j.biopsych.2010.07.005

Kimura, K., Izawa, S., Sugaya, N., Ogawa, N., Yamada, K.C., Shirotsuki, K., Mikami, I., Hirata, K., Nagano, Y., Hasegawa, T., 2013. The biological effects of acute psychosocial stress on delay discounting. *Psychoneuroendocrinology* 38, 2300–8.

doi:10.1016/j.psyneuen.2013.04.019

Kirby, K.N., Maraković, N.N., 1996. Delay-discounting probabilistic rewards: Rates decrease as amounts increase. *Psychon. Bull. Rev.* 3, 100–104.

doi:10.3758/BF03210748

Kirby, K.N., Petry, N.M., Bickel, W.K., 1999. Heroin addicts have higher discount rates for delayed rewards than non-drug-using controls. *J. Exp. Psychol. Gen.* 128, 78–87.

doi:10.1037/0096-3445.128.1.78

Koff, E., Lucas, M., 2011. Mood moderates the relationship between impulsiveness and delay discounting. *Pers. Individ. Dif.* 50, 1018–1022. doi:10.1016/j.paid.2011.01.016

- Koo-Loeb, J.H., Pedersen, C., Girdler, S.S., 1998. Blunted cardiovascular and catecholamine stress reactivity in women with bulimia nervosa. *Psychiatry Res.* 80, 13–27.
doi:10.1016/S0165-1781(98)00057-2
- Kreibig, S.D., 2010. Autonomic nervous system activity in emotion: A review. *Biol. Psychol.*
doi:10.1016/j.biopsycho.2010.03.010
- Kuhnen, C., Knutson, B., 2005. The neural basis of financial risk taking. *Neuron* 47, 763–770. doi:10.1016/j.neuron.2005.08.008
- Lagorio, C.H., Madden, G.J., 2005. Delay discounting of real and hypothetical rewards III: Steady-state assessments, forced-choice trials, and all real rewards. *Behav Process.* 69, 173–187. doi:10.1016/j.beproc.2005.02.003
- Lawyer, S.R., Schoepflin, F., Green, R., Jenks, C., 2011. Discounting of hypothetical and potentially real outcomes in nicotine-dependent and nondependent samples. *Exp Clin Psychopharmacol.* 19, 263–274. doi:10.1037/a0024141
- LeDoux, J.E., 2000. Emotion circuits in the brain. *Annu Rev Neurosci.* 23, 155–184.
doi:10.1146/annurev.neuro.23.1.155
- Lejuez, C.W., Read, J.P., Kahler, C.W., Richards, J.B., Ramsey, S.E., Stuart, G.L., Strong, D.R., Brown, R. a., 2002. Evaluation of a behavioral measure of risk taking: The Balloon Analogue Risk Task (BART). *J. Exp. Psychol. Appl.* 8, 75–84.
doi:10.1037//1076-898X.8.2.75
- Lempert, K.M., Porcelli, A.J., Delgado, M.R., Tricomi, E., 2012. Individual Differences in Delay Discounting Under Acute Stress: The Role of Trait Perceived Stress. *Front. Psychol.* 3, 251. doi:10.3389/fpsyg.2012.00251
- Lerner, J.S., Li, Y., Weber, E.U., 2013. The financial costs of sadness. *Psychol Sci* 24, 72–79.

doi:10.1177/0956797612450302

Lighthall, N.R., Mather, M., Gorlick, M. a., 2009. Acute Stress Increases Sex Differences in Risk Seeking in the Balloon Analogue Risk Task. *PLoS One* 4, e6002.

doi:10.1371/journal.pone.0006002

Lindström, B.R., Bohlin, G., 2012. Threat-relevance impairs executive functions: Negative impact on working memory and response inhibition. *Emotion* 12, 384–393.

doi:10.1037/a0027305

Liu, L., Feng, T., Chen, J., Li, H., 2013. The Value of Emotion: How Does Episodic Prospection Modulate Delay Discounting? *PLoS One* 8, e81717.

doi:10.1371/journal.pone.0081717

Logan, G.D., 1994. On the ability to inhibit thought and action: A users' guide to the stop signal paradigm, in: *Inhibitory Processes in Attention, Memory, and Language*. pp. 189–239. doi:10.1016/j.jsat.2006.09.008

Lovallo, W.R., Dickensheets, S.L., Myers, D.A., Thomas, T.L., Nixon, S.J., 2000. Blunted stress cortisol response in abstinent alcoholic and polysubstance-abusing men. *Alcohol. Clin. Exp. Res.* 24, 651–658. doi:10.1111/j.1530-0277.2000.tb02036.x

MacPherson, S.E., Phillips, L.H., Della Sala, S., Cantagallo, A., 2009. Iowa Gambling task impairment is not specific to ventromedial prefrontal lesions. *Clin. Neuropsychol.* 23, 510–22. doi:10.1080/13854040802396586

Magid, V., Colder, C.R., Stroud, L.R., Nichter, M., Nichter, M., 2009. Negative affect, stress, and smoking in college students: Unique associations independent of alcohol and marijuana use. *Addict. Behav.* 34, 973–975. doi:10.1016/j.addbeh.2009.05.007

Mason, L., O'sullivan, N., Montaldi, D., Bentall, R.P., El-Dereby, W., 2014. Decision-

making and trait impulsivity in bipolar disorder are associated with reduced prefrontal regulation of striatal reward valuation. *Brain* 137, 2346–2355.

doi:10.1093/brain/awu152

Mathias, C.W., Stanford, M.S., 2003. Impulsiveness and arousal: Heart rate under conditions of rest and challenge in healthy males. *Pers. Individ. Dif.* 35, 355–371.

doi:10.1016/S0191-8869(02)00195-2

Mauss, I.B., Robinson, M.D., 2009. Measures of emotion: A review. *Cogn. Emot.* 23, 209–237. doi:10.1080/02699930802204677

Mazur, J.E., 1993. Predicting the Strength of a Conditioned Reinforcer: Effects of Delay and Uncertainty. *Curr. Dir. Psychol. Sci.* 2, 70–74. doi:10.1111/1467-8721.ep10770907

Messer, S., 1970. The Effect of Anxiety over Intellectual Performance on Reflection-Impulsivity in Children. *Child Dev.* 41, 723. doi:10.2307/1127219

Mischel, W., Ebbesen, E.B., Zeiss, R., 1972. Cognitive and attentional mechanisms in delay of gratification. *J. Pers. Soc. Psychol.* 21, 204–218. doi:10.1037/h0032198

Mischel, W., Shoda, Y., Peake, P.K., 1988. The nature of adolescent competencies predicted by preschool delay of gratification. *J. Pers. Soc. Psychol.* 54, 687–696.

doi:10.1037/0022-3514.54.4.687

Mischel, W., Shoda, Y., Rodriguez, M., 1989. Delay of Gratification in Children. *Science* 244, 933–938.

Moeller, F.G., Barratt, E.S., Dougherty, D.M., Schmitz, J.M., Swann, A. C., 2001. Psychiatric aspects of impulsivity. *Am J Psychiatry* 158, 1783–1793.

doi:10.1176/appi.ajp.158.11.1783

Monterosso, J., Ainslie, G., 1999. Beyond discounting: possible experimental models of

- impulse control. *Psychopharmacol.* 146, 339–347. doi:91460339.213 [pii]
- Moore, B.S., Clyburn, A., Underwood, B., 1976. The Role of Affect in Delay of Gratification. *Child Dev.* 47, 273–276. doi:10.2307/1128312
- Muñoz, L.C., Anastassiou-Hadjicharalambous, X., 2011. Disinhibited behaviors in young children: Relations with impulsivity and autonomic psychophysiology. *Biol Psychiatry.* 86, 349–359. doi:10.1016/j.biopsycho.2011.01.007
- Murphy, F.C., Nimmo-Smith, I., Lawrence, A.D., 2003. Functional neuroanatomy of emotions: a meta-analysis. *Cogn Affect Behav Neurosci.* 3, 207–233. doi:10.3758/CABN.3.3.207
- Najt, P., Perez, J., Sanches, M., Peluso, M. a M., Glahn, D., Soares, J.C., 2007. Impulsivity and bipolar disorder. *Eur Neuropsychopharmacol.* 17, 313–320. doi:10.1016/j.euroneuro.2006.10.002
- Napadow, V., Dhond, R., Conti, G., Makris, N., Brown, E.N., Barbieri, R., 2008. Brain correlates of autonomic modulation: Combining heart rate variability with fMRI. *Neuroimage* 42, 169–177. doi:10.1016/j.neuroimage.2008.04.238
- Nikolaou, K., Critchley, H., Duka, T., 2013. Alcohol affects neuronal substrates of response inhibition but not of perceptual processing of stimuli signalling a stop response. *PLoS One* 8, e76649. doi:10.1371/journal.pone.0076649
- Nygren, T.E., Isen, A.M., Taylor, P.J., Dulin, J., 1996. The Influence of Positive Affect on the Decision Rule in Risk Situations: Focus on Outcome (and Especially Avoidance of Loss) Rather Than Probability. *Organ. Behav. Hum. Decis. Process.* 66, 59–72. doi:10.1006/obhd.1996.0038
- Otto, A.R., Markman, A.B., Love, B.C., 2012. Taking More, Now: The Optimality of

- Impulsive Choice Hinges on Environment Structure. *Soc. Psychol. Personal. Sci.* 3, 131–138. doi:10.1177/1948550611411311
- Pabst, S., Brand, M., Wolf, O.T., 2013. Stress effects on framed decisions: there are differences for gains and losses. *Front. Behav. Neurosci.* 7, 142. doi:10.3389/fnbeh.2013.00142
- Panksepp, J., 1998. *Affective Neuroscience: The Foundations of Human and Animal Emotions*. Oxford University Press.
- Paris, J.J., Franco, C., Sodano, R., Frye, C.A., Wulfert, E., 2010. Gambling pathology is associated with dampened cortisol response among men and women. *Physiol. Behav.* 99, 230–233. doi:10.1016/j.physbeh.2009.04.002
- Patterson, T.K., Lenartowicz, A., Berkman, E.T., Ji, D., Poldrack, R.A., Knowlton, B.J., 2016. Putting the brakes on the brakes: negative emotion disrupts cognitive control network functioning and alters subsequent stopping ability. *Exp. Brain Res.* 234, 3107–3118. doi:10.1007/s00221-016-4709-2
- Patton, J.H., Stanford, M.S., Barratt, E.S., 1995. Factor structure of the Barratt impulsiveness scale. *J. Clin. Psychol.* 51, 768–774. doi:10.1002/1097-4679(199511)51:6<768
- Pesonen, A.-K., Kajantie, E., Jones, A., Pyhälä, R., Lahti, J., Heinonen, K., Eriksson, J.G., Strandberg, T.E., Räikkönen, K., 2011. Symptoms of attention deficit hyperactivity disorder in children are associated with cortisol responses to psychosocial stress but not with daily cortisol levels. *J. Psychiatr. Res.* 45, 1471–1476. doi:10.1016/j.jpsychires.2011.07.002
- Pessoa, L., Padmala, S., Kenzer, A., Bauer, A., 2013. Interactions between cognition and emotion during response inhibition. *Emotion* 12, 192–197.

doi:10.1037/a0024109.Interactions

- Peters, J., Büchel, C., 2011. The neural mechanisms of inter-temporal decision-making: understanding variability. *Trends Cogn Sci.* 15, 227–239. doi:10.1016/j.tics.2011.03.002
- Phan, K.L., Wager, T., Taylor, S.F., Liberzon, I., 2002. Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. *Neuroimage* 16, 331–348. doi:10.1006/nimg.2002.1087
- Phan, K.L., Wager, T.D., Taylor, S.F., Liberzon, I., 2004. Functional neuroimaging studies of human emotions. *CNS Spectr.* 9, 258–266.
- Phillips, M.L., Swartz, H.A., 2014. A critical appraisal of neuroimaging studies of bipolar disorder: toward a new conceptualization of underlying neural circuitry and roadmap for future research. *Am J Psychiatry.* 171, 829–43. doi:10.1007/s12020-009-9266-z.A
- Putman, P., Antypa, N., Crysovergi, P., van der Does, W. a J., 2010. Exogenous cortisol acutely influences motivated decision making in healthy young men. *Psychopharmacology (Berl).* 208, 257–63. doi:10.1007/s00213-009-1725-y
- Puttonen, S., Elovainio, M., Kivimäki, M., Koskinen, T., Pulkki-Råback, L., Viikari, J.S.A., Raitakari, O.T., Keltikangas-Järvinen, L., 2008. Temperament, health-related behaviors, and autonomic cardiac regulation: The cardiovascular risk in young Finns study. *Biol. Psychol.* 78, 204–210. doi:10.1016/j.biopsycho.2008.03.003
- Rachlin, H., 1990. Why Do People Gamble and Keep Gambling Despite Heavy Losses? *Psychol. Sci.* 1, 294–297. doi:10.1111/j.1467-9280.1990.tb00220.x
- Rao, H., Korczykowski, M., Pluta, J., Hoang, A., Detre, J. a., 2008. Neural correlates of voluntary and involuntary risk taking in the human brain: An fMRI Study of the Balloon Analog Risk Task (BART). *Neuroimage* 42, 902–910.

doi:10.1016/j.neuroimage.2008.05.046

Rebetez, M.M.L., Rochat, L., Billieux, J., Gay, P., Van der Linden, M., 2015. Do emotional stimuli interfere with two distinct components of inhibition? *Cogn. Emot.* 29, 559–67.

doi:10.1080/02699931.2014.922054

Reynolds, B., Ortengren, A., Richards, J.B., de Wit, H., 2006. Dimensions of impulsive behavior: Personality and behavioral measures. *Pers. Individ. Dif.* 40, 305–315.

doi:10.1016/j.paid.2005.03.024

Richards, J.B., Zhang, L., Mitchell, S.H., de Wit, H., 1999. Delay or probability discounting in a model of impulsive behavior: effect of alcohol. *J. Exp. Anal. Behav.* 71, 121–143.

doi:10.1901/jeab.1999.71-121

Robinson, E.S.J., Eagle, D.M., Economidou, D., Theobald, D.E.H., Mar, a. C., Murphy, E.R., Robbins, T.W., Dalley, J.W., 2009. Behavioural characterisation of high impulsivity on the 5-choice serial reaction time task: Specific deficits in “waiting” versus “stopping.” *Behav Brain Res.* 196, 310–316. doi:10.1016/j.bbr.2008.09.021

Robinson, O.J., Bond, R.L., Roiser, J.P., 2015. The impact of threat of shock on the framing effect and temporal discounting: executive functions unperturbed by acute stress? *Front. Psychol.* 6, 1–9. doi:10.3389/fpsyg.2015.01315

Rogers, R.D., Everitt, B.J., Baldacchino, A., Blackshaw, a. J., Swainson, R., Wynne, K., Baker, N.B., Hunter, J., Carthy, T., Booker, E., London, M., Deakin, J.F.W., Sahakian, B.J., Robbins, T.W., 1999. Dissociable deficits in the decision-making cognition of chronic amphetamine abusers, opiate abusers, patients with focal damage to prefrontal cortex, and tryptophan-depleted normal volunteers: Evidence for monoaminergic mechanisms. *Neuropsychopharmacology* 20, 322–339. doi:10.1016/S0893-133X(98)00091-8

- Rosvold, H.E., Mirsky, A.F., Sarason, I., Bransome, E.D., Beck, L.H., 1956. A continuous performance test of brain damage. *J. Consult. Psychol.* 20, 343–350.
doi:10.1037/h0043220
- Rubia, K., Russell, T., Overmeyer, S., Brammer, M.J., Bullmore, E.T., Sharma, T., Simmons, A., Williams, S.C.R., Giampietro, V., Andrew, C.M., Taylor, E., 2001. Mapping Motor Inhibition: Conjunctive Brain Activations across Different Versions of Go/No-Go and Stop Tasks. *Neuroimage* 13, 250–261. doi:10.1006/nimg.2000.0685
- Sanchez-Roige, S., Baro, V., Trick, L., Peña-Oliver, Y., Stephens, D., Duka, T., 2014. Exaggerated waiting impulsivity associated with human binge drinking, and high alcohol consumption in mice. *Neuropsychopharmacology* 39, 2919–27.
- Satterfield, J. H., Dawson, M.E., 1971. Electrodermal Correlates of Hyperactivity in Children. *Psychophysiology* 8, 191–197. doi:10.1111/j.1469-8986.1971.tb00450.x
- Schlam, T.R., Wilson, N.L., Shoda, Y., Mischel, W., Ayduk, O., 2013. Preschoolers' delay of gratification predicts their body mass 30 years later. *J. Pediatr.* 162, 90–93.
doi:10.1016/j.jpeds.2012.06.049
- Schmidt, B., Mussel, P., Hewig, J., 2013. I'm too calm-Let's take a risk! On the impact of state and trait arousal on risk taking. *Psychophysiology* 50, 498–503.
doi:10.1111/psyp.12032
- Scholz, U., La Marca, R., Nater, U.M., Aberle, I., Ehlert, U., Hornung, R., Martin, M., Kliegel, M., 2009. Go no-go performance under psychosocial stress: beneficial effects of implementation intentions. *Neurobiol. Learn. Mem.* 91, 89–92.
doi:10.1016/j.nlm.2008.09.002
- Schwabe, L., Höffken, O., Tegenthoff, M., Wolf, O.T., 2013. Stress-induced enhancement of

response inhibition depends on mineralocorticoid receptor activation.

Psychoneuroendocrinology 38, 2319–2326. doi:10.1016/j.psyneuen.2013.05.001

Seeyave, D.M., Coleman, S., Appugliese, D., Corwyn, R.F., Bradley, R.H., Davidson, N.S., Kaciroti, N., Lumeng, J.C., 2009. Ability to delay gratification at age 4 years and risk of overweight at age 11 years. *Arch Pediatr Adolesc Med.* 163, 303–308. doi:10.1001/archpediatrics.2009.12

Sellitto, M., Ciaramelli, E., Mattioli, F., di Pellegrino, G., 2016. Reduced Sensitivity to Sooner Reward During Intertemporal Decision-Making Following Insula Damage in Humans. *Front. Behav. Neurosci.* 9, 367. doi:10.3389/fnbeh.2015.00367

Sharot, T., Delgado, M.R., Phelps, E. a, 2004. How emotion enhances the feeling of remembering. *Nat. Neurosci.* 7, 1376–1380. doi:10.1038/nn1353

Shed, N.W., Hodgins, D.C., 2009. Probability Discounting of Gains and Losses: Implications for Risk Attitudes and Impulsivity. *J. Exp. Anal. Behav.* 92, 1–16. doi:10.1901/jeab.2009.92-1

Shoda, Y., Mischel, W., Peake, P.K., 1990. Predicting adolescent cognitive and self-regulatory competencies from preschool delay of gratification: Identifying diagnostic conditions. *Dev. Psychol.* 26, 978–986. doi:10.1037/0012-1649.26.6.978

Smallwood, J., Fitzgerald, A., Miles, L.K., Phillips, L.H., 2009. Shifting moods, wandering minds: negative moods lead the mind to wander. *Emotion* 9, 271–276. doi:10.1037/a0014855

Smith, A., Rusted, J., Savory, M., Eaton-Williams, P., Hall, S., 1991. The effects of caffeine, impulsivity and time of day on performance, mood and cardiovascular function. *J. Psychopharmacol.* 5, 120–128. doi:10.1177/026988119100500205

- Smyth, J.M., Wonderlich, S.A., Heron, K.E., Sliwinski, M.J., Crosby, R.D., Mitchell, J.E., Engel, S.G., 2007. Daily and momentary mood and stress are associated with binge eating and vomiting in bulimia nervosa patients in the natural environment. *J. Consult. Clin. Psychol.* 75, 629–638. doi:10.1037/0022-006X.75.4.629
- Sprengelmeyer, R., Rausch, M., Eysel, U.T., Przuntek, H., 1998. Neural structures associated with recognition of facial expressions of basic emotions. *Proc. Biol. Sci.* 265, 1927–1931. doi:10.1098/rspb.1998.0522
- Sprengelmeyer, R., Young, A.W., Calder, A.J., Karnat, A., Lange, H., Homberg, V., Perrett, D.I., Rowland, D., 1996. Perception of faces and emotions in Huntington ' s disease. *Brain* 119, 1647–1665. doi:10.1093/brain/119.5.1647
- Sprengelmeyer, R., Young, A.W., Pundt, I., Sprengelmeyer, A., Calder, A.J., Berrios, G., Winkel, R., Vollmöeller, W., Kuhn, W., Sartory, G., Przuntek, H., 1997. Disgust implicated in obsessive-compulsive disorder. *Psychiatr. und Psychother.* 264, 1767–1773.
- Stankovic, A., Fairchild, G., Aitken, M.R.F., Clark, L., 2014. Effects of psychosocial stress on psychophysiological activity during risky decision-making in male adolescents. *Int. J. Psychophysiol.* 93, 22–29. doi:10.1016/j.ijpsycho.2013.11.001
- Starcke, K., Wolf, O.T., Markowitsch, H.J., Brand, M., 2008. Anticipatory stress influences decision making under explicit risk conditions. *Behav. Neurosci.* 122, 1352–1360. doi:10.1037/a0013281
- Stern, E.R., Gonzalez, R., Welsh, R.C., Taylor, S.F., 2010. Updating beliefs for a decision: neural correlates of uncertainty and underconfidence. *J Neurosci.* 30, 8032–8041. doi:10.1523/JNEUROSCI.4729-09.2010

- Swanson, J., Baler, R.D., Volkow, N.D., 2011. Understanding the effects of stimulant medications on cognition in individuals with attention-deficit hyperactivity disorder: a decade of progress. *Neuropsychopharmacology* 36, 207–26. doi:10.1038/npp.2010.160
- Talarico, J.M., Rubin, D.C., 2007. Flashbulb Memories Are Special After All; in Phenomenology, Not Accuracy. *Appl. Cogn. Psychol.* 21, 557*578. doi:10.1002/acp
- Tice, D.M., Bratslavsky, E., Baumeister, R.F., 2001. Emotional distress regulation takes precedence over impulse control: if you feel bad, do it! *J. Pers. Soc. Psychol.* 80, 53–67. doi:10.1037/0022-3514.80.1.53
- van den Bos, R., Harteveld, M., Stoop, H., 2009. Stress and decision-making in humans: Performance is related to cortisol reactivity, albeit differently in men and women. *Psychoneuroendocrinology* 34, 1449–1458. doi:10.1016/j.psyneuen.2009.04.016
- Verbruggen, F., De Houwer, J., 2007. Do emotional stimuli interfere with response inhibition? Evidence from the stop signal paradigm. *Cogn. Emot.* 21, 391–403. doi:10.1080/02699930600625081
- Volkow, N.D., Fowler, J.S., Ph, D., Wang, G., Telang, F., Logan, J., Jayne, M., Ma, Y., Pradhan, K., Wong, C., Swanson, J.M., 2010. Cognitive Control of Drug Craving Inhibits Brain Reward Regions in Cocaine Abusers. *Neuroimage* 49, 2536–2543. doi:10.1016/j.neuroimage.2009.10.088.Cognitive
- Voon, V., Irvine, M. a., Derbyshire, K., Worbe, Y., Lange, I., Abbott, S., Morein-Zamir, S., Dudley, R., Caprioli, D., Harrison, N. a., Wood, J., Dalley, J.W., Bullmore, E.T., Grant, J.E., Robbins, T.W., 2014. Measuring “waiting” impulsivity in substance addictions and binge eating disorder in a novel analogue of rodent serial reaction time task. *Biol Psychiatry.* 75, 148–155. doi:10.1016/j.biopsych.2013.05.013

- Weafer, J., Baggott, M., de Wit, H., 2013. Test-retest reliability of behavioral measures of impulsive choice, impulsive action, and inattention. *Exp Clin Psychopharmacol.* 21, 475–481. doi:10.1016/j.biotechadv.2011.08.021
- Whiteside, S.P., Lynam, D.R., 2001. The five factor model and impulsivity: Using a structural model of personality to understand impulsivity. *Pers Individ Dif.* 30, 669–689. doi:10.1016/S0191-8869(00)00064-7
- Wilcox, C.E., Pommy, J.M., Adinoff, B., 2016. Neural Circuitry of Impaired Emotion Regulation in Substance Use Disorders. *Am. J. Psychiatry* 173, 344–61. doi:10.1176/appi.ajp.2015.15060710
- Wilson, K.M., Joux, N.R. De, Finkbeiner, K.M., Russell, P.N., Helton, W.S., Zealand, N., Factors, H., 2016. The effect of task-relevant and irrelevant anxiety-provoking stimuli on response inhibition. *Conscious. Cogn.* 42, 358–365. doi:10.1016/j.concog.2016.04.011
- Wingrove, J., Bond, A.J., 1997. Impulsivity: A state as well as trait variable. Does mood awareness explain low correlations between trait and behavioural measures of impulsivity? *Pers Individ Dif.* 22, 333–339. doi:10.1016/S0191-8869(96)00222-X
- Winstanley, C.A., 2011. The utility of rat models of impulsivity in developing pharmacotherapies for impulse control disorders. *Br J Pharmacol.* 164, 1301–1321. doi:10.1111/j.1476-5381.2011.01323.x
- Winstanley, C.A., Olausson, P., Taylor, J.R., Jentsch, J.D., 2010. Insight into the relationship between impulsivity and substance abuse from studies using animal models. *Alcohol Clin Exp Res.* 34, 1306–1318. doi:10.1111/j.1530-0277.2010.01215.x
- Xie, C., Li, S.J., Shao, Y., Fu, L., Goveas, J., Ye, E., Li, W., Cohen, A.D., Chen, G., Zhang,

- Z., Yang, Z., 2011. Identification of hyperactive intrinsic amygdala network connectivity associated with impulsivity in abstinent heroin addicts. *Behav Brain Res.* 216, 639–646. doi:10.1016/j.bbr.2010.09.004
- Yuen, K.S., Lee, T.M., 2003. Could mood state affect risk-taking decisions? *J. Affect. Disord.* 75, 11–18. doi:10.1016/S0165-0327(02)00022-8
- Zadra, J.R., Clore, G.L., 2011. Emotion and perception: The role of affective information. *Wiley Interdiscip. Rev. Cogn. Sci.* 2, 676–685. doi:10.1002/wcs.147
- Zeeb, F.D., Winstanley, C. a, 2011. Lesions of the basolateral amygdala and orbitofrontal cortex differentially affect acquisition and performance of a rodent gambling task. *J Neurosci.* 31, 2197–2204. doi:10.1523/JNEUROSCI.5597-10.2011
- Zhang, S., Hu, S., Chao, H.H., Ide, J.S., Luo, X., Farr, O.M., Li, C.-S.R., 2014. Ventromedial prefrontal cortex and the regulation of physiological arousal. *Soc. Cogn. Affect. Neurosci.* 9, 900–8. doi:10.1093/scan/nst064
- Zhang, S., Hu, S., Hu, J., Wu, P.-L., Chao, H.H., Li, C.R., 2015. Barratt Impulsivity and Neural Regulation of Physiological Arousal. *PLoS One* 10, e0129139. doi:10.1371/journal.pone.0129139
- Zuckerman, M., 1984. Sensation seeking: A comparative approach to a human trait. *Behav. Brain. Sci* 7, 413. doi:10.1017/S0140525X00018938
- Zuckerman, M., 1969. Theoretical formulations: 1., in: Zubek, J.P. (Ed.), *Sensory Deprivation: Fifteen Years of Research*. Appleton-Century-Crofts, New York, pp. 407–432. doi:10.1016/j.npep.2004.07.005
- Zuckerman, M., Eysenck, S., & Eysenck, H. J. (1978). Sensation seeking in England and America: cross-cultural, age, and sex comparisons. *Journal of Consulting and Clinical*

Psychology, 46(1), 139–149. doi:10.1037/0022-006X.46.1.139