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**Psychophysics of perceptual
inference and the computational
underpinnings of intolerance of
uncertainty**

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Abstract

This thesis investigates the mechanisms and computational underpinnings of how people respond to uncertainty, with a specific focus on intolerance of uncertainty (IU), a trait characterised by the perception of uncertain situations as threatening. Given that minimising uncertainty is a fundamental aspect of perception and behaviour, this research explores IU through the framework of Bayesian inference, whereby the brain generates predictions to interpret sensory input.

Across seven experiments, behavioural responses and physiological measures (EEG and pupillometry) were used to investigate responses to uncertainty elicited through auditory stimuli. Key findings revealed that increasing the precision of sound sequences does not necessarily make otherwise equivalent sensory changes more surprising or easier to detect, and in some cases has the opposite effect. Additionally, under uncertain conditions with potential aversive outcomes, individuals with high IU anticipate upcoming stimuli to be more aversive, and also perceived aversive stimuli as more aversive than people with low IU. Unexpectedly, under particular conditions of uncertainty, people with high IU gave more nuanced and appropriate responses to the cues and stimuli presented during the experiments, and demonstrated more precise and accurate temporal expectations in their physiological responses than people with low IU.

From these findings, a pattern of results emerged that suggest that people with high IU experience uncertainty with greater sensitivity, which might lead to both advantageous and deleterious consequences. I conclude by questioning whether intolerance of uncertainty could be reframed as 'sensitivity to uncertainty', which would reflect a more balanced view of how these individuals respond to uncertainty, thereby potentially reducing stigma, highlighting the adaptive potential, and recognising associated advantages.

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i. List of Abbreviations

ASD = autism spectrum disorder

CNV = contingent negative variation

EEG = electroencephalogram

GAD = generalized anxiety disorder

IU = intolerance of uncertainty

IUS-12 = The 12-item intolerance of uncertainty scale as outlined by Carleton, Norton & Asmundson (2007)

IUS-27 = The 27-item intolerance of uncertainty scale as outline by Freeston et al. (1994)

MMN = mismatch negativity

OCD = obsessive-compulsive disorder

PSC = perceived size of change response (or perceived salience of change response)

UAMA = the uncertainty and anticipatory model of anxiety as outlined by Grupe and Nitschke (2013)

ULL = uncomfortable loudness level

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1. Introduction

1.1. Perceptual Inference

Historically perception has been assumed to be the result of passive (bottom-up) processing of external stimuli, for example, according to behaviourists such as Watson (1913), or structuralists such as Wundt (1896). However, perception is now broadly considered to involve active (top-down) processes, where incoming sensory information is used to update internal models of the environment (Parr, Pezzulo, and Friston, 2022). Perceptual inference, this process of comparing incoming sensory information against our existing representations of the world, can be understood as a form of Bayesian inference, with our brains operating as inference machines. Various generative accounts of the Bayesian brain exist with many similarities, such as those falling under the umbrellas of active sensing (Schroeder et al., 2010), the free energy principle (Friston, 2010; Friston and Kiebel, 2009), and predictive coding (Rao and Ballard, 1999).

A fundamental principle common to these generative models is the optimisation of inference under conditions of uncertainty. Using Bayes' theorem (see Figure 1), the brain constantly makes inferences by weighing its existing beliefs (*priors*, akin to hypotheses) against the likelihood that incoming stimuli support these hypotheses (*likelihood*), resulting in an updated belief (*posterior*). Put another way, perception results from a combination of internal representations of the environment (predictions generated from *priors*) with incoming sensory information (*likelihood* that this pattern of sensory information corresponds with a true environmental state).

$$P(H|E) = \frac{P(E|H)P(H)}{P(E)}$$

Figure 1. Bayes' theorem. Bayes' theorem to derive the '*posterior*' probability [P(H|E)] of the hypothesis (H) being true given the incoming evidence (E), from the '*prior*' probability [P(H)] of the hypothesis, the '*marginal likelihood*' [P(E)] of observing the evidence, and the '*likelihood*' [P(E|H)] of observing the incoming evidence assuming the hypothesis is true.

To optimise inference, prior predictions and sensory input are both weighted by their *precision*, which mathematically is defined as the inverse of variance. Incongruence between prior predictions and sensory input is termed *prediction error* (mismatch between prior and

likelihood, see Figure 2), also known as *surprise*. It is widely assumed that subjective and objective surprise responses are proportional to both the precision of the likelihood (sometimes termed *precision-weighted prediction error – PWPE*), and the precision of the prior (with the term *surprise* referring to the improbability of the sensory input based on the prior). Surprise is mathematically defined as the negative log probability of the sensory input according to the prior, and this accords well with the lay intuitive notion of surprise as the cognitive/affective sense of the unexpectedness of an event or stimulus. Perception is the act of minimising surprise through continuous updating of internal models. As well as surprise (as in prediction error), another important quantity in this process is *Bayesian surprise*, which is the extent to which the internal model is updated on account of the stimulus (i.e. the difference between the posterior and the prior, see Figure 2), essentially measuring how much this new information has changed our beliefs. As with surprise more generally, Bayesian surprise has both subjective (Baldi and Itti, 2010) and objective correlates (Sedley et al. 2016).

Mathematically, precision is the inverse of variance. In the brain, *estimated precision* is encoded largely by postsynaptic gain (Friston, 2008; Feldman and Friston, 2010). As such, precision refers to two related but distinct phenomena: the statistical properties of the sensory input from the environment, and the brain's estimate of the reliability or importance of the signal from the environment. It is often assumed that these two phenomena are closely correlated; an assumption I test in Experiments 1-4 by manipulating the environmental precision, or precision of sensory input, and measuring its effect on the perception of sensory change.

Bayesian models have been used not just to describe perception, but also decision making. Similar to predictive processing models of perception, models of Bayesian decision theory provide a framework for action selection under uncertainty. Bayesian decision theory posits that agents should make choices to maximise expected utility, defined as the probability of an outcome multiplied by its subjective reward ($P(\text{reward}) * U(\text{reward})$). However, real world human decision making has been shown to deviate from this model in economics and psychology. For example, Kahneman and Tversky's (1979) Prospect Theory explains how individuals tend to be risk averse to the detriment of utility maximisation, by preferring small certain rewards over much larger uncertain rewards. The risk aversion

described here likely reflects a broader uncertainty aversion, with individuals showing consistent preference for reduced uncertainty, potentially at the cost of expected utility.

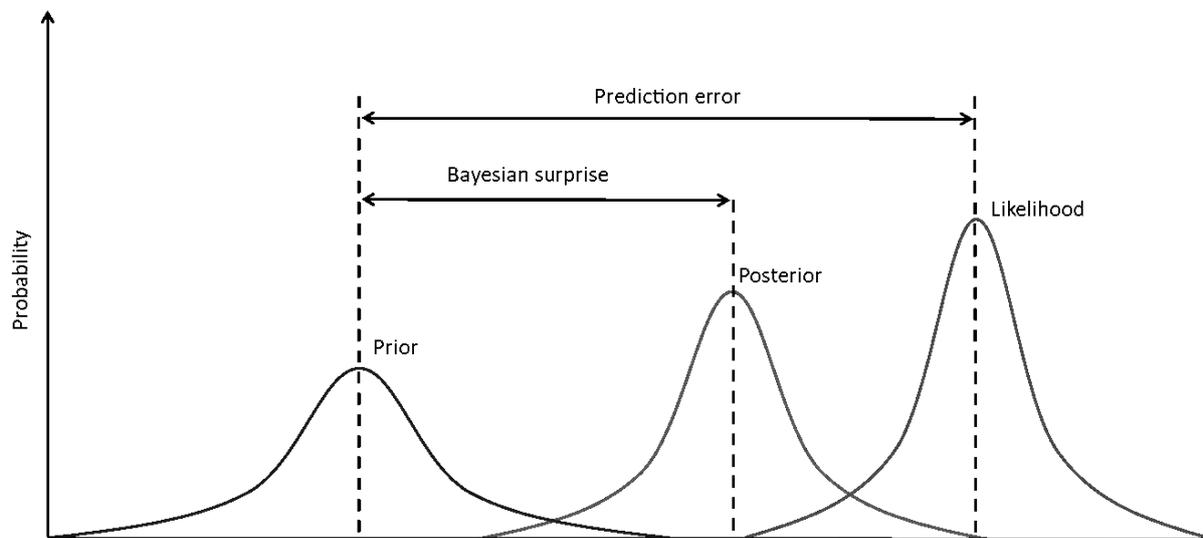


Figure 2. Bayesian Inference visualised. Precision weighting of the prior (blue curve) and the likelihood (red curve) dictates the mean and precision of the posterior. The x axis indicates a particular perceptual dimension. The y axis indicates probability. The difference between the prior and the likelihood is the prediction error. The difference between the prior and the posterior is the Bayesian surprise.

There is a growing body of empirical evidence to support predictive processing frameworks such as predictive coding. For example, Sedley et al. (2016) directly recorded electrical activity from the auditory cortex whilst participants were played semi-predictable stimuli requiring constantly updating predictions. From this they discovered distinct electrical activity relating to surprise (local field potential oscillations in the gamma band, >30Hz), updating predictions i.e. Bayesian surprise (beta band, 12-30Hz), and prediction precision (alpha band 8-12Hz). Various studies have used event-related potential mismatch negativity (MMN) as a measure of prediction error in response to deviant visual and auditory stimuli; MMN is now widely considered to quantitatively encompass prediction error in a predictive processing context (see reviews: Garrido et al., 2009; Stefanics, Kremláček and Czigler, 2014). Garrido, Sahani, and Dolan (2013) demonstrate that the size of mismatch negativity to a particular deviant depends on the precision of the background tone sequence the deviant is embedded in. Further literature supports predictive processing frameworks using behavioural evidence (see review by Summerfield & de Lange, 2014), neural correlates (see review by Arnal & Giraud, 2012), and associations with neural architecture (e.g. Bastos, 2012).

Predictive processing frameworks, such as predictive coding, have revolutionised our understanding of perception, and subsequent research has demonstrated their utility as a basis to understanding psychological symptoms and disorders. For example, hallucinations were hypothesised to result from priors with inappropriately high precision outweighing incoming sensation resulting in distorted sense of perception (Lyndon and Corlett, 2020; Corlett et al., 2019; Powers, Kelley and Corlett, 2016). Empirical research has then demonstrated a relationship with over-weighted priors and hallucination in simulated subjects (Benrimoh et al., 2019; Adams et al., 2014), neurotypical people (Alderson-Day et al., 2017; Powers, Mathys and Corlett, 2017), people with psychotic illnesses (Kafadar et al., 2020; Cassidy et al., 2018; Powers, Mathys and Corlett, 2017; Teufel et al, 2015), and people with Lewy-body disease (Zarkali et al., 2019). The importance of predictive processing is not limited to understanding clinical disorders, but also understanding the normal functioning of perceptual systems and the assumptions and biases upon which these are founded. Much research focuses on the theoretical bases and mathematical principles behind predictive processing, and their neural correlates (e.g. Friston, 2010; Rao and Ballard, 1999). It is also important to understand the psychophysics (i.e. the relationships between the physical and statistical properties of stimuli and perception) of predictive processing, in order to test these assumptions, expose inherent biases, and provide a bridge between experimental paradigms, neural correlates and subjective human experience.

Ultimately, Bayesian inference is a method of optimising judgements based on inherently uncertain information. Navigating the world under uncertainty is at the core of predictive processing theories of perception, and yet people find uncertain conditions aversive or even intolerable. Large proportions of people are intolerant of uncertainty in terms of stimuli, experiences, and events. However, literature exploring intolerance of uncertainty in terms of predictive processing is limited. In light of this gap, I aim to explore the computations of intolerance of uncertainty through a lens of predictive processing theories of perception.

1.2. Intolerance of Uncertainty

1.2.1. Definitions and measures of intolerance of uncertainty

Intolerance of uncertainty (IU) is a dispositional characteristic that results from a set of negative beliefs about uncertainty and its implications, leading to a tendency to react negatively on an emotional, cognitive, and behavioural level to uncertain situations and events. IU as a construct was described initially as “the tendency of an individual to consider the possibility of a negative event occurring as unacceptable, irrespective of the probability of occurrence” (Carleton, Norton & Asmundson, 2007). This definition was later refined to more clearly differentiate IU from similar but not identical constructs such as ‘need for cognitive closure’ (defined as an “individual’s desire for a firm answer to a question and an aversion toward ambiguity”), ‘fear of the unknown’ (defined as “an individual’s propensity to experience fear caused by the perceived absence of information at any level of consciousness or point of processing”) (Carleton, 2016). The commonly accepted definition of IU is now “an individual’s dispositional incapacity to endure the aversive response triggered by the perceived absence of salient, key or sufficient information, and sustained by the associated perceptions of uncertainty” (Carleton, 2016). An individual with high IU is not necessarily overestimating the probability of a negative outcome from an uncertain situation but has a tendency to experience the uncertainty itself as aversive, whether the outcome is negative or not (del Valle et al., 2020); i.e. “people who are intolerant of uncertainty are likely to interpret all ambiguous information as threatening” (Carleton, Norton & Asmundson, 2007).

There are likely advantages associated with being intolerant of uncertainty. For example, if one is starving any certain food reward would outweigh an uncertain one. This kind of risk-averse behaviour is often explored in economic models of decision-making, for example when individuals must balance the mean and variance of potential payoffs (Kim, 2021). The advantages and disadvantages of IU are explored further in 1.2.2. Intolerance of uncertainty (IU) as a construct was initially developed as a tool for understanding worry after the redefinition of generalized anxiety disorder (GAD) identified “unrealistic and excessive anxiety and worry” as the primary diagnostic criterion (Diagnostic and statistical manual of mental disorders, 1987). Freeston et al. (1994) first developed a measure of intolerance of uncertainty, the intolerance of uncertainty scale (IUS-27) as a self-reporting tool for investigating worry in the context of generalized anxiety disorder. The IUS-27 consists of 27

questions, using a Likert scale ranging from 1 (not at all characteristic of me) to 5 (entirely characteristic of me), that assesses 5 different factors surrounding IU. These factors are given, with one example question that exemplifies the factor, as follows. Behavioural attempts to prevent uncertainty (“One should always look ahead to avoid surprises”), inaction in the face of uncertainty (“When it is time to act, uncertainty paralyzes me”), an emotional frustration (“It’s unfair not having any guarantees in life”) or stress response (“Uncertainty makes me uneasy, anxious or stressed”), and a cognitive interpretation that being uncertain is a negative trait (“Being uncertain means that a person is disorganized”).

As a parallel to self-report measures, behavioural tasks have been developed to assess responses to uncertainty and risk in a more empirical manner. One widely used paradigm is the Balloon Analogue Risk Task (BART) (Lejuez et al., 2002), which quantifies individual differences in risk-taking under uncertainty. In this task, participants pump up a virtual balloon, earning a small monetary reward for each pump. However, the balloon can burst unpredictably with any pump, resulting in the loss of all earnings for that balloon. The task therefore gives a measure of the individual’s risk-taking behaviour, offering insight into their tolerance for escalating uncertainty. Individuals with high intolerance of uncertainty tend to engage in less risky behaviour by stopping pumping earlier to avoid potential loss (Bartoszek et al., 2022). The BART task provides a complement to questionnaire-based IU measures, by demonstrating how individuals behave in dynamic, uncertain environments, rather than how they report they respond to uncertainty.

Since its first development, understanding of intolerance of uncertainty has grown from being a measure of worry as a facet of GAD, to an overarching transdiagnostic trait that predisposes people to a range of psychiatric disorders outside of GAD; these are explored in more detail in section 1.2.2, but include depression (Bakioglu et al. 2020; Smith et al. 2020; Ferriera et al, 2020), autism (Keefer et al. 2017), and post-traumatic stress disorder (Oglesby et al 2015). As understanding of intolerance of uncertainty developed, the accepted measure of IU, the IUS-27, began to be more heavily scrutinised. The internal consistency of the IUS-27 was found to be excellent (0.91), and the IUS-27 was used as the accepted measure of IU for over a decade. However, a growing body of literature questioned the validity of the IUS, in particular the high levels of inter-item correlation and factor instability. For example, Carleton, Sharpe & Asmundson (2007) tested the fit of single, four and five factor models and

found none to of these to demonstrate adequate fit. The authors also concluded that there was significant redundancy from semantic overlap between items. Different ideal factor structures emerged when assessed with different languages and cultures. It was previously suggested that a reduced factor model would minimise cross loading and increase internal consistency (Buhr & Dugas, 2002), and a reduction in items will improve factor stability without reducing reliability (Norton 2005). A review of nine exploratory or confirmatory factor analyses of the IUS suggested that a two-factor structure was most likely to be the most stable (Birrel et al. 2011).

The IUS-27 was reduced to a 12 item, 2-factor questionnaire, after removing items that overlapped with GAD (IUS-12, Carleton, Norton & Asmundson, 2007). The first factor, prospective IU, describes a propensity to reduce uncertainty with information-seeking behaviour, or a desire to seek predictability; it is considered to reflect the cognitive aspects of IU and is more closely associated with obsessive-compulsive disorder and generalized anxiety disorder. The second factor, inhibitory IU, describes avoidance or inability to act when confronted with uncertainty; it is considered to reflect the behavioural side of IU and is more closely associated with social anxiety disorder, panic disorder and depression (Carleton 2012, McEvoy & Mahoney 2012). Khawaja & Yu (2010) used both clinical and non-clinical samples to validate both the 27-item and 12-item IUS. They found excellent convergent validity between the two scales, and demonstrated good test-retest reliability and internal consistency. As the IUS-12 has reduced redundancy, this is what the authors recommend and subsequently has been the most widely used.

1.2.2. Negative and positive associations with IU

Initially understood to be fundamentally associated with GAD (Dugas et al., 1997), intolerance of uncertainty is now understood to be a trans-diagnostic tool associated with various psychological disorders including: generalized anxiety disorder (Buhr & Dugas 2006, Freeston et al. 1994), OCD (Wheaton et al. 2020, McEvoy & Mahoney 2012), social phobia, depression, panic disorder and agoraphobia (McEvoy & Mahoney 2012), eating disorders (Renjan et al. 2015), PTSD (Oglesby et al 2015), autism (Keefer et al. 2017) and prolonged grief (Boelen et al. 2015). In addition to being present in individuals with various disorders, IU also indicates risk for the future development of anxiety symptoms and can even predict the

efficacy of future treatments. For example, IU predicted efficacy of a modified cognitive-behavioural therapy for children with Autism-spectrum disorder, as well as reported levels of anxiety post-therapy (Keefer et al. 2017); pre-trauma IU levels correlated with post-traumatic stress symptoms in individuals with varying exposure to a campus shooting, even after covarying for pre-trauma levels of anxiety sensitivity (Oglesby et al 2015). There is also a growing body of literature that has found high IU individuals to have a reduced extinction of fear (Morriss et al. 2016, Morriss et al. 2015, Dunsmoor et al. 2015). A review of current emotion literature highlights the importance of the perception and identification of unknowns in emotional processing (Carleton 2016). Literature suggests that fear of the unknown and IU are cognitive processes that are key casual factors underpinning all anxiety disorders through amplification of emotional experience (Freeston & Komes, 2023).

Individuals with high IU have been shown to be at greater risk of various mental health problems worldwide as a result of the increased uncertainty caused by the COVID-19 pandemic; e.g. in Greece (Parlapani et al. 2020), Brazil (Ferriera et al. 2020), Turkey (Deniz 2021; Karatas & Tagay 2021; Bakioglu et al. 2020; Satici et al. 2020) and the USA (Wheaton et al. 2021; Tull et al. 2020; Smith et al. 2020). In particular, intolerance of uncertainty in relation to the COVID-19 pandemic is shown to be positively correlated with: eating disorders (Scharmer et al. 2020), obsessive-compulsive disorder (Wheaton et al. 2020), health anxiety and perceived vulnerability to disease (Tull et al. 2020; Wheaton et al. 2020), loneliness in the elderly (Parlapani et al. 2020), depression (Bakioglu et al. 2020; Smith et al. 2020; Ferriera et al, 2020) stress (Bakioglu et al. 2020; Smith et al. 2020; Ferriera et al, 2020), and anxiety (Bakioglu et al. 2020; Smith et al. 2020; Ferriera et al, 2020). Additionally, intolerance of uncertainty in relation to the COVID-19 pandemic is shown to be negatively correlated with resilience to stress (Karatas & Tagay, 2021), self-compassion (Deniz, 2021), and extinction of social threat (Wake et al. 2021).

The majority of literature exploring IU focuses on the negative associations with the trait, such as its associations with various psychiatric disorders, and its inhibitory nature in uncertain situations. There is a dearth of research that investigates any potential positives aspects of intolerance of uncertainty that could explain how high IU has remained such a common trait. Evidenced by large datasets of undergraduate (e.g. n = 967 in the Netherlands (Helsen et al., 2013), n = 506 in Australia (Shihata et al., 2018), n = 696 in China (Yao et al.,

2020)) community (e.g. n = 704 in Brazil (Kretzmann & Gauer, 2020), n = 2451 in Canada (Sexton & Dugas 2009)) and clinical populations (e.g. n = 463 in Australia, (McEvoy & Mahoney, 2011)), IU is understood to be a spectrum within which all people fall, with a relatively normal distribution. As large proportions of the general population likely have moderate or high intolerance of uncertainty, it seems unlikely that IU is, or has been in previous contexts, solely a negative trait. One study exploring the interaction between intolerance of uncertainty and startle response to perceived threat found that participants with high IU had a smaller startle response under conditions of temporally uncertain threat (Nelson and Shankman, 2011). The authors found that a lack of perceived control over anxiety-related events mediated this relationship and highlight that the inhibitory qualities of intolerance of uncertainty could explain this smaller startle response. This finding is one of few that exhibits any potential positive of high intolerance of uncertainty that could explain its prevalence.

Carleton (2012) argued that whilst excessive IU is maladaptive, from an evolutionary viewpoint mild or moderate intolerance of uncertainty likely served an adaptive advantage when in a novel environment. When confronted with stimuli, the earliest analysis in the brain has been argued to simply determine if a stimulus is a threat or not (Matthews & MacLeod 1994; Matthews & MacLeod 2005). Carleton (2012) argues that perceiving uncertain environments or stimuli as a threat, and activating the autonomic nervous system early, would have been adaptive in terms of protection from predators, but in modern society IU affects survival solely by increasing risk of related disorders. However, I would argue that, even in modern society, some aspects of intolerance of uncertainty, such as a sensitivity to uncertainty or prospective behaviour towards reducing future uncertainty, would likely confer benefits which help our understanding of the prevalence of IU.

1.2.3. Precursors of intolerance of uncertainty

The developmental and neural underpinnings of IU are currently unknown. However, various studies have identified key factors in relation to the development and effects of intolerance of uncertainty in relation to related anxiety disorders, and neural correlates have been found that relate to either processing of uncertainty, anxiety in relation to uncertainty, and intolerance of uncertainty. Botessi et al. (2020) used a network analysis approach to

reveal the internal structure of IU. The authors hypothesise that discomfort occurring when confronted with surprise, and planning ahead to prevent uncertainty, are the key factors in the development of IU (Bottesi et al. 2020). Grupe and Nitschke (2013) propose an uncertainty and anticipatory model of anxiety (UAMA) that describes five potential mechanisms to explain how uncertainty can lead to excess anxiety, which seem particularly relevant to understanding the development and/or effects of intolerance of uncertainty. These five processes are as follows. 1. The severity and likelihood of an uncertain threat are inflated. 2. Hypervigilance is shown to an uncertain situation which increases attention shown to a potential threat. 3. The capacity to identify a potential threat as safe, and resolve the uncertainty, is impaired. 4. Individuals exhibit cognitive or behavioural avoidance of an uncertain situation. 5. Reactivity to uncertain threat is heightened. These processes to explain how uncertainty can lead to anxiety helped form hypotheses of intolerance of uncertainty that I test in my experiments. Experiments 5 and 6 (see Chapter 3) investigated how prospective estimates of severity and likelihood of uncertain threats differ between high and low IU participants. I hypothesised that people with high intolerance of uncertainty, when faced with an uncertain situation with potential negative outcomes, will over-anticipate the likelihood that aversive outcomes will occur, and the intensity of the aversive stimulus. The second process is tested in Experiment 7, which used physiological measures as indicators of vigilance under changing conditions of uncertainty, although these, although this is not necessarily under conditions of threat.

The third process highlights the idea of safety signals failing to relieve anxiety in uncertain situations. Converse to the assumption that noxious experiences are neurally underpinned by signals indicating danger or aversion, it has been suggested that anxiety disorders relate to aversive responding to conditions that typically signal safety, leading to lack of inhibition of fear and threat-based responses to safe stimuli (Craske and Wolitzky-Taylor, 2013; Lohr et al., 2007). It has been shown that during conditions that would typically confer safety, increased aversive responding was found in people with anxiety disorders (Lissek et al., 2010; Craske et al., 2008; Grillon et al., 1998) and people at risk of developing anxiety disorders (Craske et al., 2009; Reeb-Sutherland et al., 2009). One study found that intolerance of uncertainty moderates the relationship between panic disorder and a failure to inhibit aversive responding during safety (Gorka et al., 2014). This is used to develop a

hypothesis that people with intolerance of uncertainty are less able to understand or believe safety signals. This hypothesis is tested in Experiment 5 (Chapter 3), where I explore the effects of explicit safety cues on the anticipation of potentially aversive events in relation to intolerance of uncertainty.

The fourth process of how uncertainty can lead to anxiety (Individuals exhibit cognitive or behavioural avoidance of an uncertain situation (Grupe & Nitschke, 2013)) shows noticeable overlap with aspects of intolerance of uncertainty. In particular, the factors of the IUS-27 'behavioural attempts to prevent uncertainty', and the inhibitory factor of the IUS-12 that encompasses avoidance of uncertainty and inability to act when confronted with uncertainty. Avoidance behaviours intended to minimise or prevent exposure to uncertainty are particularly poor solutions for people with high IU for two main reasons. Firstly, avoidance behaviours are strongly linked to paralysis in the face of uncertainty; paralysis in the face of uncertainty and avoidance behaviours themselves are both thought to increase and maintain worry (Bottesi et al., 2020; Berenbaum, Bredemeier & Thompson, 2008). Secondly, the uncertainty produced by daily life cannot be reduced to zero, and when confronted with this uncertainty individuals will likely be unequipped to deal with it. Exposure to feared stimuli is shown to be one of the most effective ways to build long term coping strategies for dealing with said stimuli (Foa & Kozak 1986). For example, exposure therapy has shown to be a crucial aspect of treatment in panic disorder and agoraphobia (Meuret et al. 2012), and in anxiety disorders, OCD and PTSD (Foa & McLean, 2016).

1.2.4. Neural correlates of intolerance of uncertainty

Various studies have found relevant neural correlates of IU as an overall construct, with specific factors within IU (i.e. inhibitory or prospective IU), or the relationship between IU and related processes and disorders. Structural MRI studies found a positive relationship between IU and grey matter volume in the right superior temporal pole (Hilbert et al. 2015) which is suggested to imply enhanced emotional processing in high IU individuals. Similarly, a positive correlation was found between IU and grey matter volume in the striatum (the putamen in particular) (Hilbert et al. 2015, Kim et al. 2017), which is suggested by the authors to represent the neuroanatomic underpinning of an increased desire for predictability.

Literature suggests there is a relationship between IU and activity in the right anterior insula, which is thought to be associated with uncertainty and risk, interoceptive awareness, sensitivity to negative emotional states, and the anticipation of harm or loss (Paulus et al., 2003). Shankman et al., (2014) found unpredictable negative stimuli relates to increased activity in the right anterior insula. Inhibitory (but not prospective) IU positively correlated with this activity. Somerville et al. (2013) investigated neural activity in response to both sustained and transient threat. They found that only sustained threat correlated with increased activity in the ventral basal forebrain and anterior insula, and higher total IU score correlated with activity elicited by sustained threat in the right insula. There is also literature to suggest a relationship with the bilateral anterior insula. A positive correlation was found between total IU score and bilateral insula activation, elicited by uncertainty in face emotion (Simmons et al., 2008), and uncertainty elicited by the anticipation of and response to aversive pictures (Oathes, Hilt, & Nitschke, 2015). Gorka et al. (2016) found a positive correlation between bilateral anterior insula activation and prospective IU elicited by uncertain rewards.

Literature also suggests a positive correlation with IU and activation of the amygdala, which is thought to be involved in assigning emotional salience to stimuli, as well as processing fear and emotional stimuli related to threat detection (Hariri et al., 2003). Somerville et al. (2013) found that only transient threat (and not sustained threat) correlated with increased activity in the amygdala and midbrain, which related to a higher total IU score. Research found a similar correlation between total IU score and activity in the amygdala in adult women anticipating uncertain images (Scheinle et al., 2010). In response to uncertainty elicited in a decision-making task, adolescents with anxiety-based disorders were shown to display increased activity in the left and right amygdala, and the anterior cingulate cortex, only if they had high IU (Krain et al., 2008). Further research in adolescents has shown positive relationships between high IU and activity in the anterior cingulate cortex (Krain et al., 2016; Krain et al., 2018), but in adults a negative correlation was shown between IU and anterior cingulate cortex activation.

1.2.5. Predictive Processing and IU

There is limited literature that hypothesises how intolerance of uncertainty as a concept could be understood in terms of predictive processing. Carleton (2016) suggests IU

can be understood as an individual's inability to tolerate prediction errors or deviations from expected outcomes, and therefore leads to a heightened response to unexpected or ambiguous stimuli. Hirsh, Mar, and Peterson (2012) suggest people with high IU may struggle to update their internal models due to an over-reliance on prior predictions, (or an under-reliance on the incoming likelihood) and therefore experience higher levels of prediction errors. Finally, Grupe and Nitschke (2013) posit that people with high IU overestimate the likelihood of negative outcomes and experience greater distress from prediction errors, which results in heightened anticipation of future threats. These theories align with the idea of the predictive brain constantly trying to reduce uncertainty and minimize error, but without empirical evidence to support any particular hypothesis there is a clear gap where future research could be directed.

1.3. Uncertainty beyond IU

Predictive processing frameworks have been instrumental in a paradigm shift about understanding perception as an active, top-down process. One integral idea common amongst these frameworks is that behaviour, perception, and even learning are all results of the brain attempting to minimise uncertainty. The *Free Energy Principle* essentially posits that biological systems seek to minimise a quantity called '*free energy*' in order to maintain internal states and control their environment (Friston and Stephan, 2008; Friston, 2010). Free energy is a mathematical measure that represents the difference between predicted sensory inputs and actual sensory inputs i.e. it essentially represents the extent of uncertainty about the environment. Free energy also incorporates another component, complexity, which represents the changing of priors (similar to Bayesian surprise). The brain is continuously working to minimise prediction errors (and therefore free energy) through two main methods; adjusting internal models to better represent the environment (i.e. prediction updating, or *perception*), and changing the environment or the body's interaction with it (i.e. behaviour, or *action*).

Minimising uncertainty is now understood to be one of the core attributes of perception and behaviour; intolerance of uncertainty, therefore, could relate to an aberration in, or otherwise divergent, predictive processing. From an evolutionary perspective, it seems intuitive that adaptive bias would promote caution to uncertainty and increase the probability

an individual would overestimate (or at least prepare for) negative outcomes from uncertain situations.

Animal studies offer support for this idea that uncertainty aversion may be an evolutionarily conserved aspect of cognition. One classic paradigm is observing behaviour, in which animals are given the option to obtain information about upcoming outcomes without affecting the outcome itself. Animals often prefer to receive information in advance, even when it provides no benefit, which suggests an intrinsic value attached to uncertainty reduction (Dinsmoor, 1983). Similarly, midbrain dopamine neurons in macaques have been shown to encode a preference for advanced information about rewards, with stronger firing to cues that reduce uncertainty (Bromberg-Martin & Hikosaka, 2009). These findings suggest that the neural architecture of reward processing is sensitive to uncertainty, and that non-human animals may experience a form of uncertainty aversion. This supports the idea that uncertainty minimisation may be intrinsically motivated, possibly due to its role in maintaining adaptive predictive models of the environment.

There is also some limited empirical evidence to support this in humans. Sarinopoulos et al. (2010) used fMRI to explore the neural response to aversive pictures when preceded by either an uncertain cue (preceded aversive or neutral pictures) or a certain cue (always preceded aversive pictures). Insula and amygdala responses to aversive pictures were larger after an uncertain cue, and neural activity in the anterior cingulate cortex was inversely correlated to this. Approximately 75% of participants overestimated the frequency of aversive stimuli after uncertain cues, and the neural activity in the insula and anterior cingulate cortex correlated with this.

Even outside of high IU groups, people often display an aversion to uncertain situations with the potential of a negative outcome, to a greater degree than situations that have a guaranteed negative outcome. Increased startle response has been shown towards cues that indicate an upcoming shock of unknown intensity, as opposed to a cue that indicates a guaranteed shock of high intensity (Shankman et al., 2011). Similarly, increased startle potentiation was shown in response to uncertain cues that indicated an incoming shock in 60% or even 20% of trials, in comparison to cues indicating a shock in 100% of trials (Hefner and Curtin, 2011).

Herry et al., (2007) found that temporal uncertainty of neutrally valent auditory stimuli was sufficient to result in sustained neural activity in the amygdala and induce avoidance and anxiety-like behaviours in both human and mouse participants. The authors suggest that aversive outcomes are not necessary to increase anxiety, and that uncertainty about neutral stimuli is sufficient. However, a study investigating the anticipation of two different levels of noxious stimuli, an airblast to the larynx (less aversive) and electric shocks (more aversive), found that unpredictable contexts increased startle reflex in the more aversive stimuli group, but not in the less aversive stimuli group (Grillon et al., 2004). Here the authors suggest that uncertainty about upcoming stimuli requires the stimuli to be sufficiently noxious before the uncertain cues themselves become perceived as aversive. The conclusions of these two studies seem contradictory, although it is possible aversity is not necessary for inducing anxiety under uncertainty, but when present it interacts to increase anxiety. Although clinical literature (e.g. Mofrad et al., 2020) suggests that it is a requirement for an individual to experience both perceived threat and uncertainty for them to experience anxiety. These two studies differ in their methodologies and level of analysis (i.e. looking at responses to uncertainty at the level of neural activity vs behavioural anxiety responses). Another potential explanation for these different conclusions is that the nature of the uncertainty induced in these two studies differs. Although uncertainty as an overarching concept seems consistent, it is likely that different forms of uncertainty are processed and interpreted distinctly by entirely different networks in the brain; e.g. the temporal uncertainty elicited in Herry et al. (2007) likely relates to activity in the right anterior insula cortex, which has been shown to have increased activity when anticipating temporally unpredictable images, and the factor of inhibitory intolerance of uncertainty (Shankman et al., 2014). The uncertainty relating to consequences of a potential outcome has been shown through a lesion study to relate to the lateral prefrontal cortex in both cases where outcome probabilities are known (expected uncertainty) and unknown (unexpected uncertainty) (FeldmanHall et al., 2019). It is worth noting that both temporal and outcome uncertainty are common to the amygdala and insula (Sarinopoulos et al., 2009), regions that integrate emotional and cognitive information, yet the specific patterns of activation may differ.

With there being different types of uncertainty that likely have distinct neural mechanisms, it is perhaps important to explore how different types of uncertainty relate to

intolerance of uncertainty. Self-reported questionnaire measures of IU do not distinguish between different types and complexities of uncertainty people face day to day, and they do not capture how individuals perceive and react to uncertainty in real time (Bervoets et al., 2021). I specifically aim to examine responses to temporal uncertainty in Experiment 7. This experiment uses physiological measures to indicate anticipation of incoming stimuli and arousal to give real-time reactions to uncertainty (Chapter 4).

Sandhu et al. (2022) propose that behavioural experiments that use different forms of uncertainty are crucial in understanding how people actually interact with uncertainty, and is the next step in understanding the computations and mechanisms underpinning intolerance of uncertainty. Specifically, they categorise uncertainty into different levels of complexity. **First order uncertainty** (often termed *risk* or *expected uncertainty*) refers to the primary uncertainty about the timing or intensity of an event, e.g. a cue indicating a shock is incoming 60% of the time would represent first order uncertainty. **Second order uncertainty** (unexpected uncertainty) refers to the changeability of the probability of an event. E.g. a cue that previously indicated a 60% likelihood of an incoming shock changing to indicate an 20% likelihood of a shock. Second order uncertainty is equivalent to the principle of volatility, as laid out by Behrens (2007). If changes in event probability are not clearly signalled, there is likely uncertainty about this level of changeability which would be an example of **higher order uncertainty**, e.g. it is uncertain how the changeability of the probability of incoming shocks is changing. Finally, the authors describe **structural uncertainty** as the uncertainty about the number of stable levels of probability of an event. There is currently a notable lack of empirical literature investigating how intolerance of uncertainty interacts with higher level uncertainty such as second order, higher order, and/or structural uncertainty.

The experiments outlined in this thesis primarily explored responses to first order uncertainty, such as uncertainty relating to how aversive an incoming stimulus was going to be (Experiments 5 and 6, see Chapter 3), or uncertainty relating to when a stimulus change was going to occur (Experiment 7, see Chapter 4). I investigated intolerance of uncertainty using first order uncertainty as I am primarily interested in the computational mechanisms that underpin uncertainty, and how these relate to intolerance of uncertainty. I wanted to show differences in as early level of cognitive processing as possible to capture these early,

instinctive computations in the brain, and higher-order uncertainties likely involve more complex cognitive processes such as meta cognition. However, I would highlight that an interesting next step would be to develop experiments that explore the effects of different levels of uncertainty complexity, to more accurately represent the complex and varied levels of uncertainty faced by people in day-to-day life.

1.4. Aims and Research Questions

The broad aim of this thesis is to explore the mechanisms, computational changes, or psychophysical underpinnings of intolerance of uncertainty with a lens of predictive processing frameworks, including addressing the hypotheses outlined below. I aimed to investigate the necessary stimulus conditions of uncertainty to trigger the aversive subjective experience associated with IU, and to quantify this experience in subjective and objective terms.

Minimising uncertainty is now understood to be one of the core attributes of perception and behaviour; intolerance of uncertainty, therefore, could relate to an aberration in, or otherwise divergent, predictive processing. Through a series of psychophysics experiments (Chapter 2), I explored computational mechanisms behind predictive processing by manipulating stimulus statistics, with a particular focus on stimulus precision. These experiments were chosen to test how these changing stimulus statistics related to the perceived salience of these changes. The simplicity of the auditory stimuli allowed for precise control over signal properties while maintaining relevance to how we process in change in the sensory environment.

I then adapted this experimental structure in Chapters 3 and 4 to induce specific forms of uncertainty, partial predictability of aversive stimuli and temporal unpredictability, which are especially relevant to clinical models of IU. These paradigms were designed to elicit responses that might reveal group differences in high and low IU participants, particularly in anticipation and physiological arousal. Chapter 4 describes a lab-based temporal expectation task with physiological measures (EEG and pupillometry) to test whether intolerance of uncertainty relates specifically to temporal uncertainty.

Chapter two outlines a series of psychophysics experiments that explored the effects of changing specific stimulus statistics on predictive processing. These experiments investigated the underlying computations of surprise, and how a subjective perception of salience response changes under specific stimulus conditions. The first experiment explored specifically how “noticeable” changes in stimulus conditions were perceived to be, the second replicated the findings of this but instead asking how “surprising” participants found specific stimulus changes. This second experiment also included an IUS-12 questionnaire to see if intolerance of uncertainty related to a bias in the perception of specific stimulus statistics. The third experiment altered the timescale of the experiment, using a greater number of shorter stimuli to test the generalisability of the previous findings, and also took an accuracy response, to compare against the subjective salience of change response. The fourth experiment changed the modality of the stimulus changes, from changes in stimulus frequency to stimulus intensity, again to assess the generalisability of the findings. As a term, precision refers to two related but distinct phenomena: the statistical properties of the sensory input from the environment, and the brain’s estimate of the reliability or importance of the signal from the environment. It is often assumed that these two phenomena are closely correlated; an assumption I tested in this chapter by manipulating the environmental precision, or precision of sensory input, and measuring its effect on the perception of sensory change. If there are systematic ways in which precision in the brain deviates from environmental precision this could have important implications in understanding neurotypical and impaired brain function. I predicted that increased stimulus precision would make changes in stimuli more predictable and therefore less surprising.

Chapter three outlines two psychophysics experiments using semi-predictable potentially aversive auditory stimuli to explore the anticipation of, and perception of potentially aversive stimuli in relation to IU. These experiments were designed to simulate conditions of partially predictable uncertain threat, to elicit differences between high and low IU participants. Experiment 5 included an explicit safety cue to test whether IU is associated with a reduced ability to understand and use safety signals. Experiment 6 introduced another dimension of uncertainty by having a visual signal missing in 50% of the trials. This manipulation was chosen to reflect the idea that IU is not just fear of threat, but distress over

missing information, and therefore would differentiate anticipatory responses between high and low IU participants.

Chapter four investigates whether intolerance of uncertainty relates specifically to temporal expectation of uncertain upcoming stimuli. This experiment took physiological measures that indicate arousal and preparedness for responding to anticipated stimuli such as Contingent negative variation (CNV) from EEG measurements and pupillometry responses. This design was selected to test the hypothesis that individuals with high IU have greater difficulty predicting when events will occur under uncertainty, resulting in altered preparatory responses. Temporal uncertainty is a fundamental feature of anxiety-based disorders and is relatively understudied in relation to intolerance of uncertainty.

1.5. Hypotheses

Overall, this thesis is founded upon addressing two main hypotheses of intolerance of uncertainty. The first hypothesis is that under conditions of sensory uncertainty, people with high IU are biased towards expecting more aversive outcomes. The second is that under conditions of sensory uncertainty, people with high IU are not necessarily biased towards any particular outcome, but rather perceive uncertain situations themselves as more aversive. These two hypotheses are not necessarily mutually exclusive, although it is likely they indicate different computational mechanisms of IU.

Separate to these hypotheses, I explore a series of secondary hypotheses relating to intolerance of uncertainty and the perception of uncertainty more broadly. One hypothesis is that intolerance of uncertainty relates to an inability to either understand or believe safety signals that would indicate safety and therefore reduce anxiety (tested in Experiment 5, Chapter 3). I also test the hypothesis that when cues that indicate upcoming stimuli are missing, anticipation of and perception of aversive stimuli is increased in high IU groups (Experiment 6, Chapter 3).

I assessed the hypothesis that perceived surprise relating to a change in stimuli is positively correlated with the precision of the sensory environment (Experiments 1-4, Chapter 2). I also assess whether perceived surprise from sensory changes under uncertainty is altered depending on the IU of the participant (Experiment 2, Chapter 2).

Finally, I tested the hypothesis that people with high IU are impaired in their ability to temporally predict uncertain stimuli (Experiment 7, Chapter 4).

2. The psychophysics of surprise. Perceived change under uncertainty (Experiments 1-4)

This chapter has been submitted as a manuscript and is currently in revision with Scientific Reports. This manuscript has been submitted with the following order of contributing authors: myself (George Herbert), Choi Tim Ho, Julia Goddard, Harry Garthwaite, Jessica Komes, Christopher Petkov, and William Sedley. Choi Tim Ho, Julia Goddard, and Harry Garthwaite were undergraduate students who conducted data collection on Experiments 4, 1, and 3 respectively. Jessica Komes, Christopher Petkov, and William Sedley were involved in a supervisory role to myself and/or the undergraduate students, and advised me with experimental design and data analysis, and helped edit the manuscript. I acted in a supervisory role to two of the undergraduate students, designed and ran experiment 2, analysed all data, and wrote the manuscript.

2.1. Introduction

Contrary to classical theories of sensory processing, perception is now broadly considered an active process, where incoming sensory information is used to update internal models of the environment (Parr, Pezzulo, and Friston, 2022). Predictive coding, initially proposed by Rao and Ballard (1999), is one such generative account, describing how the brain functions as a Bayesian inference machine, constantly generating and updating an internal model of the environment. Various frameworks exist, with many similarities, such as those falling under the umbrellas of active sensing (Schroeder et al., 2010) and the free energy principle (Friston, 2010; Friston and Kiebel, 2009).

A fundamental principle common to these accounts is the optimisation of inference under conditions of uncertainty; perception results from an interplay of internal representations of the environment (priors, which generate predictions) combined with incoming sensory input (likelihood – i.e. the likelihood that the pattern of sensory input corresponds to a particular environmental state or object). To optimise this balance, prior predictions and sensory input are each weighted by precision. Incongruence between prior predictions and sensory input is termed prediction error (mismatch between prior and

likelihood), also known as surprise. It is widely assumed that subjective and objective surprise responses are proportional to both the precision of the likelihood (sometimes termed precision-weighted prediction error – PWPE), and the precision of the prior (with the term surprise referring to the improbability of the sensory input based on the prior). Surprise is mathematically defined as the negative log probability of the sensory input according to the prior, and this accords well with the lay intuitive notion of surprise as the emotional/cognitive response to unexpected events or stimuli.

Perception is the act of minimising surprise through continuous updating of internal models. As well as surprise (as in prediction error), another important quantity in this process is Bayesian surprise, which is the extent to which the internal model is updated on account of the stimulus (i.e. the difference between the posterior and the prior). As with surprise more generally, Bayesian surprise has both subjective (Baldi & Itti, 2010) and objective correlates (Sedley et al., 2016a).

Mathematically, precision is the inverse of variance. In the brain, however, one hypothesis posits that estimated precision is encoded largely by postsynaptic gain (Friston, 2008; Feldman and Friston, 2010). ‘Precision’ thus refers to two related but distinct phenomena: the statistical properties of the sensory input from the environment, and the brain’s estimate of the reliability or importance of the signal from the environment. It is often assumed that these two phenomena are closely correlated. However, if there are systematic ways in which the brain’s estimated precision deviates from environmental precision, this could have important implications in understanding neurotypical, atypical and disordered brain function. A related general assumption is that higher sensory precision is associated with greater perceptual salience of a change than the same change under lower precision conditions. However, to my knowledge this has not been directly tested.

This study describes the implementation of a behavioural Bayesian surprise paradigm (Figure 1), over a series of several experiments (Experiments 1 to 4), to explore intrinsic bias in how stimulus sequence properties (principally precision, i.e. inverse variance of the distributions from which stimuli are drawn) influence the perception of otherwise equivalent sensory changes. I am specifically examining the perception of a systematic change in the underlying stimulus distribution, i.e. Bayesian surprise, rather than the surprise associated with individual stimuli. Hereafter I use the term ‘perceived size of change’, or ‘perceived

salience of change', (PSC) to refer to this subjective Bayesian surprise. Participants listen to sequences of pure tones drawn from Gaussian distributions with a specified mean and precision (i.e. inverse variance), in which a change in mean tone frequency (or intensity in Experiment 4) of the distribution occurs exactly half-way through the sequence, and subsequently provide ratings of PSC. In all studies reported here, the principal dependent variable was PSC, on a Likert scale of 1-4, i.e. reported sense of how much the mean of the Gaussian distribution, from which stimuli are drawn, changed during the trial. Experiment 1 asked participants how 'noticeable' they found the change in mean stimuli, and Experiments 2-4, asked how 'surprising' they found this change. Experiment 3 altered the timescale of the stimuli, having a larger number of shorter stimuli in each trial. In Exp. 4 the stimuli varied in intensity rather than frequency. Experiment 3 and 4 additionally asked participants to report the direction of mean change as well as its size, to obtain a behavioural performance measure.

The aim of these experiments was to investigate the relationship between changing statistical parameters of the auditory stimuli and this PSC, particularly the effect of stimulus precision, and the interaction of precision and mean change. As greater stimulus precision would increase the signal to noise ratio, and allow more accurate estimation of the mean stimulus change I predicted, in all four experiments, that PSC would increase with greater stimulus precision, as well as with greater absolute mean change. This relationship would indicate a Bayes-optimal response (or reflect signal-to-noise ratio), which would be reflected in the results as a positive linear relationship between mean response and precision, as shown in Figure 3C(i). A non-Bayesian response pattern would show no relationship between mean response and precision (Figure 3Cii) and would indicate that the extra noise added by reduced stimulus precision did not affect participants perception of, or ability to detect, stimulus changes. A counter-Bayesian response pattern would be indicated by a negative linear relationship between precision and PSC (Figure 3Ciii); this was not predicted, but would indicate an unexpected effect of stimulus precision with an unknown mechanism. I predicted that this behavioural response pattern would not be dependent on specific phrasing, i.e. whether Participants were asked to rate how 'surprising' (Experiments 2-4) vs. how 'noticeable' (Experiment 1) changes were. I also predicted that accuracy in task performance

would show the same relationships to precision and mean change.

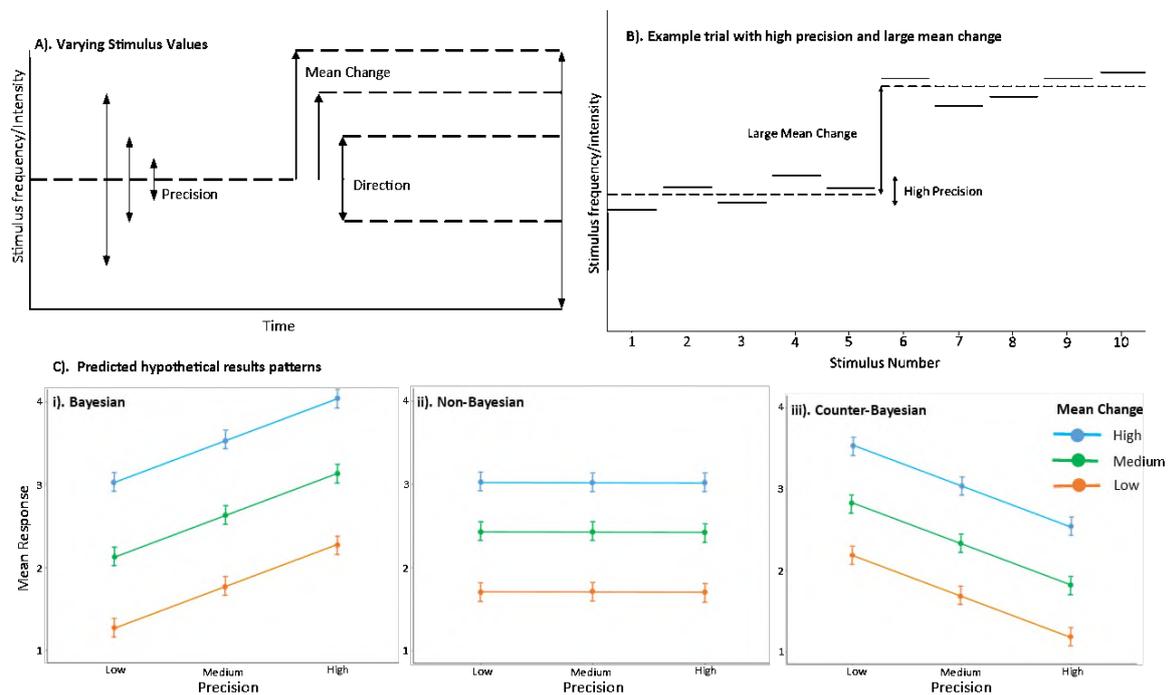


Figure 3. Overview of experimental paradigm, and canonical predicted results patterns for Experiments 1 - 4. **A)** Varying experimental stimulus parameters. Low, medium, and high precision (long, medium and short, respectively) and mean change values are indicated by arrows. Direction indicates whether the mean change was either an increase or a decrease in either frequency or intensity. **B)** Example trial with high precision and high mean change in upward direction. Each solid horizontal line indicates one stimulus. Dashed lines indicate the mean of the Gaussian distribution from which stimuli are drawn. **C)** Predicted results patterns based on three hypothesised canonical relationships between stimulus precision and perceived size of change (note: direction of mean change not specified): **i)** Bayesian, or signal-to-noise ratio (preferred); **ii)** Non-Bayesian, or precision-indifferent (possible); **iii)** Counter-Bayesian (not anticipated). Note: combinations of response patterns might also be seen.

2.2. Combined Methods

2.2.1. Participants

All studies were run online. Participants were collected using convenience sampling, with participants for Experiments 1 and 2 collected online through questionnaire/experiment sharing Facebook groups, and participants for experiments 3 and 4 collected through www.prolific.co and paid £5 for participation. Experiments 1, 2, 3, and 4, had 74, 48, 70, and 93 participants respectively (see table 1). All participants gave informed consent, and ethical approval was granted under the reference code 15229/2021.

Experiment	Mean Age	SD Age	Male ppt.	Female ppt.	NB ppt.	Total ppt.
1	30.70	16.33	28	46	0	74
2	24.79	6.68	12	35	1	48
3	35.09	12.35	38	38	2	78
4	25.60	8.98	33	60	0	93

Table 1: Demographic information for Experiments 1-4: mean and standard deviation participant age, number of male, female, and non-binary participants, and total number of participants.

2.2.2. Procedure

Each study followed the same overall procedure; differences in stimulus parameters, stimulus values, and experimental design are highlighted in Table 1. Each experiment consisted of 180 trials: 10 exemplars of each of the 18 different combinations of stimulus properties (low, medium, high precision; low, medium, high mean change; mean change direction upward or downward – see Figure 1). What differed between experiments was the values of these parameters, the instruction given to participants, the number and duration of stimuli, and/or whether stimulus frequency or intensity was the varied parameter. Experiment 4 featured intensity changes, and first required Participants to set a comfortable maximum intensity level prior to starting the experiment, with stimulus intensities set relative to (always below 90% of) this reference (maximal) value. In all experiments, Participants were instructed to wear headphones. All Participants performed four practise trials to familiarise them with the task, before completing all 180 trials continuously without breaks, taking approximately 20 minutes. Each trial consisted of a series of pure tones being played, with a change in mean frequency (or intensity, see Table 1) occurring exactly half-way through each trial. Participants were prompted, after each trial, to give a behavioural response on a four-point Likert scale; how “surprising” (or “noticeable”, see Table 1) the change was e.g. “How noticeable was the change between the first half and the second half of the stimuli?” responding 1-4 on the keyboard. 1 = ‘Not at all noticeable’, 2 = ‘Slightly noticeable’, 3 = ‘Quite noticeable’, 4 = ‘Very noticeable’. In Experiments 3 and 4, Participants gave an additional rating after each trial to indicate whether they perceived the change to be upward or downward. Experiment 2 also measured the intolerance of uncertainty of each participant using the IUS-12 (Carleton, et al., 2007).

2.2.3. Stimuli

Stimuli were generated in MATLAB (R2021b, version 9.11.0.1769968). Each trial of 10 (or 30) auditory stimuli varied in frequency (or intensity), drawn from a Gaussian distribution with a mean that changed halfway through each trial and a fixed precision (inverse of variance). The main stimulus properties that were altered for each trial were: mean change (octaves or dB), precision (inverse of variance, measured in octaves⁻¹ or dB⁻¹) and the direction of the mean change (up or down). Mean change and precision values for each experiment were designated either 'high', 'medium', or 'low' (see Figure 1), the values for these can be seen in Table 2.

	Experiment 1	Experiment 2	Experiment 3	Experiment 4
Varied parameter	Frequency	Frequency	Frequency	Intensity
Stimuli per trial	10	10	30	10
Stimulus duration (s)	0.3	0.3	0.08	0.3
Trial Length (s)	3.36	3.36	3.56	3.36
Subjective change response	'Noticeability'	'Surprise'	'Surprise'	'Surprise'
Performance measure	N/A	N/A	Change direction	Change direction
Precision (low, medium, high) ($\text{oct}^{-1}/\text{dB}^{-1}$)	16, 32, 64	16, 32, 64	16, 32, 64	1/32, 1/8, 1/2
Mean change (low, medium, high) (oct/dB)	0.25, 0.5, 1	0.25, 0.5, 1	0.25, 0.5, 1	2.5, 5, 10

Table 2: Differences in stimulus parameters and experimental design between experiments 1 – 4.

2.2.4. Data Analysis

Data analysis was conducted in RStudio (R version 4.2.2 (2022-10-31 ucrt)). As an initial step, each subject's responses were averaged across trials within each of the 18 stimulus conditions, and these subject averages formed the basis of statistical testing. For each experiment, normality of the distribution of data was visually assessed using the qqplot function, and a three-way repeated measures ANOVA with full interaction terms was used to determine if perceived stimulus change (reported noticeability or surprise) related to the size of the change in stimulus mean between the first and second half of the stimuli (mean

change), the inverse variance of the stimuli (precision), and whether the stimulus change was an increase or decrease in frequency (direction), or in intensity in experiment 4. For experiments 3 and 4, a three-way repeated measures ANOVA was run to determine if accuracy of response (proportion of correct responses indicating whether the mean change went up or down in frequency) related to the size of the change in stimulus mean between the first and second half of the stimuli (mean change), the inverse variance of the stimuli (precision), and whether the stimuli change was an increase or decrease in frequency or intensity (direction). For all ANOVAs, Mauchly's Test for Sphericity was used with Greenhouse-Geisser corrections if assumptions of sphericity were not met. Post hoc tests were run for each significant interaction effect, first by breaking the three-way interaction into two-way interactions, and then by comparing simple main effects for each significant two-way model. Finally, pairwise comparisons were run for each significant main effect for precision. At each stage Bonferroni adjustment was used for multiple comparisons.

The analysis in experiment 2 differed slightly in that it included an extra variable of IU score (either high or low based on a median split) into the analysis, making it a four-way ANOVA.

2.3. Results

Participants in all four experiments utilised the full range of perceived size of change values in their responses, which ranged from 1 – 4. Means (and standard deviations) of all response values experiments 1, 2, 3, and 4, were respectively: 2.66 (± 0.70), 1.87 (± 0.69), 2.05 (± 0.62), 2.03 (± 0.68). Mean accuracy measures of experiments 3 and 4, were 0.79 (± 0.20), and 0.74 (± 0.23), respectively (with chance level being 0.5).

Mean PSC response increased with greater mean change (Figure 4). However, contrary to the Bayesian hypothesis (Figure 3Ci), PSC did not appear to consistently increase with stimulus precision (Figure 4). Experiments 1, 2, and 4 had mean change conditions in which higher precision resulted in lower PSC, which indicates a counter-Bayesian response pattern (Figure 3Ciii). Full results are described in their respective experiment sections below. In Experiments 1 and 2, generally, larger mean change conditions were associated with positive relationships between precision and subjective change (Bayesian response pattern), whilst smaller mean

changes were associated with an inverse relationship (counter-Bayesian response pattern). Experiment 4, where stimulus intensity rather than frequency was the varied parameter, showed only the counter-Bayesian pattern. Experiment 3, featuring a larger number of shorter stimuli, had effects of precision that were neither simply positive or negative correlations, but showed more complicated relationships, characterised by non-Bayesian or mixed response patterns (Figure 3Cii).

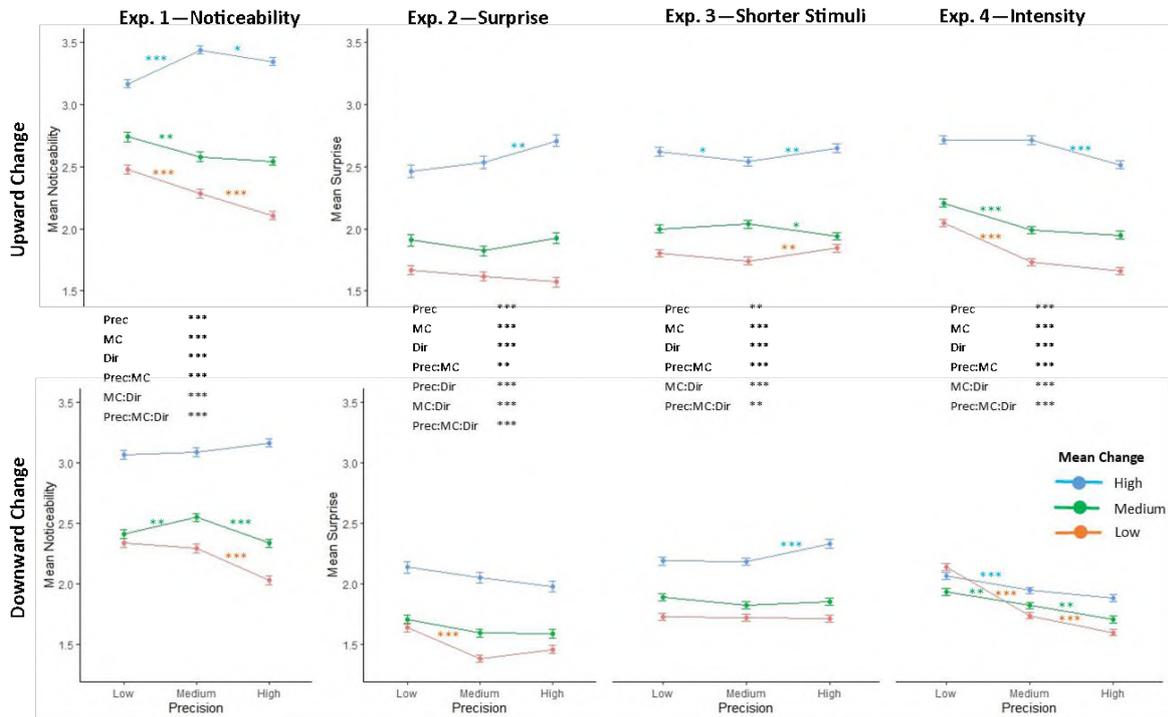


Figure 4. Perceived size of mean change (PSC) response patterns for Experiments 1 - 4. Mean PSC ratings across participant group for each stimulus category, from Experiments 1, 2, 3, and 4 in their respective columns. Y axis labels ‘noticeability’ and ‘surprise’ refer to what participants were asked to rate to indicate PSC. The x axis indicates precision of stimulus sequence, colour indicates size of mean change (response scale range 1-4). The row indicates the direction of the mean change (in frequency or intensity): top row = upward, bottom row = downward. Significant main effects and interaction effects are shown in black text for each experiment. Shorthand for stimulus parameters are as follows: Prec = stimulus precision, MC = mean change size, Dir = direction of the mean change. Coloured asterisks indicate statistical significance between neighbouring precision values for each stimulus-mean-change combination based on pairwise post-hoc testing of significant main and interaction effects. Significance is indicated as * if $p < 0.05$, ** if $p < 0.01$, and *** if $p < 0.001$.

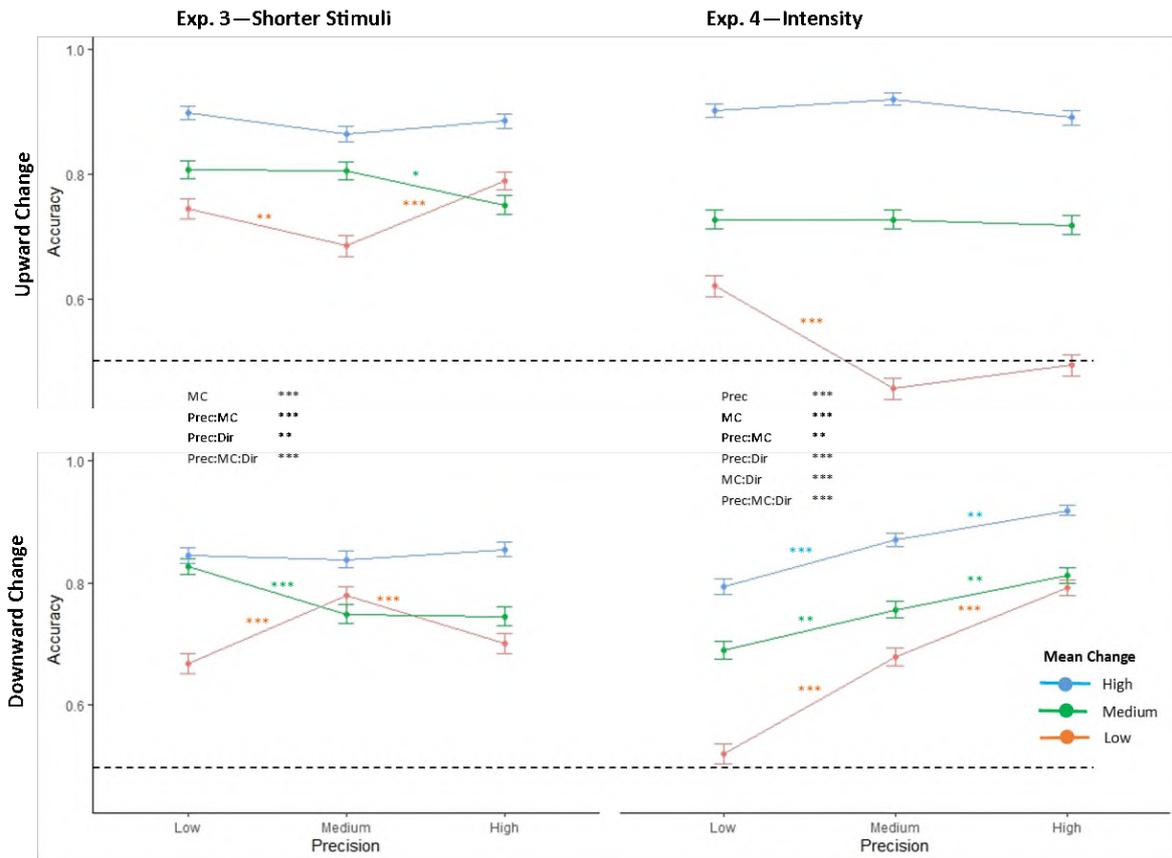


Figure 5. Accuracy of identifying direction of mean change in Experiments 3 and 4. Mean accuracy (proportion of mean change values correctly identified as increases or decreases in frequency/intensity) values for Exp 3 and Exp 4. The x axis indicates precision, colour indicates mean change. Top row indicates mean increases (in frequency/intensity), and bottom row mean decreases. Dashed line indicates chance level (0.5). Significant main effects and interaction effects are shown in black text for each experiment. Shorthand for stimulus parameters are as follows: Prec = stimulus precision, MC = mean change size, Dir = direction of the mean change. Coloured asterisks indicate significant differences between neighbouring precision values for each stimulus condition, based on post-hoc pairwise testing of significant main and interaction effects. Significance is indicated as * if $p < 0.05$, ** if $p < 0.01$, and *** if $p < 0.001$.

2.3.1. Experiment 1 – ‘Noticeability’ as subjective response

A three-way repeated measures ANOVA on subjective change response showed significant main effects of precision ($F(1.8, 131.52) = 26.965, p < 0.001$), mean change ($F(1.1, 80.26) = 191.220, p < 0.001$), and direction ($F(1,73) = 35.665, p < 0.001$). Significant interaction effects were shown between: precision and mean change ($F(4, 292) = 33.531, p < 0.001$); mean change and direction ($F(2, 146) = 9.808, p < 0.001$); and mean change, precision, and direction ($F(4, 292) = 12.794, p < 0.001$). PSC was greater for larger mean changes and for upward

changes of frequency. PSC did not increase with precision in the predicted Bayesian response pattern (Figure 3Ci); with medium and low mean change size, PSC decreased with increased precision, in a counter-Bayesian manner. With a high mean change size for downward frequency changes, the results indicated a non-Bayesian response pattern (Figure 3Cii). The high mean change for upward frequency changes seemed to indicate conflicting patterns, with medium precision giving the highest PSC response.

2.3.2. Experiment 2 – ‘Surprise’ as subjective response

A four-way repeated measures ANOVA on subjective change response showed significant main effects of precision ($F(2, 92) = 8.596, p < 0.001$); mean change ($F(1.13, 52.08) = 117.841, p < 0.001$); and direction ($F(1, 46) = 51.177, p < 0.001$). IU group did not come out as significant ($F(1, 46) = 0.291, p = 0.592$). Interaction effects were found between: precision and mean change ($F(4, 184) = 4.239, p = 0.003$); precision and direction ($F(2, 92) = 17.571, p < 0.001$); mean change and direction ($F(1.49, 68.67) = 32.312, p < 0.001$); and precision, mean change, and direction ($F(4, 184) = 7.743, p < 0.001$). No other interaction effects were found to be significant, including any relationship with IU group.

With downward changes, precision behaved solely in a counter-Bayesian manner, albeit generally not to a statistically significant degree (with the notable exception of low precision responses being higher than medium precision responses at a low mean change). Upward changes showed more complicated relationships. High mean change indicated a Bayesian response pattern: medium and low mean change indicated non-Bayesian response patterns (or at low mean change a trend towards counter-Bayesian response pattern).

2.3.3. Experiment 3 – Larger number of shorter stimuli

2.3.3.1. Subjective change response

A three-way repeated measures ANOVA on subjective change response showed significant main effects of: precision ($F(2, 154) = 6.109, p = 0.003$); mean change ($F(1.11, 85.75) = 130.075, p < 0.001$); and direction ($F(1, 77) = 79.995, p < 0.001$). Interaction effects were found between: precision and mean change ($F(4, 308) = 5.580, p < 0.001$); mean change and direction ($F(2, 154) = 34.560, p < 0.001$), and precision, mean change, and direction ($F(4, 308) = 4.605, p$

= 0.001). Relationships between PSC and precision largely indicate a non-Bayesian response pattern, or potentially conflicting effects, with some instances of Bayesian or counter-Bayesian patterns between related stimulus conditions, e.g. with a high mean change, medium precision seemed to give the lowest response.

2.3.3.2. Accuracy of direction responses

A three-way repeated measures ANOVA on accuracy change response showed significant main effects of: mean change ($F(1.79, 137.73) = 100.019, p < 0.001$). Interaction effects were found between: precision and mean change ($F(3.41, 262.83) = 9.609, p < 0.001$); precision and direction ($F(2, 154) = 5.121, p = 0.007$); and precision, mean change, and direction ($F(4, 308) = 14.118, p < 0.001$). Relationships between accuracy of direction response and precision largely indicate conflicting response patterns, with some instances of Bayesian or counter-Bayesian patterns between related stimulus conditions, e.g. In the low mean change condition, upwards frequency change found medium precision to give the lowest accuracy, but for the downward frequency change condition it gave the highest accuracy. High mean change indicated a non-Bayesian response pattern (Figure 3Cii).

2.3.4. Experiment 4 – Intensity rather than frequency changes

2.3.4.1. Subjective change responses

A three-way repeated measures ANOVA on subjective change response showed significant main effects of: precision ($F(1.37, 128.91) = 90.050, p < 0.001$), mean change ($F(1.19, 111.61) = 119.075, p < 0.001$), and direction ($F(1, 94) = 124.812, p = < 0.001$). Interaction effects were found between precision and mean change ($F(4, 376) = 25.673, p < 0.001$); mean change and direction ($F(1.39, 130.91) = 125.923, p < 0.001$); and precision, mean change, and direction ($F(4, 376) = 7.558, p < 0.001$). Relationships between PSC and precision largely indicate a counter-Bayesian response pattern, with greater PSC at lower levels of precision.

2.3.4.2. Accuracy of direction Responses

A three-way repeated measures ANOVA on accuracy change response showed significant main effects of: precision ($F(2, 188) = 39.306, p < 0.001$), and mean change ($F(1.69, 158.91) = 563.735, p < 0.001$). Interaction effects were found between: precision and mean change ($F(3.44, 323.41) = 4.319, p = 0.003$); precision and direction ($F(1.84, 173.29) = 92.633, p < 0.001$), mean change and direction ($F(1.78, 167.43) = 34.347, p = < 0.001$); and precision, mean change, and direction ($F(4, 376) = 23.731, p < 0.001$). In the downward intensity change condition, relationships between accuracy of change response and precision indicated a Bayesian response pattern, with greater precision leading to greater accuracy. In the upward intensity change condition, precision largely indicated non-Bayesian response pattern. The low mean change condition deviated from this pattern, with significantly better accuracy for low precision than medium or high precision, which were both around 50% accuracy (chance level).

2.4. Discussion

2.4.1. Quality control measures

Our prediction that PSC would show a positive relationship with mean change was met in all four experiments, indicating that participants understood the task and responded appropriately. All four experiments found a main effect of direction on the subjective change response, with higher responses to an increase in either stimulus frequency or intensity. This corresponds to findings in previous literature, e.g. loudness and duration of stimuli have been shown to be overestimated when stimuli are increasing in intensity (Bach et al., 2009; Bach et al., 2007). This is likely the result of auditory *looming bias*: an increase in saliency to auditory stimuli with increasing intensity as an evolutionary response to approaching sounds (Ignatiadis et al., 2021; Neuhoff, 1998). Higher frequency sounds are often associated with sources of (or reporting of) threat, and therefore a similar bias seems understandable. In Experiment 2, no effect was found between IU group and PSC, or any interaction effect with any combination of changing stimulus statistics. This suggests that intolerance of uncertainty is not simply an aberration of the perception of (and/or response to) changes in stimulus statistics relating to the calculation of uncertainty. This finding is explored more thoroughly in Chapter 3.

2.4.2. Bayesian and counter-Bayesian relationships between stimulus sequence precision and PSC

Our prediction that stimulus precision would positively relate to the behavioural response in a Bayesian response manner (Figure 3Ci), as opposed to non-Bayesian (Figure 3Cii) or counter-Bayesian (Figure 3Ciii), was not met. All four experiments found main and/or interaction effects of precision, however, in many cases precision was inversely related to PSC; e.g. in Experiment 1 & Experiment 4, when mean change was low, PSC response decreased with increased precision in a counter-Bayesian manner. This is unexpected and counter-intuitive, as more precise stimulus sequences would reduce noise in the data and therefore indicate more reliable information via increased signal to noise ratio. This paradoxical effect of precision potentially indicates the dissociability of informational precision of the sensory signals in the environment from encoded estimated precision within the brain, as an indicator of the reliability and importance of those signals. Put another way, many instances were observed where participants responded to less precise sensory input as if it carried a higher salience or behavioural relevance. Interactions of mean change and precision indicate that the paradoxical effect of precision applies particularly to smaller absolute stimulus changes, whilst larger absolute changes were more often Bayesian, and intermediate changes precision-indifferent or mixed. Interactions of precision and direction may reflect looming and related biases, and indicate biases in direction of inferred change under uncertain conditions. Interactions of all three are a combination of the above factors. In the following paragraphs I consider why this might be the case and its potential relevance for my understanding of perceptual inference and its disorders.

One trivial interpretation of these results was that participants were responding to differences between individual stimuli, as opposed to the overall change between halves of the stimulus trials. Therefore, lower precision trials would favour increased perception of change through greater distinction between individual stimuli. The results of Experiment 1 were scrutinised to investigate this potential explanation. Change between the last stimulus from the first half and the first stimulus of the second half of each trial were compared with mean response for each combination of precision and mean change condition, and no systematic relationship was observed. Similarly, I observed no relationship between each

trial's response, within each mean change condition, and the maximal difference between any two individual stimuli within the trial. Therefore, participants were likely responding to a combination of all stimuli in each half, and not simply individual outliers or stimuli in specific sequence positions.

Findings that indicate increased perceived change with lower precision, especially in conjunction with lower mean change as a proxy for low signal-to-noise ratio stimuli, could therefore be explained as an inflated estimated precision of sensory signals in the brain compared to statistical precision of the sensory input. Alternatively, or additionally, these findings could be the result of a phenomenon similar to stochastic resonance, a robust effect where additional noise increases sensitivity to the detection of weak signals (Wiesenfeld and Moss, 1995). Whilst not identical, the effect I observe here could be analogous in terms of a mechanism to aid the detection of subtle changes in the sensory environment under conditions of additional noise.

A further explanation could be that low-precision stimulus streams contain more variability between individual stimuli, which increases stimulus-driven attention, in effect increasing the effective precision of those stimuli in the brain (an effect shown by Feldman and Friston, 2010). More difficult listening conditions (reduced signal to noise ratio) demand greater listening effort which results in an increased attention to these trials making them more salient. Detecting a change through greater noise could increase the perceived difficulty of the task, with more care and attention directed to tasks that demand higher levels of thought.

It is also possible that more variable stimulus sequences reduce the extent of stimulus-specific adaptation, leading to greater sensitivity to similar stimuli.

Finally, whilst I have discounted the explanation of outlier values within each trial dominating perception, it is possible that the added noise associated with low precision results in a greater number of individual stimuli that are relative outliers in the context of the entire experiment, and that over-weighting of the salience these rarer values might lead to greater influence on the processes of perceptual inference.

2.4.3. Behavioural accuracy and stimulus sequence precision

Findings relating to the performance measure of how accurately participants could indicate the direction of change suggest that performance increased with size of mean change, which indicates participants understood the task and that differences in mean change size changed the difficulty of the task. Experiment 4, which varied stimulus intensity, found a main effect of precision, and both experiments found all interaction effects involving precision to be significant. In Experiment 4, downward intensity changes were detected more accurately with higher precision in a Bayesian response pattern, whilst upward intensity changes showed a non-Bayesian response pattern, except the smallest mean increase, which was more accurate in the low precision condition reflecting a counter-Bayesian response pattern.

In some situations, such as the medium downward mean change condition in Experiment 3, lower precision improved performance. This result could be indicative of opposing mechanisms, e.g. that decreased precision aids performance (through one or more of the mechanisms suggested previously, e.g. stochastic resonance or increased salience), but this is specific to a certain difficulty of identification. i.e. If the mean change is high, the decision may be too easy for precision to have much of an effect on accuracy. If the mean change is low, the mechanism(s) that increases performance in low precision conditions may be insufficient to outweigh the increased noise. A recent study exploring how rule-based cues and stimulus-based cues elicit bias in perception similarly found contrasting effects of stimulus cues affecting perception at different levels of signal to noise ratio (Tardiff et al., 2022). High signal to noise ratio biased participants' responses away from recent stimuli, whereas low signal to noise ratio biased participants towards recent stimuli. E.g. after hearing high frequency stimuli participants were less likely (and slower) to report a high frequency test tone as high frequency when signal to noise ratio was high.

Findings show the subjective change response to be largely distinct from accuracy, suggesting it was not merely indicating salience. However, it is noteworthy that the increased perception of subjective change with low precision largely (with some exceptions) occurred in the same conditions where accuracy was lower. Although, all accuracy measures were above chance level, which discounts a simplistic explanation that participants were simply guessing about the size of change in low-precision conditions.

2.4.4. Wider implications of counter-Bayesian precision effects

It is important to highlight that this paradoxical effect of precision indicates the brain behaving in a non-Bayes optimal manner, and making objectively sub-optimal inferences. If there are instances where the neurotypical and healthy brain is already behaving in a Bayes-suboptimal manner in normal processes, this could be valuable in further understanding clinically disordered states associated with sub-optimal Bayesian inference, in which these biases might be quantitatively or qualitatively different. It is beyond the scope of this article to fully outline the myriad possible clinical implications of these observations, but to name just a few examples: tinnitus is proposed to be the result of stimulus precision overriding the default prediction of silence to instead expect sound (Sedley et al., 2016b; Hullfish et al., 2019); the imprecision hypothesis of chronic pain posits that the precision of information about a painful event determines the degree to which this pain will generalize to similar events (Moseley and Vlaeyen, 2015); the somatic error hypothesis of anxiety posits that anxiety disorders can be explained as a discrepancy between body state predictions and sensed body state (somatic error) (Khalsa & Feinstein, 2018), and over-inference of sensory changes might predispose to anxiety; several phenotypic features of autism spectrum disorder have been accounted for as a discrepancy in ability to form predictions between individuals with ASD and neurotypical people (Cannon et al., 2021).

Hallucinations were hypothesised to result from priors with inappropriately high precision outweighing incoming sensation resulting in distorted sense of perception (Lyndon and Corlett, 2020; Corlett et al., 2019; Powers, Kelley and Corlett, 2016). Subsequent empirical research has since demonstrated a relationship with over-weighted priors and hallucination in simulated Participants (Benrimoh et al., 2019), neurotypical people (Alderson-Day et al., 2017; Powers, Mathys and Corlett, 2017), people with psychotic illnesses (Kafadar et al., 2020; Cassidy et al., 2018; Powers, Mathys and Corlett, 2017; Teufel et al, 2015), and people with Lewy-body disease (Zarkali et al., 2019). Similarly, Friston (2012) proposed that an addict's reward-seeking behaviour is a consequence of suboptimal perceptual learning, specifically resulting from overweighted precision as a result of dopaminergic neuromodulation.

There is likely an evolutionary benefit to the over-caution of erring towards perceiving a larger change (or a change vs. no change) in uncertain conditions, as signals indicating potential threats might be largely obscured by noise in some situations, and a bias towards over-perception of potential threats might confer more benefits in more sensitive detection of true positives than detrimental consequences of false alarms. The findings of this study suggest a mechanism to facilitate the detection of subtle signals in noisy environments.

Although replicated between these four studies, this paradoxical effect of precision was observed in a limited parameter space, including low numbers of stimuli per sequence, and therefore it is important to understand how generalisable it is. Varying the signal to noise ratio more widely (i.e. greater variance between mean change and precision) would help explain how far this effect generalises.

2.5. Conclusions

I have shown that increasing precision of stimulus sequences does not necessarily make otherwise equivalent sensory changes more surprising or easier to detect, and in some cases that it has the opposite effect. This paradoxical effect of precision indicates the brain behaving in a counter-Bayesian manner, with inherent biases towards over-inferring small changes in noisy conditions, and towards detecting small increases, mainly in intensity. These observations are important for our fundamental understanding of perceptual inference. The myriad possible clinical implications of these observations include further understanding tinnitus, chronic pain, anxiety disorders, and ASD.

Further exploration of behavioural and neurophysiological correlates of this discrepancy between environmental precision and encoded estimated precision could shed light on the mechanisms underlying a potentially vast range of common clinical disorders, and potentially indicate targets for intervention.

3. Intolerance of Uncertainty – Behavioural studies of aversivity predictions

3.1. Background

One of the previous discussed experiments (Experiment 2, Chapter 2) explored the perception of sensory change under conditions of uncertainty. Specifically, participants rated how surprising they found changes in frequency of auditory stimuli, with varying stimulus statistics dictating how noticeable these changes were for each trial. This study found no difference between high and low IU groups in behavioural responses reporting perception of changes in stimulus statistics (2.4.2 ‘Surprise’ as a subjective response).

If these results are true reflections of the effects of changing stimulus statistics on perceptual inference, this result implies that, at least in general, the computations of Bayesian inference occur similarly in people with high and low intolerance of uncertainty, and that intolerance of uncertainty is not simply an aberration of the perception of (and/or response to) changes in stimulus statistics relating to the calculation of uncertainty. Either the uncertainty elicited through surprise from this previous experiment is of insufficient magnitude to reveal differences related to IU symptoms, or is distinct from the uncertainty processing mechanisms that are implicated in IU. If IU is unrelated to, or at least more complex than, biases in the processing of stimulus statistics, under what stimulus conditions is this uncertainty elicited that does distinguish people with high and low IU?

This previous paradigm was altered to incorporate multiple new elements anticipated to reveal differences between high and low IU groups, with the intention of subsequent work then removing elements to uncover the requisite components of experimentally eliciting intolerance of uncertainty. If the computational underpinnings of intolerance of uncertainty can be identified, this will help further understand intolerance of uncertainty and related anxiety-based disorders, as well as potential novel approaches to treatment and therapy.

To explore the computational mechanisms behind intolerance of uncertainty, the following two online psychophysics experiments compared the responses of high and low IU participant groups to auditory stimuli varying in intensity. These responses indicated both the anticipation of, and subsequent perception of, potentially aversive stimuli. Participants set an individual uncomfortable loudness level, and the probability that a probe stimulus will exceed this threshold was semi-predictable, based on specific context stimulus statistics.

I had two primary hypotheses for these experiments. The first was that under conditions of sensory uncertainty, people with high IU are biased towards expecting more aversive outcomes. The second was that under conditions of sensory uncertainty, people with high IU are not biased towards any particular outcome, but rather perceive aversive stimuli as more aversive. If the first hypothesis is true, I predicted that participants with high IU will give higher mean anticipation responses than low IU groups, as this indicates they are consistently expecting the subsequent probe stimulus to be more aversive. If the second hypothesis is true, I predicted that participants with high IU will report the aversity perception response to be higher, as this would indicate that they are perceiving the stimuli as more aversive. These two predictions are not necessarily mutually exclusive, and one might carry over to the other (i.e. more aversive predictions might make subsequent perception more aversive, and/or increased perceived aversity might carry through to subsequent predictions of greater aversity), although it is likely the hypotheses that underpin them indicate different computational mechanisms of IU. As a secondary hypothesis, I was also interested in exploring whether increasing the sensory uncertainty of the experimental conditions exaggerates the relationship between IU group and anticipation/perception of aversity. In these experiments, stimulus precision related to the uncertainty of the potential aversity in the probe trial, so I predicted that lower precision would be associated with increased responses (anticipation response and/or aversity perception response depending on whether either or both responses to uncertainty show a relationship with IU group).

Conversely, if IU does not result from a bias in perceptual inference, and is unrelated to the aversity of stimuli, I would likely find no distinction between low and high IU groups in either the anticipation response, or aversity perception response, to aversive stimuli. However, the feelings experienced by IU groups may still differ when experiencing uncertainty about these potentially aversive stimuli. Behavioural measures indicating anticipation of, or experience of, potentially aversive stimuli may not capture this felt sense of unease from the uncertainty itself, but a measure of general discomfort or unease may capture differences between groups. To capture this measure, the second experiment also had a measure of general unease given prior to the probe stimuli, in order to distinguish the anticipation of potentially aversive stimuli and unease felt as the result of the uncertainty itself. Therefore, my third hypothesis was that under conditions of sensory uncertainty,

people with high IU are not biased towards any particular outcome, but rather find the uncertainty of the situation itself aversive. If this is the case, I would predict that there would be no difference in anticipation and aversity perception response, but high IU participants would have higher unease responses than low IU participants.

As a further element to differentiate responses between high and low IU participants, Experiment 6 has the addition of visual cues. Information that helps predict upcoming potentially aversive stimuli might alleviate felt uncertainty, through either reduction in the uncertainty itself (more predictable stimuli) or forewarning potentially aversive stimuli so people can prepare and potentially reduce the felt surprise relating to aversive stimuli when it arrives (leading to reduced expected surprise, i.e. uncertainty). These visual stimuli give accurate indications of the aversity of the upcoming stimuli in 50% of trials. In the other 50%, the visual stimulus indicates the requisite information is missing. This extra dimension of information, and in 50% of trials increased uncertainty from missing information, could affect the results in several ways. Participants encountering trials where the visual stimuli are missing might feel greater uncertainty than if this information were never present to begin with (e.g. in Experiment 5). People with high IU are particularly sensitive to a lack of information about upcoming uncertainty, and therefore I predicted that people with high IU will rate perceive the trials with missing information as more aversive than the low IU group. I also predict that the uncertainty elicited by the missing information will elicit more unease in the high IU group than low IU group.

Converse to the assumption that noxious experiences are neurally underpinned by signals indicating danger or aversion, it has been suggested that anxiety disorders relate to aversive responding to conditions that typically signal safety, leading to lack of inhibition of fear and threat-based responses to safe stimuli (Craske and Wolitzky-Taylor, 2013; Lohr et al., 2007). It has been shown that during conditions that would typically confer safety, increased aversive responding was found in people with anxiety disorders (Lissek et al., 2010; Craske et al., 2008; Grillon et al., 1998) and people at risk of developing anxiety disorders (Craske et al., 2009; Reeb-Sutherland et al., 2009). One study found that intolerance of uncertainty moderates the relationship between people with panic disorder and a failure to inhibit aversive responding during safety (Gorka et al., 2014).

It is possible, therefore, that intolerance of uncertainty results in an aberration in the ability to perceive or believe safety signals. To search for a potential relationship with safety signals and IU, Experiment 5 has an extra block of trials which follows the same trial structure as the other blocks, but participants are correctly informed that stimuli will not reach the uncomfortable loudness level. The reduced uncertainty from less aversive and more predictable stimuli should lead to reduced anticipation and aversity perception responses. I hypothesise that IU is related to an incapacity to trust implicit safety signals given in conditions of uncertainty, and therefore I predict that high IU groups will give higher anticipation responses in the ‘safe’ block compared to the lower groups.

Primary Hypothesis	Secondary Hypothesis	Prediction
IU is related to uncertainty about potentially aversive outcomes	Predictions are biased towards aversive outcomes	IU will positively relate with anticipation response
	IU affects how strongly aversive stimuli are perceived to be	IU will positively relate with aversity perception response
IU is unrelated to the aversity of an outcome, and results from feelings about uncertainty itself	IU is a feeling of unease in any uncertain situation that does not affect expectations	IU will positively relate with unease rating only
	IU is related to an incapacity to trust safety signals	IU will positively relate with anticipation response in conditions where stimuli are ‘safe’
	IU is exacerbated by a lack of key information about a situation	IU will positively relate to responses in conditions where visual stimulus is missing

Table 3. Hypotheses of Experiments 5 and 6

3.2. Experiment 5 – Aversity psychophysics with safety cue

3.2.1. Method

3.2.1.1. Participants

143 participants were recruited for the study through prolific.co and paid £5 for their participation. All participants were English speakers from the UK or USA. From an initial 150 recruited participants, 7 unfinished responses were removed from the study. Median participant age was 37 (± 13.7) years old. 64 identified as male, 77 identified as female, and 2 identified as non-binary. Participants completed the IUS-12 questionnaire (Carleton, et al., 2007) and were categorised as either high or low intolerance of uncertainty, based on a median split (33). All participants gave informed consent at the start of the study, and ethical approval was granted under reference code 38257/2023.

3.2.1.2. Procedure

Participants were required to wear headphones throughout. Participants were first asked demographic questions and completed the IUS-12 (Carleton, et al., 2007). They were then informed of the trial structure, i.e. that five initial sounds will be followed by one 'probe' sound, with an increase in loudness between the initial and probe sounds. They were informed that the loudness of the final sound in each trial was based on the initial five sounds, and that in between these five initial sounds and the final sound they would be asked to rate how aversive they expect the final sound to be, and then after they have heard the sound they will be asked to rate how aversive they found it in retrospect. Participants were told that stimuli were defined as aversive if "they cause discomfort to the degree that you would actively avoid the sound in your day to day life". In the instructions, participants were encouraged to respond instinctively with the following instruction, "we recommend having your fingers resting on the '1', '2', '3', and '4', keys for faster answering".

Prior to the first block, and three further times between blocks of trials, an uncomfortable loudness level (ULL) was determined, and repeated to compensate for any habituation or adaptation that might have occurred. Participants were instructed to set their system volume at 100%, listen to the pure tones played (initially at very low volumes), and adjust the volume (within the experiment software) to the loudest level they are comfortable

listening to. Intensity was adjusted in the experiment, by the participant using a linear percentage scale, between 0% (indicating silence) and 100% indicating the maximum volume possible for the participant's audio setup. After the ULL had been set, participants were played pure tones just below this intensity as a final confirmation of comfort, and then given the option to restart the sound check if the sounds were perceived as uncomfortable, or to move onto the practice trials. All stimulus intensities thereafter were expressed in dB, relative to the most recently determined ULL (i.e. ULL = 0 dB).

Participants then familiarised themselves with the task with six practise trials. These trials were replicates of 6 trials used in the main experiment, chosen to show the breadth of stimulus parameters and therefore probability of the probe stimulus exceeding the ULL. After the practice trials the first block of trials began.

Each trial consisted of a series of five pure tones, referred to as the 'context' stimuli, the stimulus parameters of which influenced the probability that the following stimulus (hereafter probe stimulus) would surpass the ULL, and, if so, by how much. Participants were then prompted to indicate how aversive they predicted the following probe stimulus would be on a four-point Likert scale; 1 = 'Not at all aversive', 2 = 'Slightly aversive', 3 = 'Somewhat aversive, 4 = 'Aversive'. They were also given the option to end the study during any trial with 'esc' if they found the sounds to be painful or intolerable. After the context stimuli and anticipatory rating, the probe stimulus was presented, which was a single pure tone with an intensity influenced by the stimulus parameters of the context stimuli (see Figure 6C and Section 3.2.1.3), followed by a post-probe rating according to the prompt "How aversive was the sound?", using the same four-point Likert scale.

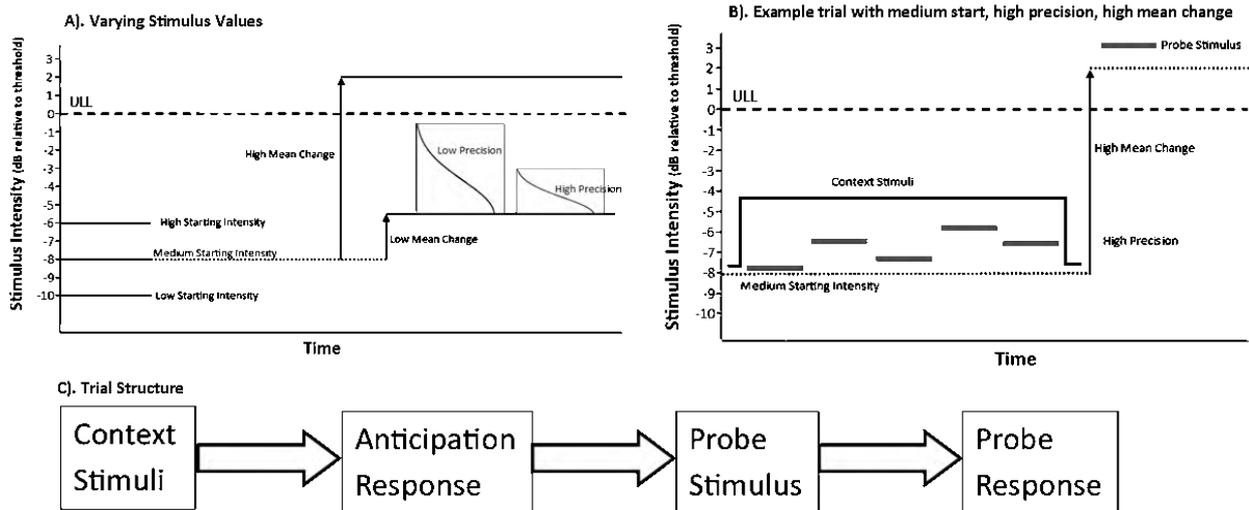


Figure 6. Overview of experimental paradigm, and trial structure for Experiment 5. A). Varying experimental stimulus parameters that affect the probe stimulus intensity relative to the ULL. Low, medium, and high starting intensity, low and high mean change size, low and high precision. **B).** An example trial, with a medium starting intensity, high precision, and high mean change values. The red lines indicate the context and probe stimuli, the y axis indicates their intensity relative to the ULL. The dashed lines indicate the minimum values from which stimuli were drawn in a half-gaussian distribution based on the precision values. i.e. the medium starting intensity and the medium starting intensity plus the high mean change values. **C).** The sequence of stimuli and responses during each trial in chronological order.

3.2.1.3. Stimuli

Each experiment consisted of 300 trials in five blocks of 60 trials. Before each of the first four blocks, participants set an uncomfortable loudness level (ULL) above which sound intensity is reported as aversive. This ULL dictated the intensity of the stimuli of each trial, with certain stimulus properties resulting in trials exceeding the ULL. The first four blocks consisted of a total of 20 exemplars of each of the 12 different combinations of stimulus properties, in random order. The final block (hereafter referred to as the ‘safe’ block) was preceded by a message informing participants that trials would not exceed the ULL, and altered stimulus statistics ensured trial stimuli were unlikely to reach the ULL. The mean total experiment duration was 31 minutes.

Stimuli were generated in MATLAB (R2021b, version 9.11.0.1769968). Each stimulus was a pure tone at 3 kHz, with a duration of 300ms including an onset ramp and offset ramp of 10ms each. Gaps between consecutive tones were 40ms. Each trial began with five context stimuli varying in intensity drawn from a half-Gaussian distribution, specifically the right-hand

side of the Gaussian distribution. There were three possible means and two possible precisions (inverse of variance) of this distribution, which were factorially varied over trials, in randomised order. The probe stimulus was a single tone drawn from the same half-Gaussian distribution as the context stimuli for that trial, but with its intensity increased by one of two possible values (i.e. the *mean change*), which were also parametrically varied over trials.

These three stimulus parameters; hereafter referred to as *start mean* (the mean the context stimuli were drawn from), *precision* (precision of the context and probe half-Gaussian distributions within a trial), and *mean change* (the step size between the start mean and the mean the probe tone was drawn from); gave a total of 12 possible combinations of parameters for a given trial (see Figure 5A. to see how the 12 different stimulus parameter combinations affect the probability of probe stimuli exceed the ULL). These stimulus parameters determined the probability that the probe stimulus would reach or exceed the ULL, and by how much. Start mean was either 'low', 'medium', or 'high' (-10dB, -8dB, -6dB, relative to the ULL): mean change was either 'low' or 'high' (2.5 or 10 dB increase from the start mean), precision was either 'low' or 'high' ($\frac{1}{8}$ dB⁻¹ or $\frac{1}{2}$ dB⁻¹). As the probe stimulus was drawn from a half-Gaussian distribution, increased variance also increased the mean intensity of the distribution of possible probe tones to be drawn from, therefore decreased precision also meant an increase in probe stimulus intensity.

3.2.1.4. Data Analysis

Data analysis was conducted in RStudio (R version 4.2.2 (2022-10-31 ucrt)). As an initial step, each subject's responses were averaged across trials within each of the 12 stimulus conditions, and these subject averages formed the basis of statistical testing. For each experiment, normality of the distribution of data was visually assessed using the qqplot function, and a repeated measures ANOVA with full interaction terms was used to determine whether: 1) anticipatory aversity response significantly related to the IU group of the participant, start mean, and/or precision; 2) whether reported aversity response related to the IU group of the participant, start mean, precision, and/or mean change. Mean change was not included as a factor in the anticipatory response as it was not meaningful at this point in

the trial. For all ANOVAs, Mauchly's Test for Sphericity was used with Greenhouse-Geisser corrections if the assumptions of sphericity were not met.

Post hoc tests were run for each significant interaction effect, first by breaking the three-way interaction into two-way interactions, and then by comparing simple main effects for each significant two-way model. Finally, pairwise comparisons were run for each significant main effect for precision. At each stage Bonferroni adjustment was used for multiple comparisons.

An ANOVA was also run to determine if the volumes set as the ULLs related to the IU group and the time within the experiment the ULL was set (i.e. before block 1, before block 2, before block 3, or before block 4).

3.2.2. Results

3.2.2.1. Participant Responses and IUS results

Participants utilised the full range of values (1 – 4) in both their anticipatory responses based on the context tones (anticipation response) and their actual reported aversity of the probe tone (aversity perception response), as well as the anticipation and aversity perception responses in the block after the safety message had been given and stimulus parameters have been reduced (safety anticipation response and safety aversity perception response respectively). The grand mean and standard deviation for each response was as follows: mean anticipation response was 2.46 (± 0.99), mean aversity perception response was 2.50 (± 1.03), mean safety anticipation response was 2.35 (± 0.96), and mean safety aversity perception response was 2.39 (± 0.97).

Group	Median	Mean	SD	Min	Max	n
Full Dataset	33	34.25	10.09	12	58	147
Low IU (≤ 33)	27	26.15	5.27	12	33	75
High IU (> 33)	42	42.69	6.27	34	58	72

Table 4: Descriptive statistics for IUS -12 scores for Experiment 5

3.2.2.2. Uncomfortable Loudness Level

A two-way repeated measures ANOVA on the volume set as the uncomfortable loudness level, showed a significant main effect of timepoint (either before the 1st, 2nd, 3rd, or

4th trial block) within the experiment ($F(3, 572) = 4.763, p = 0.0027$). A strong negative trend approaching significance was shown for a main effect of the IU group of participants ($F(1, 572) = 3.579, p = 0.059$). An interaction effect between timepoint and IU was not significant ($F(3,572) = 0.075, p = 0.97$).

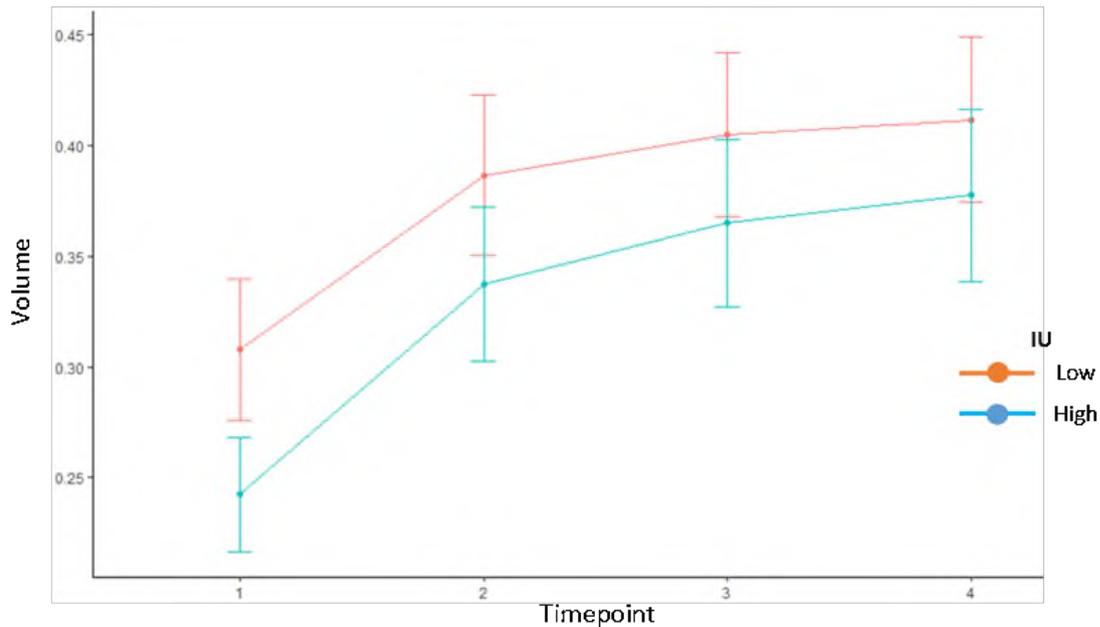


Figure 7. Mean uncomfortable loudness level set in Experiment 5. The mean (with standard deviation) uncomfortable loudness level set by participants at four different timepoints within the experiment. The y axis indicates the volume set as the uncomfortable loudness level as a proportion of the potential maximum system volume of the device used, with 0 indicating no sound, and 1 indicating maximum system volume. The x axis indicates the 4 timepoints in consecutive order, immediately before the 1st, 2nd, 3rd, and 4th block of trials respectively. The orange line indicates the low IU group, and blue line indicates the high IU group.

3.2.2.3. Anticipation Response

A three-way repeated measures ANOVA on the anticipatory response to upcoming potentially aversive stimuli, based on related context stimuli, showed significant main effects of IU group ($F(1, 1752) = 4.285, p = 0.039$), stimulus precision ($F(1, 1752) = 13.430, p < 0.001$), and start mean ($F(2,1752) = 99.305, p < 0.001$). No significant interaction effects were shown. This aversity anticipation response was higher in the high IU group than the low IU group,

lower with increased precision, and higher with a higher mean starting intensity (see Figure 8).

3.2.2.4. Aversity Perception Response

A four-way repeated measures ANOVA on the behavioural response to the aversity of the probe stimuli, showed significant main effects of precision ($F(1, 1740) = 13.666, p < 0.001$), start mean ($F(2, 1740) = 168.961, p < 0.001$), and mean change ($F(1, 1740) = 116.523, p < 0.001$). The relationship between behavioural response to the aversity of the probe stimuli and IU group was not significant ($F(1, 1740) = 2.711, p = 0.100$). No significant interaction effects were shown. This aversity perception response was higher when the mean change size was increased, higher when the starting intensity was higher, and lower when the stimulus precision was higher (see Figure 8). Although not found significant in the ANOVA, there was a visual trend that indicated a similar positive relationship between IU group and the aversity perception response as was observed as a significant finding in the anticipatory ratings.

3.2.2.5. Safety Block - Anticipation Response

A three-way repeated measures ANOVA on the anticipatory response to upcoming potentially aversive stimuli within the safety block, showed significant main effects of precision ($F(1, 1605) = 37.715, p < 0.001$), and start mean ($F(2, 1605) = 15.792, p < 0.001$). There was no relationship between the anticipation response in the safety block and IU group ($F(1, 1605) = 0.002, p = 0.96$). No significant interaction effects were shown. This anticipation response was higher when the starting intensity was higher, and lower when the stimulus precision was higher (see Figure 8).

3.2.2.6. Safety Block - Aversity Perception Response

A four-way repeated measures ANOVA on the behavioural response to the aversity of the probe stimuli within the safety block, showed significant main effects of precision ($F(1, 1595) = 13.999, p < 0.001$), start mean ($F(2, 1595) = 17.957, p < 0.001$), and mean change ($F(1, 1595) = 34.370, p < 0.001$). The relationship between the aversity perception response in the

safety block and IU group was not significant ($F(1, 1595) = 0.785, p = 0.38$). This aversity perception response was higher when the mean change size was increased, higher when the starting intensity was higher, and lower when the stimulus precision was higher (see Figure 8). One significant interaction effect was seen between stimulus precision and mean change size ($F(1, 1595) = 5.729, p = 0.017$). The interaction effect indicated that when mean change size was low, precision had a large impact on aversity perception response, with lower precision eliciting larger aversity response. When mean change size was high, precision had less of an effect, with the low and high precision groups eliciting similar aversity responses.

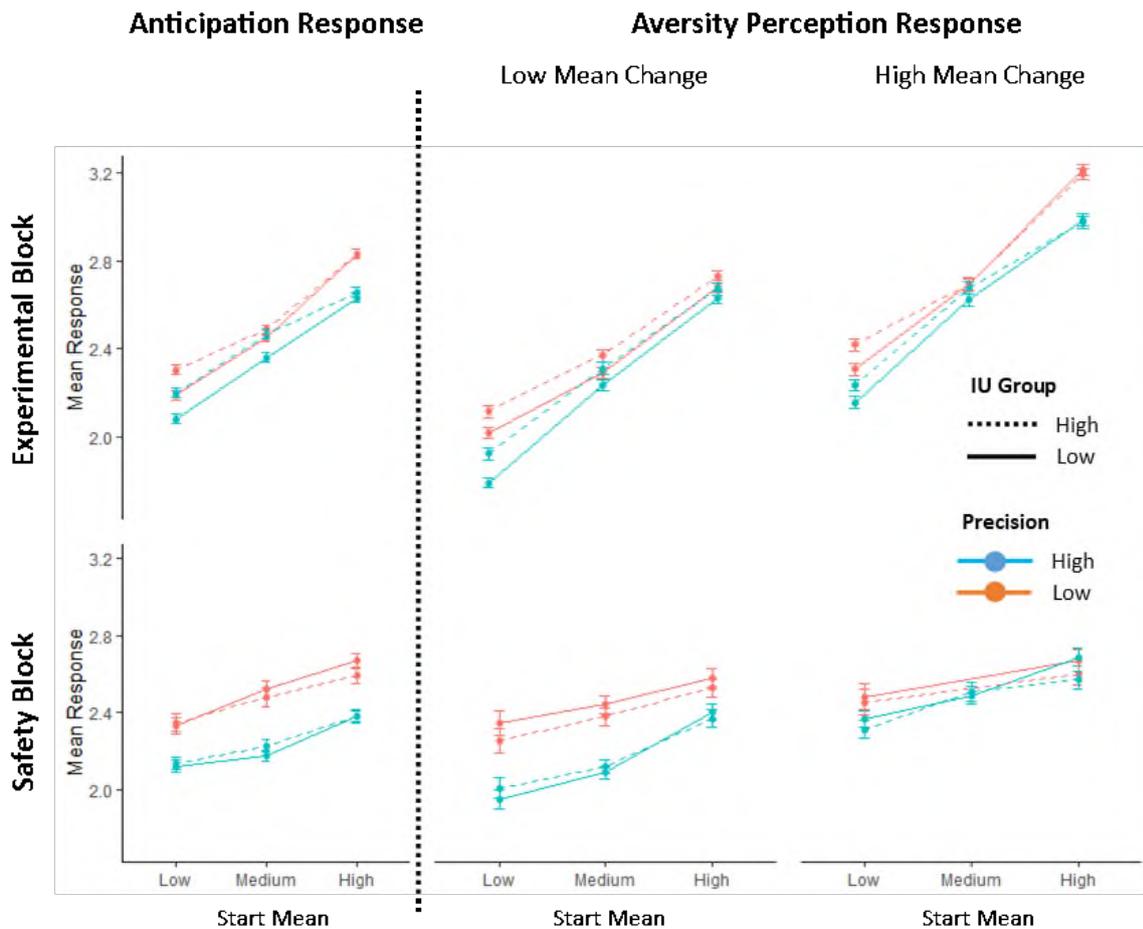


Figure 8. Mean anticipation responses and aversivity perception responses across all stimulus conditions in Experiment 5. Mean behavioural responses to context and/or probe stimuli across all participants for each stimulus category. The y axis indicates mean anticipation/aversivity perception response given in response to the relevant stimuli in a 1-4 scale. Y axis rows indicated by ‘Experimental Block’ and ‘Safety Block’ refer to the section of the experiment these results correspond to, with the safety block having altered stimulus statistics to reduce the probability of aversive stimuli. The x axis indicates the starting mean of the context stimuli, which indicates how likely stimuli were to exceed the ULL. Colour indicates stimulus precision (blue = high precision, orange = low precision). Solid lines and dashed lines indicated how these results varied across participants with high IU (dashed lines) and low IU (solid lines).

3.2.3. Discussion

3.2.3.1. Trivial and expected results

All four behavioural measures showed a positive relationship with starting mean, and the aversivity perception responses showed a positive relationship with mean change. This

likely indicates that participants understood the task and responded appropriately to stimuli with higher intensity. All four measures also found a main effect of precision, with higher responses relating to decreased precision. As the probe stimulus was drawn from a half-Gaussian distribution, with variance only able to increase the intensity and not reduce it, low precision likely indicated stimuli with higher intensity. Therefore, this relationship also indicated that participants noticed and responded to, albeit smaller, intensity changes in the context and probe stimuli.

The volume of the ULL was shown to increase significantly with the timepoints across the experiment. This is an expected and established effect of habituation. A trend approaching significance showed that participants in the high IU group consistently set lower ULL volume levels relative to the low IU group. This could indicate a higher degree of hyperacusis as I did not test for this as part of the experiment, and despite no literature exploring the relationship between hyperacusis and IU, hyperacusis has been shown to relate to anxiety (Jüris et al., 2012).

3.2.3.2. Intolerance of uncertainty results and interpretations

A significant relationship was found between intolerance of uncertainty group and anticipation response, with participants in the high IU group anticipating the probe to be more aversive than those in the low IU group, based on the equivalent context stimuli (already adjusted to the individual ULL). No relationship was found between intolerance of uncertainty group and either of the aversity perception measures, or the safety anticipation response. In fact, results in the safety block did not show even a trend in the same direction, and under conditions of low precision, the high IU group provided slightly lower ratings than the low IU group.

There was a non-significant trend that indicated that mean aversity perception response followed a similar response pattern to the anticipation response, with regards to higher responses in the high IU groups than low IU group, at the low starting intensity. I considered whether the reason I found significance in the relationship between the anticipation response and IU, and not between the aversity perception response and IU, was a result of the extra factor of mean change size in the aversity perception ANOVA. To check if

this was an effect of non-equivalent analyses, I reran the anticipation response ANOVA with the mean change size factor included, and still found this relationship to be significant ($F(1,1740) = 4.268, p = 0.039$).

These results imply that intolerance of uncertainty does not necessarily primarily affect how aversive participants find stimuli, but that people with high IU predict upcoming uncertain stimuli to be more aversive than people with low IU. This finding can be interpreted in a few different ways.

1. People with high IU are more likely to anticipate a negative outcome from some uncertain situations than people with low IU.
2. When a negative outcome is possible (or likely), people with high IU anticipate this negative outcome to be more aversive than people with low IU would.
3. The uncertainty of not yet having the full information of the trial causes sufficient distress to distinguish high IU and low IU participants, and this distress is picked up through the anticipation response.
4. Participants with high IU are showing more careful attention to the task itself, i.e. they are correctly anticipating the increase in aversity of the probe stimuli as opposed to low IU participants merely rating the aversity of the context stimuli.

The following experiment (Experiment 6) has additions that can potentially address some of these possible interpretations of findings. The addition of visual cues in 50% of the trials that accurately indicate the mean change size (and therefore upcoming aversity), would likely go some way in exploring the first two interpretations of the findings, because it would reduce the uncertainty in half of the trials, and the upcoming anticipation of aversity can be more accurate, so if high IU participants still anticipate more aversity than low IU participants, it would support the second interpretation. This could also address the fourth interpretation, as it would make the upcoming aversity easier to predict and reduce the chance of misunderstanding the task. An additional measure of general unease was added to address the third interpretation by differentiating general unease from the anticipation of aversive stimuli.

The results did not find that stimulus precision (which relates to the uncertainty of upcoming stimuli) relates to IU level in either anticipation response or aversity perception

response. This means the hypothesis that increased uncertainty of stimuli will exaggerate differences in response found between IU groups has not been supported.

3.3. Experiment 6 – Aversity psychophysics with present or absent visual cue

3.3.1. Introduction

This experiment essentially functioned as a replication of Experiment 5 with three major exceptions. The first is the addition of a general unease measure, to help distinguish between a sense of unease elicited by trial uncertainty, and anticipation of potentially aversive outcomes. The second difference is the introduction of a visual cue present in 50% of trials that accurately indicated the mean change size of the upcoming stimulus. This addition of salient information that is missing 50% of the time was intended to further differentiate responses between IU groups, as well as address some potential implications of findings from Experiment 5. The third is the removal of the safety block. To prevent over-complication.

3.3.2. Methods

3.3.2.1. Participants

129 participants were recruited for the study through prolific.co and paid £5 for the study. All participants were English speakers from the UK or USA and used headphones. From an initial 150 recruited participants, 21 unfinished responses were removed from the study. Median participant age was 37 (± 12.2) years old. 46 identified as male, 78 identified as female, and 5 identified as non-binary. Participants completed the IUS-12 questionnaire (Carleton, et al., 2007) and were categorised as either high or low intolerance of uncertainty, based on a median split (36). All participants gave informed consent at the start of the study, and ethical approval was granted under reference code 38257/2023.

3.3.2.2. Procedure

The experiment followed the same procedure as Experiment 5 (aversity psychophysics with or without safety cue), with three notable exceptions. The first is that there was no safety block. Therefore, the experiment consisted of 240 trials in four blocks of 60 trials. As with Experiment 5, before each block participants set an uncomfortable loudness level (ULL) above

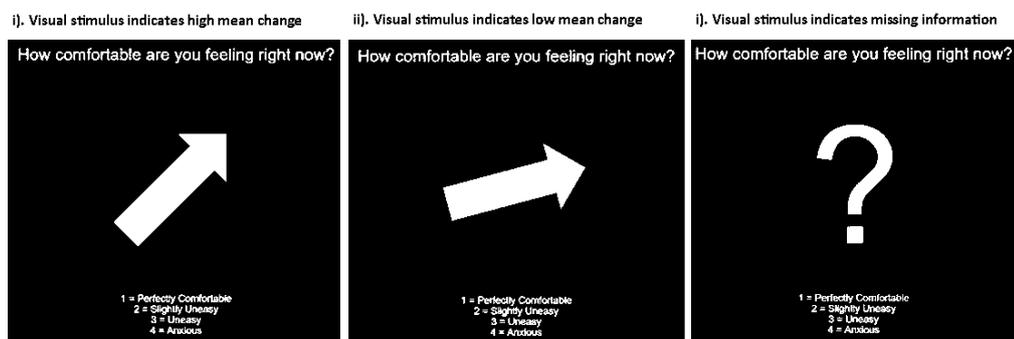
which sound intensity is reported as aversive. This ULL dictated the intensity of the stimuli of each trial, with certain stimulus properties resulting in trials exceeding the ULL. Each block consisted of 20 exemplars of the 12 different combinations of stimulus properties. The mean total experiment duration was 33 minutes.

The second alteration was that after hearing the context stimuli, but prior to giving the context response, participants were asked to give a rating of their current unease (unease response). Specifically, they were asked “How comfortable are you feeling right now?”, with the options of “perfectly comfortable”, “slightly uneasy”, “uneasy”, “anxious”.

The third alteration was the addition of a visual stimulus to correctly indicate the mean change size. This visual stimulus only gave any information 50% of the time. The visual stimulus was either a steep arrow (45° angle) to indicate a high mean change, a shallow arrow (75° angle) to indicate low mean change, or a question mark to indicate missing information. This was presented immediately after hearing the context stimuli whilst participants could answer the unease response.

Stimulus generation was performed using the same procedure as Experiment 5.

A). Visual stimuli given during unease response



B). Trial Structure

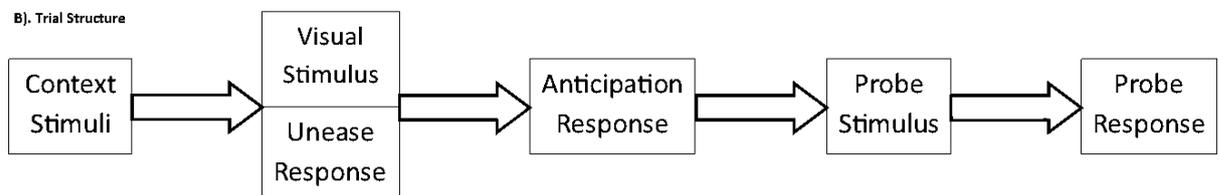


Figure 9. The visual stimuli and trial structure used in Experiment 6. A). The visual stimulus given during the unease response in the trial, indicating **i).** high mean change, **ii).** Low mean change, or **iii).** information about mean change size is missing (this occurred 50% of the time). **B).** The overall trial structure for this experiment.

3.3.2.3. Data Analysis

Data analysis was conducted using the same software and methods as Experiment 5. Repeated measures ANOVAs with full interaction terms were used for statistical analysis. A different measure of the visual stimulus variable used for the aversity perception ANOVA compared to the unease response and anticipation response ANOVAs. For the unease response and anticipation response ANOVAs, the visual stimulus measure was a three-way factor: either visual stimulus absent, visual stimulus indicating low mean change, and visual stimulus indicating high mean change. In the aversity perception response ANOVA, the visual stimulus measure was a two-way factor (either present or absent), and mean change size was added as a separate two-way factor (either high or low).

3.3.3. Results

3.3.3.1. Participant Responses and IUS score

Participants utilised the full range of values (1 – 4) in their anticipatory responses based on the context tones (anticipation response), their unease scale response (unease response), and their actual reported aversity of the probe tone (aversity perception response). The mean and standard deviation for each response is as follows: mean unease response was 2.10 (± 1.02), mean anticipation response was 2.26 (± 0.99), and mean aversity perception response was 2.22 (± 1.02).

Group	Median	Mean	SD	Min	Max	n
Full Sample	36	36.63	10.38	14	60	129
Low IU (≤ 36)	29	28.4	5.79	14	36	68
High IU (> 36)	46	45.78	5.57	37	60	61

Table 5: Descriptive statistics for IUS -12 scores for Experiment 6

3.3.3.2. Unease Response

A four-way repeated measures ANOVA on the level of general unease felt during a trial, showed significant main effects of IU group ($F(1, 2286) = 21.619, p < 0.001$), and starting intensity ($F(2, 2286) = 30.236, p < 0.001$). The relationships between the unease response and precision ($F(1, 2286) = 0.860, p = 0.35$), and the visual stimuli ($F(2, 2286) = 0.324, p = 0.72$) were not significant. This unease response was higher in the high IU group than the low IU group, and higher with a higher mean starting intensity (see Figure 10). There was a significant

interaction effect between precision and mean starting intensity ($F(2, 2286) = 4.305, p = 0.014$), which indicated that when the starting mean was higher, low precision elicited greater unease response than high precision stimuli. When the starting mean was lower, this effect of stimulus precision was not seen (see Figure 10).

3.3.3.3. Anticipation Response

A four-way repeated measures ANOVA on the anticipatory response to upcoming potentially aversive stimuli, based on related context stimuli, showed significant main effects of IU group ($F(1, 2286) = 9.764, p=0.0018$), and starting intensity ($F(2, 2286) = 14.296, p<0.001$). The relationships between anticipation response and precision ($F(1, 2286) = 0.510, p = 0.48$), and visual stimuli ($F(2, 2286) = 1.744, p = 0.18$) were not significant. This anticipation response was higher in the high IU group than the low IU group, and higher with a higher mean starting intensity (see Figure 10). There was a significant interaction effect between precision and mean starting intensity ($F(2, 2286) = 3.025, p = 0.049$), which indicated that when the starting mean was higher, low precision elicited greater anticipation response than high precision stimuli. When the starting mean was lower, this effect of stimulus precision was not seen (see Figure 10).

3.3.3.4. Aversity Perception Response

A five-way repeated measures ANOVA on the behavioural response to the aversity of the probe stimuli, showed significant main effects of IU group ($F(1, 3048) = 5.483, p = 0.019$), start mean ($F(2, 3048) = 120.549, p<0.001$), presence of the visual stimulus ($F(2, 3048) = 4.061, p = 0.044$), and mean change size ($F(2, 3048) = 212.944, p<0.001$). The relationship between aversity perception response and precision ($F(1, 3048) = 2.244, p = 0.13$) was not significant. Aversity perception response was higher when the mean change size was larger, higher when the starting intensity was higher, and lower when the stimulus precision was higher (see Figure 10). Aversity perception response was lower when the visual stimulus was present as opposed to when it was absent. There was a significant interaction effect between precision and mean starting intensity ($F(2, 3048) = 10.588, p <0.001$), which indicated that when the precision was low starting mean exhibited greater positive influence on the aversity

perception response. When precision was high this relationship was lessened (see Figure 10). There was also a significant three-way interaction effect between precision, mean change size, and visual stimulus presence ($F(1, 4.3) = 7.394, p = 0.0066$). There was also a significant interaction effect between precision and mean change size ($F(1, 3.7) = 6.335, p = 0.012$). This indicated that under low precision conditions, the distinction in aversity perception responses between high and low mean change values are more pronounced than in low precision conditions. No further interaction effects were found.

3.3.3.5. Notable Visual Trends

These ANOVA analyses were run with many factors, and ANOVAs make a lot of assumptions that potentially lead to missed findings. I believe there are notable visual trends in the data worth exploring that did not reach significance in the ANOVA. Although it is important to emphasise that these trends have not shown significance and must be tested before any interpretations of them can be considered with any weight. Firstly, with high precision, and absent visual cue, the anticipation responses (both unease and anticipation response) seem unaffected by mean start value, which was unexpected (See Figure 11). As this experiment had the extra dimension of the visual cue as a more concrete indication of incoming stimuli, it is possible that when it was missing and replaced with a question mark (indicating absence of information), participants interpreted this to mean other cues were also invalid for this trial (i.e. the starting value), or participants found the visual cue indicating absence distracting enough that they paid less attention to the other cues.

This same relationship, where high precision and absent visual cue lead to no effect of mean starting value, was visible in the aversity perception response but only when the mean change size was low and only in the low IU group. The high IU group did seem to correctly incorporate the start value into their aversity perception response. As such, the high IU group's responses did more accurately reflect the stimuli, whereas the low IU group carry forward this relative indifference or suppression of starting value information. With this same combination of variables but in the high mean change condition, the low IU group were similarly less affected by starting value, but in this case the high IU group seemed over reactive, giving higher aversity ratings than expected based on the stimuli.

Finally, in the high-precision conditions, the visual cue largely appeared to bias perceptual judgements (of aversity of the probe) away from the direction of the cue whereas in low-precision conditions it seemed to bias towards the direction of the cue. I.e. in high precision conditions, the visual cue indicating high mean change resulted in lower aversity perception, and the cue indicating low mean change resulted in higher aversity perception. Whereas, in low precision conditions, the visual cue indicating high mean change resulted in higher aversity perception, and the visual cue indicating low mean change resulted in lower aversity perception.

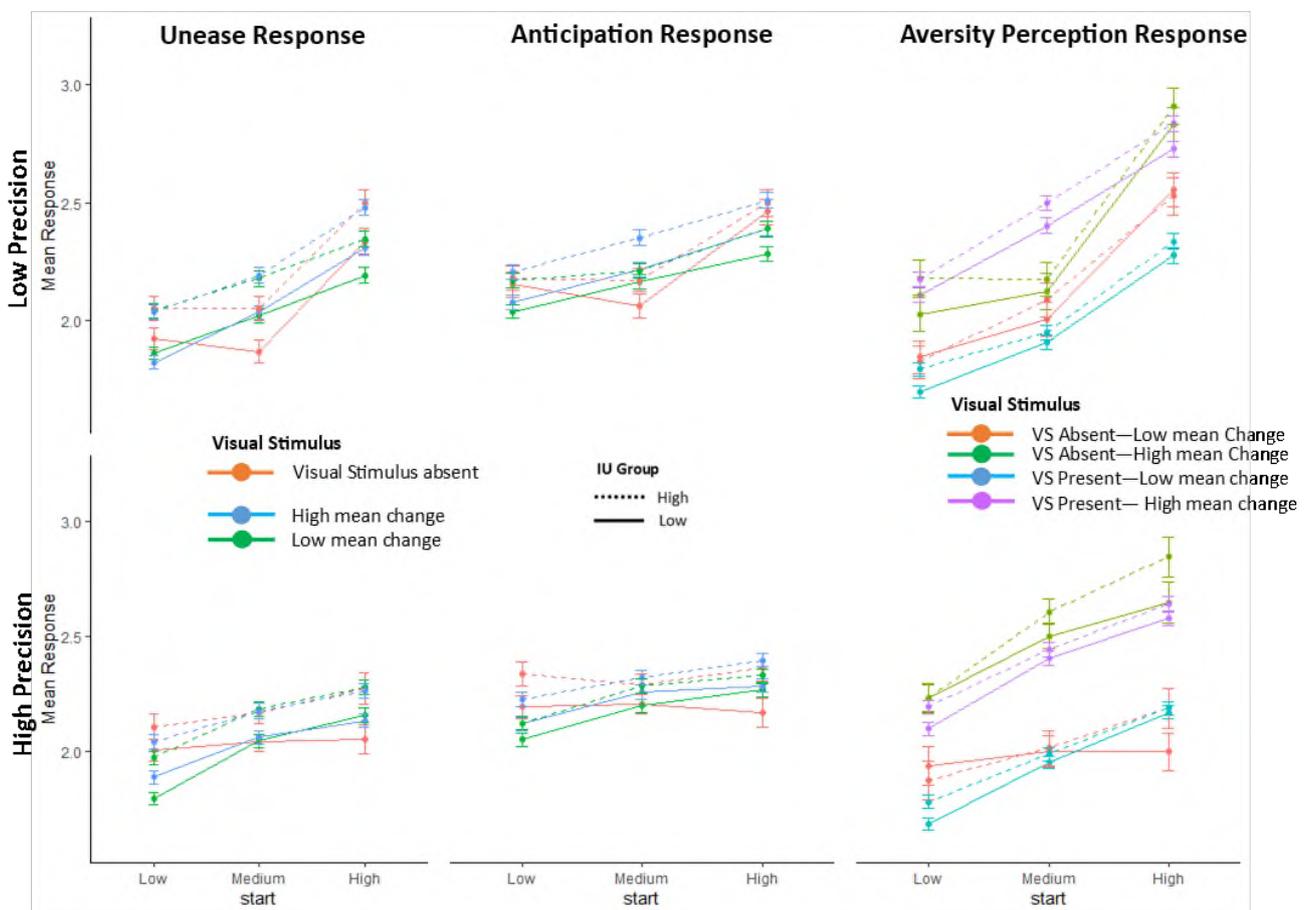


Figure 10. Mean unease, anticipation, and aversity perception responses across all stimulus conditions in Experiment 6. Mean behavioural responses to context and/or probe stimuli across all participants for each stimulus category. The y axis indicates mean unease/anticipation/aversity perception response given in response to the relevant stimuli in a 1-4 scale. Y axis rows indicate levels of stimulus precision, with the low precision condition on the top row, and the high precision condition on the bottom row. The x axis indicates the starting mean of the context stimuli, which indicates how likely stimuli were to exceed the ULL. Colour indicates the state of the visual stimulus and the mean change size. With the unease and anticipation responses, blue = visual stimulus indicated high mean change, green = visual stimulus indicated low mean change, orange = the visual stimulus was missing. With

the aversity perception response, orange = the visual stimulus was missing and mean change was low, green = the visual stimulus was missing and the mean change was high, blue = visual stimulus was present and indicated low mean change, magenta = visual stimulus was present and indicated high mean change. Solid lines and dashed lines indicated how these results varied across participants with high IU (dashed lines) and low IU (solid lines).

3.3.4. Discussion

3.3.4.1. Effects of mean change size, starting mean, and precision

All three behavioural measures showed a positive relationship with starting mean size, and the aversity perception response showed a positive relationship with mean change size. This likely indicates that participants understood the task and responded appropriately to stimuli with higher intensity.

None of the measures found a main effect of precision. I am interpreting this at least partially as a result of the increased complexity of this experiment compared to experiment 5 which found a main effect of precision in every measure. In this experiment (6), the visual cue adds an extra dimension of information that also highlights to the participants the effects of the mean change size. The more subtle effects of stimulus precision may become lost to the participants when they are able to rely on visual information (in 50% of the trials). With the anticipation rating, there is now more valid predictive cue available (the visual cue indicating mean change size) and therefore the relative contribution of the precision is lowered. With the aversity perception rating, however, there is no difference in the probe stimulus aversity between experiments. I can only conclude that either the presence of this main effect of stimulus precision in Experiment 5, or its absence in Experiment 6, must be mediated by differences in predictions made prior to hearing the probe stimulus.

However, precision did seem to effect results outside of a main effect; these effects indicate an increase in trial uncertainty which in turn affected how participants responded to other stimulus properties. For example, all three response measures found an interaction effect between precision and starting mean intensity. Overall, this relationship indicated that under low stimulus precision conditions (and increased uncertainty of incoming stimuli) starting mean exerted more influence.

Interestingly, with high precision, and an absent visual cue, the anticipation responses (both unease and anticipation response) seem unaffected by mean start value, which was unexpected. As this experiment (6) had the extra dimension of the visual cue as a more concrete indication of incoming stimuli, it is possible that when it was missing and replaced with a question mark (indicating absence of information), participants interpreted this to mean other cues were also invalid for this trial (i.e. the starting value), or participants found the visual cue indicating absence distracting enough that they paid less attention to the other cues. The interpretation of stimulus precision's role in this relationship again seems to be that under low stimulus conditions, starting mean exerted more influence.

The unease response and anticipation response showed very similar overall response patterns, and both the respective ANOVAs showed significance with the same main effects and interaction effects. One interpretation of these results is that they indicate the unease and anticipation measures have been conflated into a single subjective feeling, which forms the basis of both measures. This may be a result of these measures taken consecutively within the trial structure (see Figure 8b), as well as participants encouraged to respond instinctively; in the instructions participants were informed that "we recommend having your fingers resting on the '1', '2', '3', and '4', keys for faster answering". I.e. participants likely had their fingers resting on the respective keys and were quickly and instinctively giving two measures based on the context stimuli and visual stimulus, immediately prior to experiencing a potentially aversive probe stimulus. Although an alternate explanation is that within the structure of this trial, participants' current unease might at least in part form the basis of the anticipation of upcoming aversity.

3.3.4.2. Visual Stimulus Results

Overall, the absence of the visual cue resulted in increased mean aversity perception scores compared to trials where the visual cue was present. In relation to mean change size (indicated by the visual cue) specifically, participants gave highest mean aversity scores to trials where visual stimulus was absent and mean change was highest, next highest scores were given to trials where the visual stimulus was present and mean change was high, followed by trials where the visual stimulus was absent with low mean change. The lowest mean aversity response was to the trials where visual stimulus was present and showed low

mean change. Although when split by high or low precision, this relationship seems slightly more complex, e.g. in the high precision condition, high mean change and present visual stimulus scores higher in aversity perception response than high mean change and absent visual stimulus in the medium starting condition.

The unease response and anticipation responses found no relationship with the visual stimulus measure (which in these analyses was included as a single 3-way factor, indicating either high mean change, low mean change, or missing information). The aversity perception response found a negative relationship with the visual stimulus variable (in this analysis, visual stimulus was included as a 2-way factor, either present or absent, and mean change was included as its own 2-way factor, either high or low). Both the presence and content of the visual cue did not influence predictions of upcoming aversity, but both of these variables influenced how aversive the probe stimulus was perceived to be. Therefore, the visual cue has influenced perception, but without participants prospectively realising it influenced it. These results indicate that under the same sensory conditions, the absence of a cue does not necessarily increase the anticipation of a potentially aversive outcome, but it does increase how aversive the outcome is perceived as.

It is worth noting that the visual information given in the experiment would likely be processed as a rule-based cue, as opposed to the stimulus-based cues of the stimulus statistics, which would bias auditory perception and responses through distinct neural mechanisms to stimulus-based cues (Tardiff et al., 2022). The cues of experiment 5 were entirely stimulus-based, which are understood to reflect to bottom-up neural processes in the auditory system and are thought to result in responses that are faster, more instinctual, and less accurate (Chambers et al., 2016; Tardiff et al., 2022). Rule-based cues, such as the visual stimulus used in experiment 6, are thought to be processed through top-down mechanisms that result in slower responses that are more accurate as a result of higher-level neural processes (Summerfield & de Lange, 2014; Tardiff et al., 2022).

Upon visual inspection, the aversity perception results indicated that the level of precision altered the effects of the visual stimulus. In the high-precision conditions, the visual cue largely biases perceptual judgements (of aversity of the probe) away from the direction of the cue whereas in low-precision conditions it biases towards the direction of the cue. Recently, Tardiff et al. (2022) found that auditory cues with low signal-to-noise ratio bias

responses towards recent stimuli, and cues with high signal-to-noise ratio bias responses away from recent stimuli. This result supports this finding that altering levels of stimulus precision can change how responses are biased towards or away from cues.

3.3.4.3. Intolerance of Uncertainty Results and Interpretations

A main effect of intolerance of uncertainty group was found with all three measures: unease, anticipation, and aversity perception. As the unease and anticipation measures shared all results and showed a very similar response pattern, I have interpreted these results as indicating the measures have been conflated into one general anticipatory response, or that alterations in anticipated aversity have their basis in current sense of unease. Regardless, this implies that the high IU group anticipated the probe stimulus to be more aversive based on the context stimulus and once the probe stimulus arrived, they also perceived it as more aversive than the low IU group. As the perception of the aversive stimuli was higher in the high IU group, their increased anticipation of aversive stimuli (compared to the low IU group) seems a reasonable response and does not necessarily indicate an over-anticipation of aversity. Although the relationship is likely not this simple, as the degrees of increased responses relating to intolerance of uncertainty varied under different stimulus conditions.

The greatest distinction shown between aversity perception responses from high and low IU participants was when responding to stimuli with high mean change size, high starting intensity, high precision, and the visual stimulus absent (i.e. indicating missing information). The most aversive aversity perception response would likely be elicited by the highest mean change size and highest starting intensity, and these conditions with a missing visual stimulus elicited the most aversive responses. When these stimuli are expected (with informative visual stimulus) the difference in aversity response between high and low IU groups is small, but when these stimuli are unexpected, participants with high IU rate these responses as more aversive than low IU participants. This finding could be indicative of a wider pattern of results relating to IU discussed below.

As previously discussed (see 3.3.4.1), during conditions of high precision, and an absent visual cue, the anticipation responses (both unease and anticipation response) seem unaffected by mean start value. This same relationship was found in the aversity perception

response but only when the mean change size was low and only in the low IU group. The high IU group did correctly reflect the start value in their aversity perception responses. As such, the high IU group's responses do more accurately reflect the stimuli, whereas the low IU group may carry forward this relative indifference or suppression of starting value information. With this same combination of variables but in the high mean change condition, the low IU group are similarly less affected by starting value, but in this case the high IU group seem over-reactive, giving higher mean aversity perception ratings than expected based on the starting value. When considering both of these findings together, I could infer that, under certain conditions of uncertainty, high IU is associated with a tendency to make fuller use of multiple sources of predictive and stimulus information (such as correctly using the starting mean size) when making perceptual judgements. But this also leads to a tendency to exaggerate unexpectedly aversive stimuli.

3.4. General Discussion

3.4.1. Notable findings

In experiment 5, all response measures found a main effect of precision. In experiment 6, none of the measures found a main effect of precision, however, all measures found an interaction effect of precision and starting mean intensity. I am interpreting this lack of a main effect of precision at least partially as a result of the increased complexity of experiment 6, as well as the replacement of a main effect of precision with an interaction effect. This finding is perhaps more understandable with the anticipation rating, as there is now a more meaningful predictive cue available (the visual cue indicating mean change size) and therefore the relative contribution of the precision is lowered. With the aversity perception rating, however, there is no difference in the probe stimulus aversity between experiments. I can only conclude that either the presence of this main effect of stimulus precision in Experiment 5, or its absence in Experiment 6, must be mediated by differences in predictions made prior to hearing the probe stimulus (relating to the visual cue). Interestingly, both the presence and the content of the visual cue did not influence predictions of upcoming aversity, but both of these variables influenced how aversive the probe stimulus was perceived to be once it occurred. Therefore, this variable has influenced perception, but without participants prospectively realising it has influenced it.

3.4.2. Hypotheses

The hypothesis that, under conditions of uncertainty, people with high IU are biased towards predicting more aversive outcomes was supported by the results. In both experiments, anticipation response was shown to be higher in the high IU group compared to the low IU group.

The hypothesis that under conditions of sensory uncertainty, people with high IU perceive aversive stimuli as more aversive than low IU people, was partially supported by the results. Experiment 6 showed that high IU participants gave higher aversity perception responses than the low IU group. The results from Experiment 5 did not show a significant relationship between IU group and aversity perception response. The interpretation of this difference in finding between experiments is discussed in Chapter 3.4.3.

I hypothesised that participants with high IU would report a greater sense of unease under conditions of uncertainty, than low IU participants. Despite finding a significant relationship between IU and the unease response in Experiment 6, I do not assume the results confirm this hypothesis, as I believe the unease response and aversity anticipation responses may have been conflated into one general anticipation response. This is discussed in more detail in Chapter 3.3.4.1.

The hypothesis that differences between IU groups are exaggerated under more uncertain conditions is not met, as increased precision did not relate to intolerance of uncertainty score in either experiment. However, trends seem to indicate a more complex relationship between stimulus precision and IU (discussed in Chapter 3.3.4.3). Interestingly, Experiment 6 showed the largest effects of IU group, and this experiment had less uncertainty (but more sources of predictive information).

The hypothesis that effects of intolerance of uncertainty will be more exaggerated under conditions of missing information was not supported by the results from the ANOVA, as there were no interaction effects of IU and presence of visual cue. However, trends in the data imply a more complex relationship between IU and presence of a visual cue, and one that could at least partly support this hypothesis (discussed in Chapter 3.3.4.3).

The hypothesis that IU is related to an incapacity to trust safety signals is not supported, as the results of Experiment 5 do not show any relationship between IU and any measure in the safety block.

3.4.3. Intolerance of uncertainty findings

Overall, in both experiments IU was found to have a main effect on the anticipation of potentially aversive stimuli. Participants with high IU anticipated incoming stimuli to be more aversive than low IU participants. Experiment 5 did not find IU to have an effect on aversity perception response, although a visual trend in the data indicated the mean aversity response followed a similar response pattern to the significant relationship found with the anticipation response. Specifically, that in the low starting intensity condition higher responses were found in the high IU groups than low IU group. Experiment 6 did find a main effect of intolerance of uncertainty on the aversity perception response. This may indicate that the added complexity of Experiment 6 strengthened a trend present but not quite showing significance in Experiment 5.

Under particular conditions of uncertainty (see Chapter 3.3.4.3 for details), the high IU group gave more nuanced and appropriate aversity perception responses to the cues given during the trial. However, under similar conditions of uncertainty, but with increased stimulus aversity, the high IU group also gave higher aversity perception responses, but to a seemingly overreactive degree. When considering both of these findings together, I could infer that, under certain conditions of uncertainty, high IU is associated with a tendency to make full use of multiple sources of predictive and stimulus information when making perceptual judgements. But this also leads to a tendency to exaggerate unexpectedly aversive stimuli.

3.4.4. Limitations and Future Directions

One limitation is the potential conflation of the unease response and the anticipation response, possibly as a result of a methodological flaw, within Experiment 6. These measures were taken consecutively within the trial structure (see Figure 8b), as well as participants encouraged to respond instinctually, e.g. in the instructions participants were informed that “we recommend having your fingers resting on the ‘1’, ‘2’, ‘3’, and ‘4’, keys for faster

answering". The response patterns were very similar (see Figure 10) and found the same main and interaction effects of stimulus statistics in their respective ANOVAs. If these measures have been conflated into one general anticipatory measure, replication with an unease measure taken at an alternate time, e.g. after every block or at another timepoint within each trial (e.g. at the end of each trial), would be valuable. A valid unease measure would be an important step in distinguishing whether intolerance of uncertainty results from the anticipation or perception of aversive outcomes in the context of sensory uncertainty, or whether it results from a general feeling of discomfort in the face of uncertainty itself.

These experiments adapted a previous paradigm (Experiments 1-4, Chapter 2) with multiple alterations anticipated to induce sufficient uncertainty to reveal differences between high and low IU groups, with the intention of subsequent work then removing elements to uncover the requisite components of experimentally eliciting intolerance of uncertainty. In particular, replication that explores the full spectrum of valence, from pleasant to unpleasant stimuli, could be invaluable in understanding how IU varies with sensory uncertainty that is not necessarily tied to potentially aversive outcomes.

Further limitations worth highlighting are that these experiments were run online. Therefore, we had less control over the stimuli with regards to system volume, distractions, and headphones usage. In-person replication may be useful to validate these results. These experiments began with an IUS-12 which could potentially have a priming effect on participant responses during the experiment. However, the task itself being repetitive, uncertain, and potentially aversive in some conditions is also likely to prime the results of the intolerance of uncertainty score. Nonetheless, future studies may consider counterbalancing or delaying a self-reported IUS to mitigate order effects.

IU was operationalised using a median split on IUS-12 scores, to classify participants into high and low IU groups. While IU is a continuous construct with no established thresholds to indicate high/low IU, the use of a median split was motivated by the need to directly compare patterns of behavioural responses across clearly distinguishable groups. This categorical approach facilitates interpretability, and supports the goal of identifying conditions that could distinguish individuals with high IU in a clinically meaningful way. I acknowledge, however, that this comes at the cost of statistical power, and therefore may

obscure more nuanced findings. Future work could complement this approach with regression-based analyses to investigate individual variability more precisely.

The IUS-12 contains two subscales, prospective and inhibitory IU; the analysis in this study used the total IUS-12 score as a unidimensional measure of general intolerance of uncertainty (Carlton et al., 2007). This decision to not analyse subscales was made primarily to maintain statistical power and minimise Type I errors associated with multiple comparisons. However, a crucial next step is to explore how inhibitory vs. prospective IU differentially relate to behavioural and physiological responses under uncertainty.

Future directions could also explore the stimulus conditions found to create the greatest distinction between IU groups to understand the individual contributions and relationships that contribute to differences in intolerance of uncertainty.

3.4.5. Conclusions

The results of these two experiments showed that participants with high IU anticipated incoming stimuli to be more aversive than low IU participants. Experiment 6, but not Experiment 5, found intolerance of uncertainty to positively related to aversity perception. This may indicate that the added complexity of Experiment 6 strengthened a trend present but not quite showing significance in Experiment 5. Under certain conditions of uncertainty the high IU group gave more nuanced, and appropriate to the cues and probes presented, aversity perception responses during the trial. However, under similar conditions of uncertainty, but with increased stimulus aversity, the high IU group also gave higher aversity perception responses, but to a seemingly overreactive degree. This finding indicates that high IU is associated with a tendency to make full use of multiple sources of predictive and stimulus information when making perceptual judgements. But this also leads to a tendency to exaggerate unexpectedly aversive stimuli. These findings require replication and an exploration into their generalisability, but this suggests a pattern of increased sensitivity shown by people with high IU to specific conditions of uncertainty that implies a more nuanced understanding of the trait that comes with advantages and disadvantages.

4. Experiment 7 – Temporal expectation with physiological measures

4.1. Introduction

4.1.1. Temporal Expectation

Temporal expectation refers to the ability to predict when an event will occur. People use both sensory cues, and internal priors, to anticipate when future events will occur, enhancing behavioural outcomes (Nobre, 2001). Temporal processing is likely a factor in anxiety-based disorders, as it has been shown that compared with a control group, people with anxiety have been shown to consistently underestimate time periods (Mioni et al., 2016). Similarly, experimentally induced anxiety (relating to unpredictable events) was shown to associate with underestimating time intervals, which was not found with induced transient fear (Sarigiannidis et al., 2020). Flores et al., (2020) found that increased prospective intolerance of uncertainty (a subfactor of IU) related to worse discrimination between threatening and safe time periods. However, one study exploring the interaction between intolerance of uncertainty and startle response to perceived threat found that participants with high IU had a smaller startle response under conditions of temporally uncertain threat (Nelson and Shankman, 2011).

This literature implies that impaired temporal processing relates to anxiety-based disorders, but the mechanisms behind this relationship are unclear. It seems logical that if people struggle to predict when an event will occur, it would lead to more surprise when it does occur, and would lead to an increase in uncertainty from everyday situations. If people with high intolerance of uncertainty are impaired in their ability to make temporal predictions, this could at least partially explain why people with high IU feel the need to control their life in order to prevent uncertain situations. However, there is a lack of literature experimentally investigating the relationship between intolerance of uncertainty and temporal expectations.

4.1.2. Physiological Measures

When investigating the neural computations of intolerance of uncertainty, physiological measures, alongside behavioural ones, are invaluable. Crucially, some physiological measures can be made continuously without interrupting a task, and offer high temporal resolution,

and thus provide a detailed response over a time course. Whilst the behavioural responses to uncertainty used in my previous experiments were encouraged to be instinctual and were intended to represent as early processing of uncertainty as possible (e.g. the anticipation response and aversity perception response used in Experiments 5 and 6, Chapter 3), these responses still represent responses to uncertainty through action that requires some level of decision making. Physiological measures can reveal unconscious responses from the brain and provide insight into the preconscious processing of uncertainty, as well as being able to show more subtle responses beyond what is observable by behaviour alone. For example, Endrass et al., (2008) showed that event-related potentials, measured through EEG, indicated over-active performance monitoring in people with OCD that was not captured by behavioural correlates of performance monitoring. This study uses three physiological measures to investigate the relationship between IU and temporal expectations, contingent negative variation, alpha oscillations, and pupil dilation.

Contingent negative variation (CNV) is an event-related potential recorded through electroencephalography (EEG) that appears as a negative shift in the EEG signal that occurs between two events, typically a warning signal and a target stimulus (Walter et al., 1964). CNV is understood to be a reliable physiological measure of anticipation of upcoming stimuli, as well as showing attention to, and the preparedness of motor responses to, the stimuli (Tecce, 1972; Leuthold & Jentsch, 2001; Fan et al., 2007) (e.g. pressing a button when you notice a change).

Alpha oscillations are patterns of brain activity in the frequency range of 8-12Hz, and are most prominent in the posterior regions of the brain (i.e. occipital and parietal lobes) (Niedermeyer, 1993). Alpha oscillations are associated with the brain being in a relaxed but wakeful state, and they relate to inhibition of sensory input. Alpha activity in the auditory system is desynchronised by auditory stimuli (Tiihonen et al., 1991). Alpha oscillations are inversely related to attention; when attention is required for a specific task, alpha oscillations in the relevant brain regions desynchronise which reflects increased cognitive engagement in the task (Uusberg et al., 2013). After completion of a task, alpha oscillations then resynchronise, relating to a more relaxed, less focussed state.

Pupillometry is the measurement of pupil size and dynamics to indicate arousal levels, as well as to give more complex insight into autonomic nervous system responses to stimuli

relating to attention, cognitive load, listening effort, emotional arousal, and stress (Stanners et al., 1979; Bradley et al., 2008; Zénon, 2019). Pupil dilation has also been shown to increase when confronted with uncertainty in a gambling task (Lavín et al., 2014). Pupillometry as a measure has good temporal resolution and has been used as a measure of surprise and attention in temporally uncertain tasks (e.g. Preuschoff et al., 2011; Lempert et al., 2023). It is important to highlight that, as the autonomic nervous system must process the stimulus and initiate the physiological response before visible changes in pupil dilation can take place, there is a short time lag between stimulus onset and pupil dilation. This is commonly between 200 ms and 500 ms, but can range up to 1000 ms in cases of more complex or emotionally valent stimuli (Einhäuser et al., 2008; Laeng, Sirois, and Gredebäck, 2012).

4.1.3. Hypotheses and Predictions

Hypothesis 1 – Intolerance of uncertainty relates to an aberration in temporal expectation; people with high IU are less able to selectively attend to when an event is likely to happen, and will deploy increased attention outside of optimum windows.

Hypothesis 2 – Intolerance of uncertainty is unrelated to people’s accuracy of temporal expectations; people with high IU are not impaired in their ability to predict when events will happen, but simply find the experience of temporal uncertainty aversive.

In order to test these hypotheses, the following experiment manipulates temporal precision relating to stimulus change that participants must respond to as quickly as possible. This stimulus change occurs in 50% of trials. The three physiological measures used in this study are expected to respond to time points associated with increased temporal probability of change in the following ways: pupil dilation is expected to increase, the CNV response is expected to show increased negative potential, and/or the alpha oscillations are expected to decrease in amplitude. If the physiological measures support these hypotheses, I predict the following results patterns.

- For the physiological results to support hypothesis 1, I predict a distinct response pattern between IU groups. I predict physiological response in the high IU group to show no differentiation between precision conditions, and show a general level of increased physiological response across the trial period. I predict the physiological

responses in the low IU group to approximately follow the changing probability of stimulus change (Figure 11).

- For physiological results to support hypothesis 2, I predict both high and low IU groups to follow a similar pattern in the time course of physiological response approximately matching the changing probability of stimulus change (Figure 11), but with the high IU group showing a stronger physiological response: i.e. increased pupil dilation, more negative CNV, decreased alpha amplitude.

4.2. Methods

4.2.1. Participants

22 participants with IU score of 25 and lower formed the low IU group; mean and standard deviation of the low IU group was 20.13 ± 2.93 . 22 participants with IU score of 31 or higher formed the high IU group; mean and standard deviation of the high IU group was 39.00 ± 6.19 . These groups were selected to be matched in demographics. Full demographic breakdown can be found in Table 5. To avoid effects of IU-related co-morbidities, potential participants were excluded from the study after pre-screening if they had a formal diagnosis of GAD or were currently taking any medication for a neurological or mental health disorder. These criteria disproportionately excluded potential high IU participants, with 1 potential low IU participant excluded and 7 potential high IU participants excluded.

81 Participants were pre-screened with the IUS-12 collected with an opportunity sample, advertised to friends and colleagues, on University social media (Yammer), and posters put up in the University Medical and Dental School. The sample was collected with the intention of a quartile split with the 1st quartile of 20 participants being the low IU group, and the 4th quartile of 20 participants becoming the high IU group. However, as rates of attrition and co-morbidities were higher in the high IU group, the IU threshold was moved to allow sufficient participants. The 1st and 4th quartile IU scores were 21 and 34 respectively. The actual low/high IU thresholds used in the study were ≤ 25 and ≥ 31 , respectively. There is no established clinically validated threshold score to distinguish high and low IU. However, one study suggests an IUS-12 score of 28 as an optimal cutoff for distinguishing individuals with GAD from non-clinical cases (Wilson et al., 2020). The thresholds used in this study, ≤ 25 and ≥ 31 , should therefore serve as sufficient to differentiate high and low IU participants. All

participants gave informed consent at both the pre-screening stage and in-person experiment and had the opportunity to withdraw at any time. University ethical approval was granted under the reference code 41990/2023.

IU Group	Mean Age	SD Age	Male ppt.	Female ppt.	NB ppt.	Total ppt.
Low (≤ 25)	25	4.5	11	11	0	22
High (≥ 31)	25	5.5	11	9	2	22

Table 6: Demographic information for each IU group. Mean and standard deviation participant age, number of male, female, and non-binary participants, and total number of participants.

4.2.2. Procedure

The experiment was run through MATLAB (R2021a, version 9.10.0.1602886). After receiving experiment instructions and completing ten practice trials, participants completed 220 trials in four blocks of 55 trials. In between the blocks, participants were prompted to take a break. Trials consisted of listening, through headphones, to a continuous auditory stimulus (in the form of regular interval noise; RIN, first used by Yost (1996)), of 10s duration, which changed to a target stimulus (spectrally equivalent Gaussian noise) in 50% of trials, at a semi-predictable time. The transition from RIN to Gaussian noise was not accompanied by any change in spectral energy, but only the cessation of a pitch percept, to minimise the chance of eliciting any stimulus-driven alerting response.

The mean time of the change occurring was always five seconds into the trial, the standard deviation was different in the two precision conditions; the high precision condition had a standard deviation of 0.5 seconds, and the low precision condition had a standard deviation of 2 seconds (see Figure 11). Participants were instructed to press a button as quickly as possible if they notice the stimulus change into the target stimulus. There were two different pitch values at which the auditory stimulus was played. The pitch value consistently indicated the variance of the time when the context stimulus would change into the target stimulus. The association between the higher (512 Hz) and lower (128 Hz) frequency stimulus and the temporal precision condition was randomized. This meant that in 50% of experiments the higher frequency context stimulus (512 Hz) indicated a standard deviation of 0.5s, the low frequency context stimulus (128 Hz) indicated a variance with a standard deviation of 2s (see

Figure 11). This relationship was reversed in the other 50% of experiments, so that high frequency stimulus indicated higher variance etc.

Participants received immediate feedback as soon as they pressed the button, or when the trial ended. This feedback indicated whether they correctly pressed the button after a change occurred (correct hit), incorrectly pressed the button when a change did not occur (false alarm), incorrectly did not press the button when a change did occur (miss), or if they correctly did not press a button when a change did not occur (correct reject). With correct hits, participants were also given their reaction time from the moment the change occurred to when they pressed the button. They were encouraged to try to minimise this reaction time.

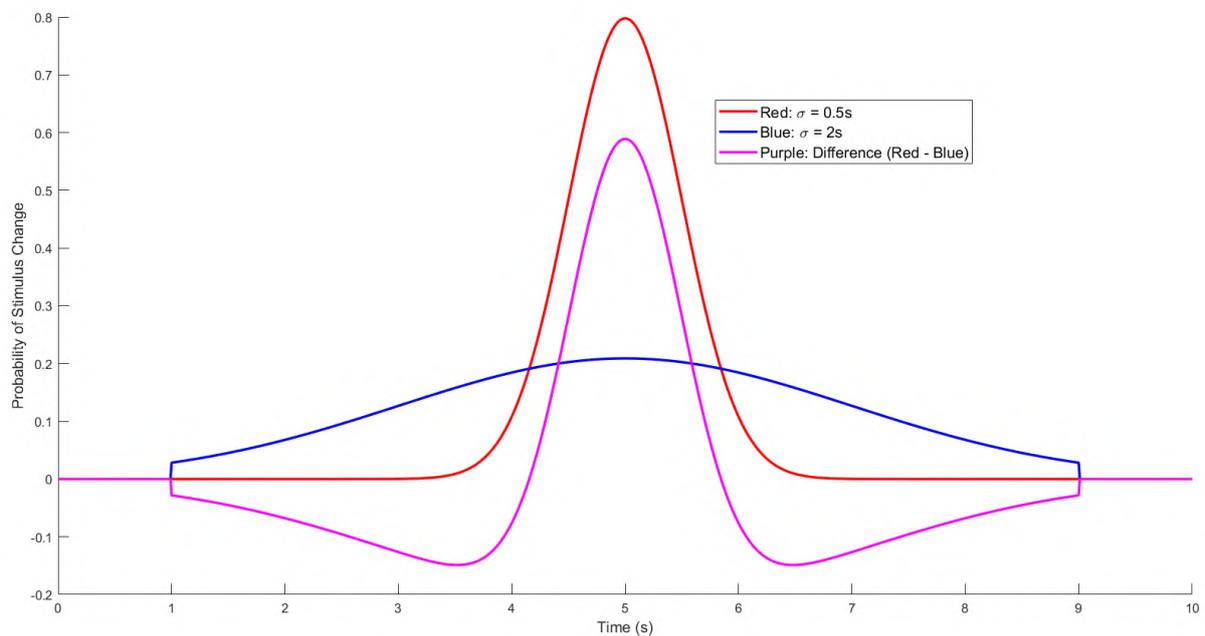


Figure 11. The changing probability of stimulus change in Experiment 7. The changing probability of stimulus change over the trial time in the 50% of trials where a change occurred, in the two different precision conditions. The y axis indicates the probability of stimulus change at that timepoint. The x axis indicates the time (in seconds) within the trial. The probabilities in both conditions followed a gaussian distribution with a mean time of stimulus change at 5 seconds, and a minimum and maximum time of stimulus change at 1 and 9 seconds respectively. The blue curve indicates the low precision condition (indicated to participants by stimulus frequency) where the standard deviation of the probability is 2 seconds. The red curve indicates the high precision condition where the standard deviation of the probability of stimulus change is 0.5 seconds. The magenta line indicates the difference between the two temporal conditions.

4.2.3. Physiological measures

Participants performed the experiment in a dimly-lit soundproofed room. EEG data were continuously recorded during stimulus presentation using a 64-channel cap using the Biosemi ActiveTwo system. Electrode offset was kept within manufacturer recommended limits (± 10 mV). Pupillometry data were recorded using an Eyelink Pro eye tracker, without head fixation, tracking the left pupil.

4.2.4. Data Analysis

All data analysis was performed using MATLAB (R2021a, version 9.10.0.1602886). Only correct reject trials (i.e. no stimulus change, and no button press) were subject to physiological data analysis. This was to avoid any noise or artefacts in the EEG/pupillometry data relating to the perception of the stimulus change and/or movement when pressing the button. Mean reaction times were taken from correct hit trials only. A two-way mixed measures ANOVA was used to investigate how mean reaction times changed in different precision conditions in the high and low IU groups. To test if there was a difference in accuracy, Wilcoxon rank-sum test was used to compare the number of hits and misses between high and low IU responses.

For the pupil analysis, blinks and other aberrant values were removed and missing values were interpolated. Trials without a sufficient baseline period, or with more than 15% missing data, were excluded. All trials were baseline corrected, smoothed, and trials in each condition were averaged for each subject.

For the two EEG analysis measures, CNV and alpha oscillations, the responses were referenced to channels P9 and P10, and the channel of interest was selected (Fz for the CNV response and POz for the alpha response). Data were filtered using 0.01 Hz and 15 Hz cutoffs for the CNV response, and using 8 Hz and 12 Hz cutoffs for the alpha response. The data was then epoched to each trial, and an independent component analysis was performed to remove eye blinks and other ocular artefacts from the data. For the alpha response, the data were converted to the amplitude envelope, via the Hilbert transform, to focus on the strength of alpha activity over the trial. Trials with outlying values were rejected, based on visual inspection of the histogram of the maximal absolute value for each trial. Trials were averaged

within each experimental condition, and baseline correction was performed. For the CNV response the baseline of -0.1 to 0 s peristimulus time was subtracted from the signal. For the alpha response the signal was divided by the mean baseline across all experimental conditions, and then the data were log transformed.

Due to the low low-pass filter setting required in light of the long trial duration, and the potential for large low-frequency artefacts to be present, CNV trial-average data were visually inspected for an N100 and P200 response to the stimulus onset, and data from 8 participants were removed from analysis on the basis of these responses not being discernible, or being of much lower amplitude than other deflections in the waveforms. Both EEG responses, and the pupillometry responses, were then subject to non-parametric permutation analysis, with 1,000 permutations. This analysis compared t-scores of: high and low precision in the high IU group (randomising trial precision category in each permutation), high and low precision in the low IU group (again, randomising trial precision), high precision condition in both IU groups (randomising IU group in each permutation), low precision in both IU groups, and the difference between two precision conditions (high minus low temporal precision) between both IU groups. The null distribution was generated based on the maximal absolute t score at any post-baseline time point for each permutation, thus any points in the actual data exceeding that threshold (the 50th largest value, to correspond to $p = 0.05$) were deemed significant.

4.3. Results

4.3.1. Participant Responses and reaction time data

Participant response accuracy was high (see table 3), with participants overall responding correctly (either with a hit or correct rejection) in 98.8% of trials. The high IU group had slightly higher accuracy overall (mean low IU accuracy was 98.2%, mean high IU accuracy was 99.4%), with no single trial where any high IU participant missed the stimulus change.

To compare the accuracy measures between low and high IU groups, a Wilcoxon rank-sum test was used to compare accuracy between high and low IU groups. . There was no significant difference in the number of hits between the low IU group ($M = 0.1$, $SD = 0.3$) and

the high IU group ($M = 0.05$, $SD = 0.21$), $z = 0.61$, $p = 0.545$. As there was no variance in the misses in the high IU group, statistical comparison could not be performed.

Group	Metric	Mean (%)	SD (+/-)
Low IU	Hits	98.14	5.38
	Misses	0.41	1.75
	Correct rejections	98.31	5.56
	False Alarms	0.86	1.03
High IU	Hits	99.50	0.72
	Misses	0.00	0.00
	Correct rejections	99.38	0.86
	False Alarms	1.12	1.12

Table 7. Response accuracy from Experiment 7. Participant response data indicating the percentage of hits, misses, correct rejections, and false alarms made when attempting to react as fast as possible when noticing the stimulus change.

A two-way repeated measures ANOVA investigated how mean reaction times changed with intolerance of uncertainty and precision group. This ANOVA found a main effect of precision ($F(1, 84) = 25.062$, $p < 0.001$). The effect of IU ($F(1, 84) = 0.175$, $p = 0.68$) and the interaction measure ($F(1, 84) = 0.0336$, $p = 0.85$) were not significant. Mean reaction time was higher in the low precision condition than the high precision condition (see Figure 12). Mean reaction time was similar between high and low IU groups within the same precision conditions.

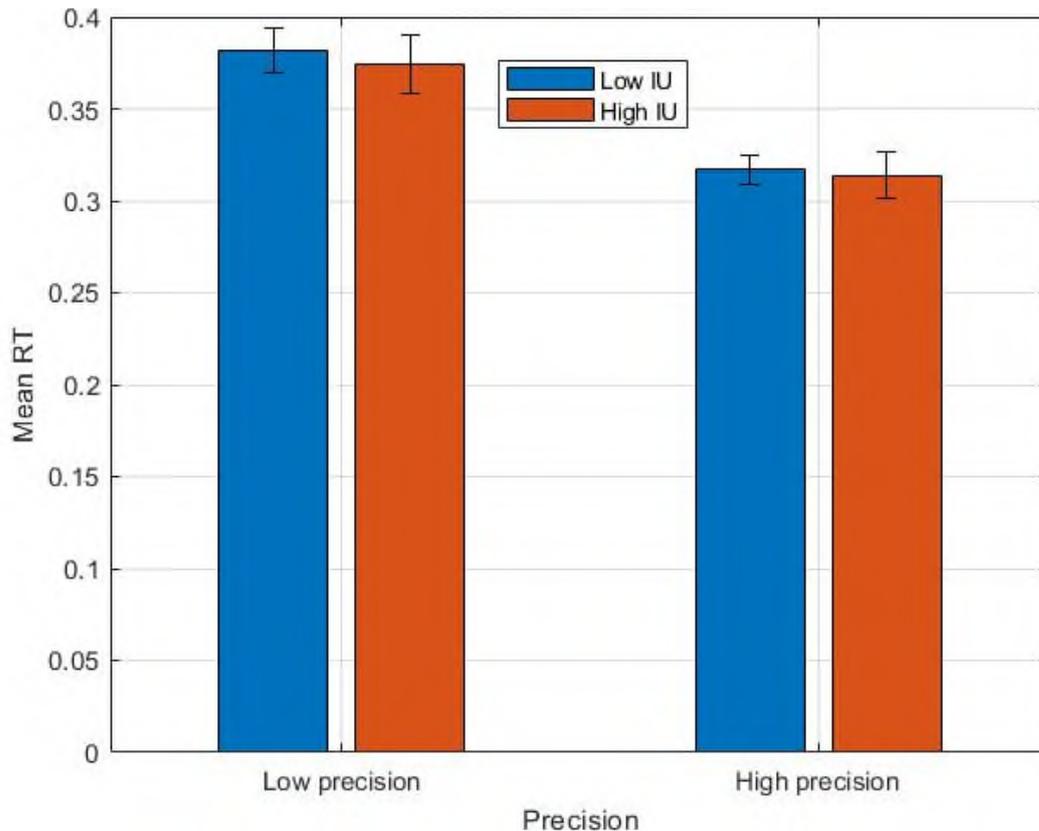


Figure 12. Mean reaction time in each experimental condition in Experiment 7. Mean reaction time in the high and low precision condition trials, in high and low IU groups. The y axis indicates the mean reaction time from the onset of the change in stimulus to the response in seconds. The x axis indications the level of precision of the trial, with the bars on the left indicating the low precision condition and the bars on the right indicating the high precision condition. The colour of the bars indicates the IU group of the participants, with blue indicating low IU and red indicating high IU. The error bars indicate standard error.

4.3.2. Pupillometry results

Results from the low IU group showed a similar pattern of mean pupil dilation over the course of the trial in both low and high precision conditions. From the baseline, mean pupil dilation increased to approx. 0.1 mm dilation over the first two seconds of the trial, plateaus for approx. two seconds, and then gradually decreases back to the baseline by the end of the trial (see Figure 13). The non-parametric permutation analysis indicated no significant difference in pupil dilation between precision conditions in the low IU group.

Results from non-parametric permutation analysis indicated a significant difference ($p < 0.05$) in pupil dilation, in the high IU group, between the low and high precision conditions for a short time window around the two second mark (significance at $p < 0.05$ is

indicated by the solid black line at the baseline in Figure 13). Beyond this window, non-parametric permutation analysis did not indicate any other significant difference between groups, including: high and low precision in the low IU group, high precision condition in both IU groups, low precision in both IU groups, and the difference measure of the two precision conditions between both IU groups.

Visual inspection of Figure 13 suggests differences in the shape and timing of the dilation curves between IU groups in the low precision and high precision conditions, particularly later in the trial. However, these trends did not reach statistical significance, and any description of them should be considered exploratory and speculative. For example, in the high IU group, the low precision condition showed a gradual decrease in dilation after the initial peak, crossing baseline around eight seconds, and ending at approx. -0.05mm. In contrast, the high precision condition exhibited a second dilation peak at around six seconds, before returning to baseline near the end of the trial. This potential divergence in response is reflected in the difference measure (high precision response minus low precision response), which shows a trough at two seconds, and a peak at six seconds. These patterns may suggest differential attentional or cognitive dynamics under uncertainty, but without further testing these should be interpreted with caution, and used solely for hypothesis development.

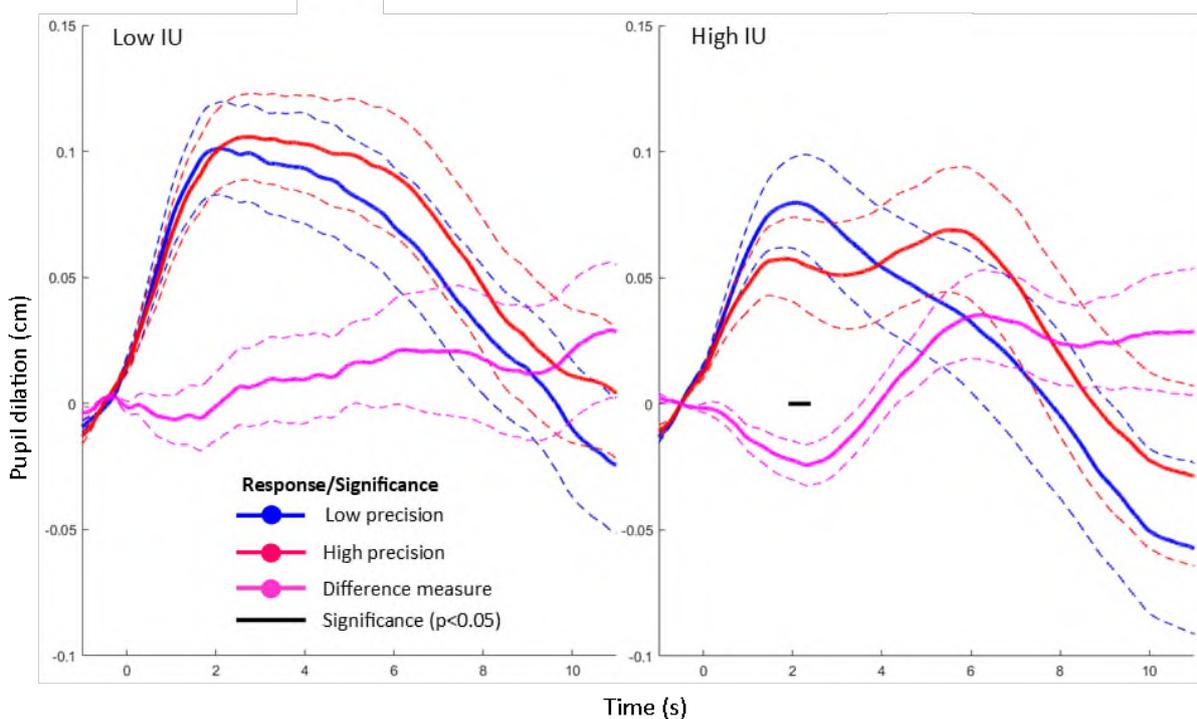


Figure 13. Pupil dilation from Experiment 7. Mean changes in pupil dilation over the timescale of each trial in low and high IU groups in both precision conditions in the correct rejection trials, where no stimulus change occurred. The y axis indicates pupil dilation in mm. The x axis indicates the time in seconds within each trial. The left column indicates the median pupil size change for the low IU group, and the right column indicates the high IU group. The solid lines indicate the mean response in that response group, with the dashed lines indicating the standard deviation. The blue lines indicate the low precision response group, the red lines indicate the high precision response group, and the magenta lines indicate the difference measure. The solid black line indicates the epochs where the difference in pupil dilation between the low and high precision group is significant ($p < 0.05$).

4.3.3. CNV results

Non-parametric permutation analysis indicated there was no significant difference at any timepoint in CNV response between: high and low precision in the high IU group, high and low precision in the low IU group, high precision condition in both IU groups, low precision in both IU groups, and the difference measure of the two precision conditions between both IU groups.

Although no statistically significant differences were found, visual inspection of Figure 14 suggests potentially distinct patterns of CNV activity over time between IU groups and across precision conditions. These should be interpreted with caution, as they are exploratory and not supported by inferential statistics.

In the low IU group, both high and low precision conditions showed a similar CNV response over the trial, but with the low precision condition being consistently more negative (i.e. larger in amplitude) across the trial. Amplitude in both precision conditions decreased sharply in the first second of the trial, the low precision response to approximately $-6 \mu\text{V}$, and the high precision response to approximately $-4 \mu\text{V}$. Both responses remained approximately at this level of negative amplitude until the end of the trial.

In the high IU group, both conditions similarly dropped to approximately $-4 \mu\text{V}$ within the first second. However, in the low precision condition CNV amplitude then gradually increased to a peak of approximately $-1 \mu\text{V}$ at the 7 second point, then decreased to $-3 \mu\text{V}$ and remained there for the rest of the trial. In the high precision condition, CNV amplitude increased to approximately $-3 \mu\text{V}$ by 4 seconds, then declined to approximately $-6 \mu\text{V}$ and approximately remained there for the rest of the trial. These diverging patterns were reflected in the difference measure (high precision minus low precision), which remained approximately at the baseline for the first four seconds, after which it decreased to between $-2 \mu\text{V}$ and $-5 \mu\text{V}$. These descriptive trends may suggest differences in how CNV response develops over time in relation to IU and temporal precision but cannot be taken as evidence of reliable effects.

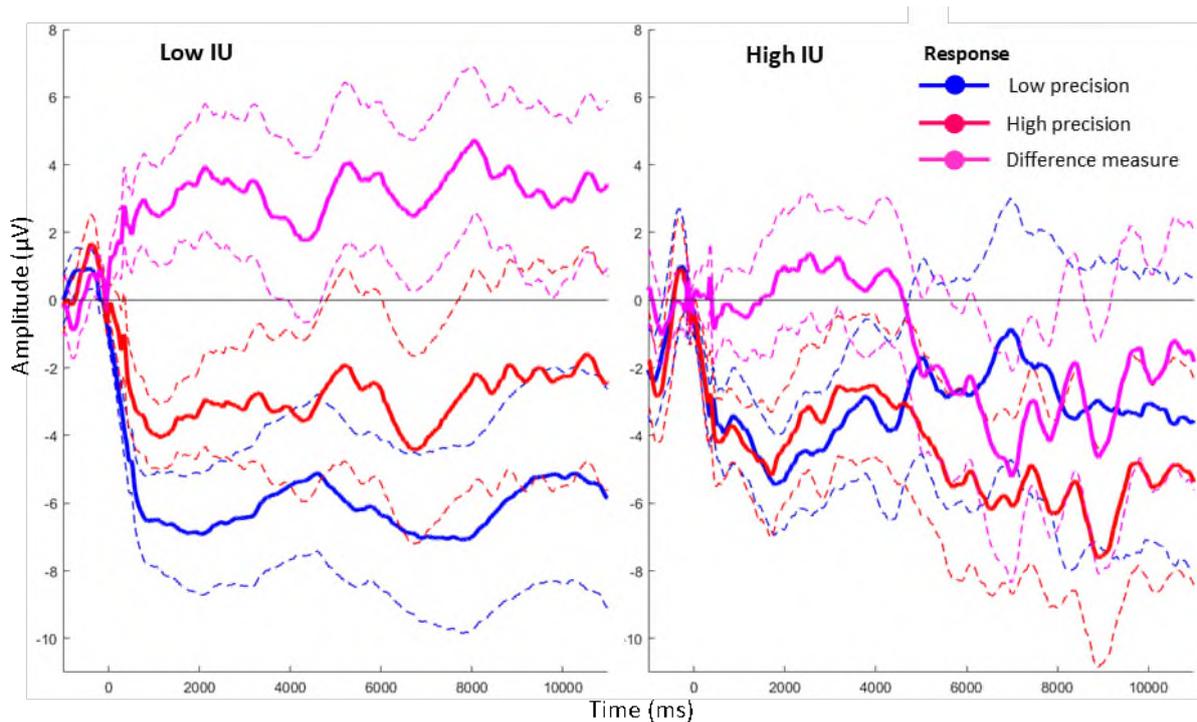


Figure 14. CNV results from Experiment 7. Mean changes in amplitude in the Fz electrode over the timescale of each trial in the low and high IU groups in both precision conditions in the correct rejection trials, where no stimulus change occurred. The y axis indicates amplitude in μV . The x axis indicates the time in milliseconds within each trial. The left column indicates the median pupil size change for the low IU group, and the right column indicates the high IU group. The solid lines indicate the mean response in that response group, with the dashed lines indicating the standard deviation. The blue lines indicate the low precision response group, the red lines indicate the high precision response group, and the magenta lines indicate the difference measure.

4.3.4. Alpha Oscillation Results

Results from non-parametric permutation analysis indicated there was no significant difference at any timepoint in alpha oscillation response between: high and low precision in the high IU group, high and low precision in the low IU group, high precision condition in both IU groups, low precision in both IU groups, and the difference measure of the two precision conditions between both IU groups.

In both precision conditions and intolerance of uncertainty groups, alpha oscillation response followed a similar pattern (see Figure 15). Alpha amplitude increased from the baseline to approx. $1.5 \mu\text{V}$ over the first 2 seconds of the trial, then gradually reduced to approximately $1 \mu\text{V}$ until the end of the trial. As there is no noticeable difference in trend

between the high and low precision condition, the difference measure does not deviate from the baseline to indicate any significant differences or even apparent trends.

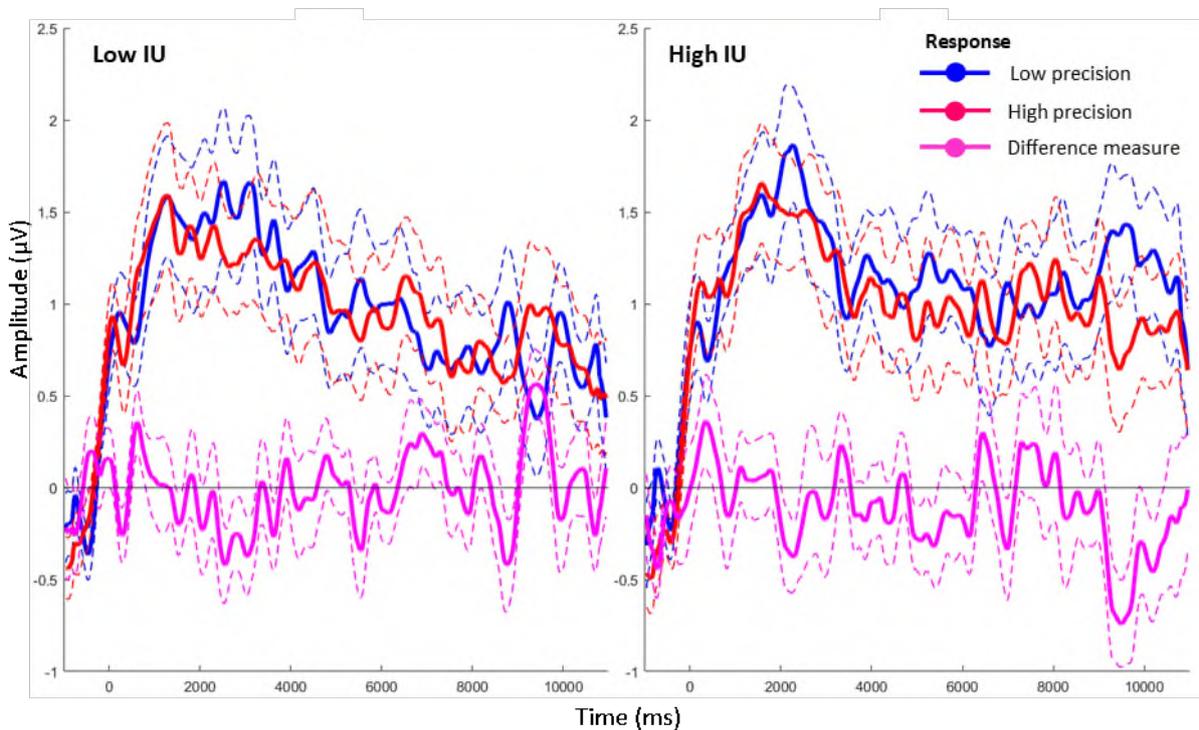


Figure 15. Alpha oscillation results from Experiment 7. Mean changes in alpha envelope amplitude in the POz electrode over the timescale of each trial in the low and high IU groups in both precision conditions in the correct rejection trials, where no stimulus change occurred. The y axis indicates amplitude in μV . The x axis indicates the time in milliseconds within each trial. The left plot indicates the low IU group, and the right plot indicates the high IU group. The solid lines indicate the mean response in that response group, with the dashed lines indicating the standard error. The blue lines indicate the low precision response group, the red lines indicate the high precision response group, and the magenta lines indicate the difference measure.

4.4. Discussion

4.4.1. Participant Response

Participant accuracy was high, with 98.8% of trials given the correct response (either a hit or correct rejection). This likely indicates that participants detected and understood the stimulus change and responded accordingly within the trials. Mean reaction time was similar between high and low IU groups within the same precision conditions. Combined mean reaction time was higher in the low precision condition than the high precision condition (see Figure 12), which likely indicates that participants understood the difference in precision,

based on the stimulus frequency, and were able to selectively attend to the reduced time period where the change was likely to occur in the high precision condition (see Figure 11).

4.4.2. Pupillometry

High and low IU participants showed different pupil response patterns to the high and low precision conditions. In the low IU group, pupil dilation followed a similar pattern in both precision conditions, indicating elevated arousal and anticipation of the stimulus change from the earliest point the stimulus change could happen (one second) until the six second mark (after the mean stimulus change time of five seconds).

In the high IU group, distinct pupil response pattern was shown in the two different precision conditions. In both precision conditions, pupillometry results indicate an increase in anticipation to a peak two seconds into the trial. This peak in dilation at the two second mark was shown to be significantly lower in the high precision trial than the low precision trial by non-parametric permutation analysis (see 5.3.2 Pupillometry results, and Figure 13). This indicates they showed less vigilance to the first section of the trial in the high precision condition, when less vigilance was required as stimulus change was less likely.

Beyond this window, no statistically significant differences were found, but visual inspection suggests that dilation patterns diverged further over time. The pupil response in the low precision condition gradually reduced to the end of the trial, dropping below the baseline level eight seconds in, which could imply that participants had become convinced that this trial did not have a stimulus change in. Whereas in the high precision condition pupil dilation increased to a second peak between 4 and 7 seconds into the trial (the section where the stimulus change was most likely to occur. This peak at six seconds into the trial likely reflects an appropriate level of selective attention towards the most likely time period in the study (five seconds) that stimulus change is likely to occur. It is worth highlighting however, that this trend was not statistically supported and should be considered exploratory only. However, if this pattern is replicated and found to show significance, this difference in response patterns would suggest that the high IU groups were showing more appropriate allocation of attention to the different precision conditions, specifically showing relatively more attention to time period in the high precision condition when the stimulus change was

most likely to occur, and less vigilance when a stimulus change was unlikely. The hypothesis that people with high IU are less able to selectively attend to when an event is likely to happen and will deploy increased attention outside of optimum windows is therefore not supported.

4.4.3. Alpha Oscillations

Alpha oscillation response patterns were similar in both IU groups and precision condition and indicated increased attention in all conditions towards the start of the trial. This pattern of results could have a few interpretations. It could reflect decreased engagement with the task in the first four seconds when participants presumed that stimulus change was not as likely, and then increased as participants started to expect stimulus change and attended to the task more closely. However, it could also reflect the participants intentionally being in an inactive state to ensure they are receptive to the stimulus when it arrives. There is also some literature to suggest that during vigilance-based experiments, increased alpha oscillations in task-irrelevant cortical areas will actually promote sustained attention by suppressing distracting sensory information, and only alpha oscillations from task-relevant areas will indicate a negative relationship with attention (Clayton, Yeung, and Cohen Kadosh, 2015). This experiment measured alpha oscillations from the POz electrode which is commonly used as a measure of alpha oscillations. However, POz is associated with activity from the parieto-occipital cortex, as at the scalp the greatest alpha amplitude is seen over the parietal and occipital areas (e.g., Johnson, Hamidi, and Postle, 2010). As this measure is associated with activity from the parieto-occipital cortex, measuring alpha oscillations from task-specific areas (in this case the auditory cortex) may provide results indicative of more task-specific activity.

4.4.4. CNV Response

CNV amplitude patterns differed between IU groups across the trial, although no significant differences were detected by permutation analysis. Visual inspection suggests that the high IU group showed increased negativity in the high precision condition from the mid-point to the end of the trial, which encompasses most of the period where the probability of

stimulus change is highest. Conversely, the low IU group showed similar response patterns across precision conditions.

These patterns should be interpreted with caution, as they were not statistically significant. However, if found to be reliable, they would suggest high IU participants respond more appropriately by showing more focussed attention to the section of the trial where the stimulus change was more likely. The hypothesis that people with high IU are less able to selectively attend to when an event is likely to happen and will deploy increased attention outside of optimum windows is therefore not supported.

4.4.5. Intolerance of Uncertainty

Despite both IU groups showing similar levels of accuracy and reaction times, results from the CNV and pupillometry responses suggest possible differences in how attention was allocated over time. In both CNV and pupillometry measures, low IU participants showed largely similar response profiles across precision conditions. Conversely, the high IU participants showed distinct time courses of physiological markers of vigilance in the different precision conditions, in keeping with more specific targeting of vigilance to the period in the high precision condition where stimulus change was most likely to occur.

Contrary to initial hypotheses, these findings offer preliminary evidence consistent with the idea that people with high IU may be more efficient in applying attentional resources to these tasks involving temporal uncertainty, attending more selectively to periods of time where attention is necessary. However, these interpretations are based in part on non-significant patterns and should be considered tentative and hypothesis-generating. Replication is needed to determine whether these apparent differences reflect true IU related traits or sample-specific noise. But this does indicate an interesting pattern that would benefit from future investigation.

This pattern of the high IU group potentially showing more selective attention did not necessarily result in better performance than low IU participants. No significant difference was shown in accuracy or reaction time between IU groups. However, accuracy was very close to the maximum ceiling which makes it unlikely that consistent differences in accuracy would be visible. One could also argue that the high IU group achieving an equal performance to the

low IU group whilst expending fewer cognitive resources is itself advantageous. Although again this is highly speculative and not a conclusion I can make without further study.

4.4.6. Limitations and Future Directions

There is one key limitation with this experimental design. As 50% of the trials have no stimulus change, the responses to the later time points in the trials likely start to reflect the increasing probability that no change will occur in that trial, perhaps more so than the stimulus change probability functions I intended to investigate. It is not straightforward to compensate for this in the design, trials with no stimulus change are crucial to explore responses across the trial to changing probabilities of stimulus change, without being affected by the actual stimulus change itself. However, this makes it hard to interpret results towards the end of the trials, and it may mean that only responses to the early and mid-points of the trial accurately reflect the probability functions I intended to investigate.

Literature suggests that alpha oscillations should be taken from task-related areas of the brain. This experiment measured alpha oscillations from the POz electrode which is commonly used as a measure of alpha oscillations. However, POz is associated with activity from the parieto-occipital cortex (e.g., Johnson, Hamidi, and Postle, 2010). As this measure is associated with activity from the parieto-occipital cortex, measuring alpha oscillations from the auditory cortex may provide results more indicative of attentional differences related to this task.

4.4.7. Conclusions

The results showed that under specific circumstances, high IU and low IU participants demonstrated distinct patterns of attention and arousal in response to uncertainty. Results from physiological measures indicated that under some conditions of uncertainty, people with high IU show more precise temporal expectations than people with low IU. This finding suggests that people with high IU may be more efficient in applying attentional resources to these tasks involving temporal uncertainty, attending more selectively to periods of time where attention is necessary. However, several of the observed differences were not statistically significant, and some interpretations are based on exploratory trends. These

should be considered tentative and hypothesis-generating, rather than conclusive. Replication in future studies is essential to validate and clarify these findings. If replicated, this pattern could reframe how intolerance of uncertainty is viewed as a more nuanced trait that comes with advantages and disadvantages.

5. Discussion

5.1. Aims and Hypotheses

The broad aim of this thesis is to explore the mechanisms, computational changes, or psychophysical underpinnings of intolerance of uncertainty with a lens of predictive processing frameworks, including addressing the hypotheses outlined below. I aimed to investigate the necessary stimulus conditions of uncertainty to trigger the aversive subjective experience associated with IU, and in some way quantify this subjective experience. Minimising uncertainty is now understood to be one of the core attributes of perception and behaviour; intolerance of uncertainty, therefore, could relate to an aberration in, or otherwise divergent, predictive processing. Through a series of psychophysics experiments, I explored computational mechanisms behind predictive processing. I then adapted this experiment structure to induce sufficient uncertainty to distinguish results from high and low intolerance of uncertainty participants. I then ran a lab-based temporal expectation task with physiological measures using EEG and pupillometry to test whether intolerance of uncertainty relates specifically to temporal uncertainty.

Overall, this thesis is founded upon addressing two main hypotheses of intolerance of uncertainty. The first hypothesis is that under conditions of sensory uncertainty, people with high IU are biased towards expecting more aversive outcomes. The second is that under conditions of sensory uncertainty, people with high IU are not necessarily biased towards any particular outcome, but rather perceive uncertain situations themselves as more aversive. These two hypotheses are not necessarily mutually exclusive, although it is likely they indicate different computational mechanisms of IU.

Separate to these hypotheses, I explored a series of secondary hypotheses relating to intolerance of uncertainty and the perception of uncertainty more broadly. One hypothesis is that intolerance of uncertainty relates to an inability to either understand or believe safety signals that would indicate safety and therefore reduce anxiety (tested in Experiment 5, Chapter 3). I also tested the hypothesis that when cues that indicate upcoming stimuli are missing, anticipation of and perception of aversive stimuli is increased in high IU groups (tested in Experiment 6, Chapter 3).

I assessed the hypothesis that perceived surprise relating to a systematic change in stimulus environment is positively correlated with that precision of the sensory environment (Experiments 1-4, Chapter 2). I also assessed whether perceived surprise from sensory changes under uncertainty is altered depending on the IU of the participant (Experiment 2, Chapter 2).

Finally, I tested the hypothesis that people with high IU are impaired in their ability to temporally predict uncertain stimuli (Experiment 7, Chapter 4).

5.2. Summary of findings

5.2.1. Chapter 2 Findings – The psychophysics of surprise

Chapter 2 describes a series of four psychophysics experiments that investigate the influence of stimulus precision on the perception of stimulus changes; participants reported their perceived size of change (PSC) in the mean value of sequences of sounds, with trials varying in sequence precision. I hypothesised that PSC, for a particular absolute change, would be positively correlated to stimulus precision, however this hypothesis was not supported by the results. All four experiments found main and/or interaction effects of precision, but in many cases precision was inversely related to PSC. E.g. in Experiment 1 and Experiment 4, when mean change was low, PSC response decreased with increased precision in a counter-Bayesian manner. This is unexpected and counter-intuitive, as more precise stimulus sequences would reduce noise in the data and therefore indicate more reliable information via increased signal to noise ratio. These results demonstrate circumstances, characterised by low signal-to-noise ratio, where human perception potentially behaves in a counter-Bayesian manner.

This paradoxical effect of precision can be interpreted in a few ways. Findings that indicate increased perceived change with lower precision, especially in conjunction with lower mean change as a proxy for low signal-to-noise ratio stimuli, could therefore be explained as an inflated estimated precision of sensory signals in the brain compared to statistical precision of the sensory input. Alternatively, or additionally, these findings could be the result of a phenomenon akin to stochastic resonance, a robust effect where additional noise increases sensitivity to the detection of weak signals (Wiesenfeld and Moss, 1995).

Whilst not identical, the effect I observe here could be analogous in terms of a mechanism to aid the detection of subtle changes in the sensory environment under conditions of additional noise.

A further explanation could be that low-precision stimulus streams contain more variability between individual stimuli, which increases stimulus-driven attention, in effect increasing the effective precision of those stimuli in the brain (an effect shown by Feldman and Friston, 2010). More difficult listening conditions (reduced signal to noise ratio) demand greater listening effort which results in an increased attention to these trials making them more salient. Detecting a change through greater noise could increase the perceived difficulty of the task, with more care and attention directed to tasks that demand higher levels of thought. It is also possible that more variable stimulus sequences reduce the extent of stimulus-specific adaptation, leading to greater sensitivity to similar stimuli.

There is likely an evolutionary benefit to the over-caution of erring towards perceiving a larger change (or a change vs. no change) in uncertain conditions, as signals indicating potential threats might be largely obscured by noise in some situations, and a bias towards over-perception of potential threats might confer more benefits in more sensitive detection of true positives than detrimental consequences of false alarms. The findings of this study suggest a mechanism to facilitate the detection of subtle signals in noisy environments.

Although replicated between these four studies, this paradoxical effect of precision was observed in a limited parameter space, including low numbers of stimuli per sequence, and therefore it is important to understand how generalisable it is. Varying the signal to noise ratio more widely (i.e. greater variance between mean change and precision) would help explain how far this effect generalises.

These findings represent the effects of changing stimulus precision on a subjective change perception response measured through self-report. The experiments use different phrasing for the subjective change perception response (Experiment 1 asked “how noticeable” changes were, Experiments 2-4 asked how “surprising” the change was). Whilst the results imply that these different questions were interpreted similarly, replication with a more objective measure of response to this changing stimulus precision would aid in our understanding of the computations of perceptual inference. To investigate this, I have since

designed and run an experiment that follows a similar methodology but where a change only occurs 50% of the time, and requires participants to press a button as quickly as possible as soon as they notice a stimulus change. This reaction time measure, as well as response accuracy, should give more objective measures of their perception of stimulus change, which may help validate this paradoxical effect of precision. I have not yet had time to analyse these results, and therefore this experiment unfortunately could not be used as part of this thesis.

Another point to highlight is the idea that in a high precision trial a stimulus change would likely be perceived as larger than in a low precision trial, and therefore perception of an equivalent change in a low precision trial would likely require a greater stimulus change. Replication that compares subjective surprise responses with an implicit measure of subjective similarity could be integral in strengthening the conclusions made about this paradoxical effect of precision.

This paradoxical effect of precision indicates the brain sometimes behaving in a non-Bayesian and/or counter-Bayesian manner. If there are instances where the neurotypical and healthy brain is already behaving in a Bayes-suboptimal manner in normal processes, this could be valuable in further understanding clinically disordered states associated with sub-optimal Bayesian inference, in which these biases might be quantitatively or qualitatively different. For example, tinnitus is proposed to be the result of overestimated stimulus precision leading to spontaneous activity in the auditory pathway overriding the default prediction of silence to instead expect noise (Sedley et al., 2016b; Hullfish et al., 2019). To investigate whether people with tinnitus relate to altered use of stimulus precision, one could replicate this study, or a variant thereof, with matched participants with and without tinnitus.

Experiment 2 included an IUS-12 questionnaire to see if intolerance of uncertainty related to a bias in the perception of specific stimulus statistics and found no difference between high and low IU groups in behavioural responses reporting perception of changes in stimulus statistics. If these results are true reflections of the effects of changing stimulus statistics on perceptual inference, this result implies that, at least in general, the computations of Bayesian inference occur similarly in people with high and low intolerance of uncertainty, and that intolerance of uncertainty is not simply an aberration of the perception of (and/or response to) changes in stimulus statistics relating to the calculation of uncertainty. Either the uncertainty elicited through surprise from this experiment is of

insufficient magnitude to reveal differences related to IU symptoms, it is distinct from the uncertainty processing mechanisms that are implicated in IU, and/or the task or behavioural context surrounding the uncertainty-associated stimuli is a key determinant. Experiments 5 and 6 adapted this methodology to investigate under what stimulus conditions the sufficient and/or correct type of uncertainty is elicited that distinguishes people with high and low IU.

5.2.2. Chapter 3 findings – Behavioural studies of aversity predictions

Chapter three outlines two psychophysics experiments that give semi-predictable potentially aversive auditory stimuli and explore the anticipation of, and perception of, these potentially aversive stimuli in relation to intolerance of uncertainty. Overall, in both experiments IU was found to positively relate to the anticipation of potentially aversive stimuli. This supports the hypothesis that, under conditions of uncertainty, people with high IU are biased towards predicting more aversive outcomes.

The hypothesis that under conditions of sensory uncertainty, people with high IU perceive aversive stimuli as more aversive than low IU people, was partially supported by the results. Experiment 6 showed that high IU participants gave higher aversity perception responses than the low IU group. Experiment 5 did not find IU to have a significant effect on aversity perception response, although a visual trend in the data indicated the mean aversity response followed a similar response pattern to the significant relationship found with the anticipation response. This could indicate that the added complexity of Experiment 6 (the addition of the visual stimulus) strengthened a trend present but not quite showing significance in Experiment 5.

Regardless, this implies that the high IU group anticipated the probe stimulus to be more aversive based on the context stimulus and once the probe stimulus arrived, they also perceived it as more aversive than the low IU group. As the perception of the aversive stimuli was higher in the high IU group, their increased anticipation of aversive stimuli (compared to the low IU group) seems a reasonable response and does not necessarily indicate an over-anticipation of aversity. However, it is possible this relationship is reversed and actually predictions of greater aversity could bias perception towards perceiving greater aversity. Regardless, the relationship is likely not this simple, as the degrees of increased responses

relating to intolerance of uncertainty varied under different stimulus and experiment conditions.

The results did not support the hypothesis that effects of intolerance of uncertainty will be exaggerated under conditions of missing information (elicited by the visual cue being missing in 50% of trials), at least at the level of the individual trials. Although the increased complexity of Experiment 6 (i.e. more interacting sources of uncertainty) resulted in a larger effect of IU score on predicted and perceived aversity. Additionally, trends in the data imply a more complex relationship between IU and presence of a visual cue, and one that could at least partly support this hypothesis (Discussed further in Chapter 5.3); it may be that in some uncertain situations with low anticipated aversity, people with low IU tend to ignore certain perceptual subtleties, whilst those with high IU remain sensitive to them. Interestingly, both the presence and the content of the visual cue did not influence predictions of upcoming aversity, but both of these variables influenced how aversive the probe stimulus was perceived to be once it occurred. Therefore, this variable has influenced perception, but without participants prospectively realising it has influenced it.

Experiment 6 included a general unease measure to differentiate anticipation of incoming potentially aversive stimuli, and general unease felt under conditions of uncertainty. However, the results suggested that these two measures may have been conflated into one general anticipation response (see chapter 3.3.4.1). If this is the case, replication with an unease measure taken at a different time in the study would be valuable, e.g. after every block or at another timepoint within each trial. A valid unease measure would be an important step in distinguishing whether intolerance of uncertainty results from the anticipation or perception of aversive outcomes in the context of sensory uncertainty, or whether it results from a general feeling of discomfort in the face of uncertainty itself.

These experiments adapted a previous paradigm (Experiments 1-4, Chapter 2) with multiple alterations anticipated to induce sufficient uncertainty to reveal differences between high and low IU groups, with the intention of subsequent work then removing elements to uncover the requisite components of experimentally eliciting intolerance of uncertainty. In particular, replication that explores the full spectrum of valence, from pleasant to unpleasant stimuli, could be invaluable in understanding how IU varies with sensory uncertainty that is not necessarily tied to potentially aversive outcomes.

5.2.3. Chapter 4 Findings – Temporal Uncertainty

Chapter four describes an experiment that investigated whether intolerance of uncertainty relates to temporal expectation of uncertain upcoming stimuli. This experiment manipulated the precision of when a stimulus change was likely to occur and measured three physiological responses to this, CNV, alpha oscillations, and pupillometry responses, which indicate arousal and preparedness for responding to anticipated events. I predicted that participants with high intolerance of uncertainty would be impaired in their ability to predict when incoming stimuli changes will occur, and therefore show less selective attention in their physiological responses.

Despite similar levels of accuracy and reaction times, results from the CNV and pupillometry measures indicated that high IU and low IU participants demonstrated distinct patterns in attention and arousal. In both CNV and pupillometry measures, low IU participants showed a time course of attention that did not distinguish high and low temporal precision conditions. Conversely, high IU participants showed distinct time courses of physiological markers of vigilance in the different precision conditions, in keeping with more specific targeting of vigilance to the period in the high precision condition where stimulus change was most likely to occur.

Contrary to the original hypothesis, this pattern may suggest that people with high IU show in fact show *more* precise temporal expectations than people with low IU, applying attentional resources more selectively under conditions of sensory uncertainty. However, this interpretation is based in part on trends in the data that did not reach statistical significance. As such, these findings should be considered exploratory and hypothesis generating, requiring replication before conclusions can be drawn. But this does indicate an interesting pattern that would benefit from future investigation.

This more selective attention shown by the high IU group did not necessarily result in better performance than low IU participants; no significant difference was shown in accuracy or reaction time between IU groups. However, accuracy was very close to ceiling which makes it unlikely that consistent differences in accuracy would be visible. One could also argue that the high IU group achieving an equal performance to the low IU group whilst expending fewer cognitive resources is itself advantageous. Although again this is highly speculative and not a conclusion I can make without further study.

Alpha oscillation response patterns were similar in both IU groups and precision conditions. These results therefore do not support the hypothesis that people with high IU are less able to selectively attend to when an event is likely to happen. This pattern of results could have a few interpretations. There is also some literature to suggest that during vigilance-based experiments, increased alpha oscillations in task-irrelevant cortical areas will actually promote sustained attention by suppressing distracting sensory information, and only alpha oscillations from task-relevant areas will indicate a negative relationship with attention (Clayton, Yeung, and Cohen Kadosh, 2015). This experiment measured alpha oscillations from the POz electrode which is commonly used as a measure of alpha oscillations. However, POz is associated with activity from the parieto-occipital cortex, as at the scalp the greatest alpha amplitude is seen over the parietal and occipital areas (e.g., Johnson, Hamidi, and Postle, 2010). As this measure it is associated with activity from the parieto-occipital cortex, measuring alpha oscillations from task-specific areas (in this case the auditory cortex) may provide results indicative of more task-specific activity.

5.3. Differences in methodological design and IU findings

Experiment 2 found no difference between high and low IU groups in behavioural responses reporting perception of changes in stimulus statistics under conditions of sensory uncertainty (Chapter 2.4.2). Experiments 5, 6 and 7 all found main effects of intolerance of uncertainty on measures of anticipation of aversive stimuli, aversity perception, and physiological measures in response to temporal uncertainty. This lack of an effect of IU in Experiment 2 implies that either the uncertainty elicited through surprise from this experiment was of insufficient magnitude to reveal differences related to IU, or was distinct from the uncertainty processing mechanisms that are implicated in IU, or the associated task was not one sufficient to reveal IU-related differences. This also implies that the uncertainty elicited in Experiments 5, 6, and 7 was of sufficient magnitude and/or activates the correct processing mechanisms to differentiate responses from high and low IU groups. Therefore, scrutinising the methodological differences used to induce uncertainty between these experiments could aid in revealing correlates relevant in inducing uncertainty that relates to intolerance of uncertainty.

The differences in experimental design and measures between Experiment 7 and Experiment 2 will likely make direct comparisons difficult. Although the addition of physiological measures used in Experiment 7 to the other experiments may aid in characterising differences related to IU. Experiments 5 and 6 did share a basic methodological design with Experiment 2, but with alterations intended to elicit sufficient uncertainty to differentiate responses from high and low IU participants. Primarily, stimulus statistics in Experiments 5 and 6, such as stimulus precision, dictated the intensity of the stimuli relative to an uncomfortable loudness level. This added a dimension of negative valence to the study, compared to the neutrally valent stimuli used in Experiment 2. It is possible that this addition of potentially aversive outcomes from uncertain situations was essential in differentiating responses between IU groups. However, the accepted definition of intolerance of uncertainty indicates that “people who are intolerant of uncertainty are likely to interpret all ambiguous information as threatening” (Carleton, Norton & Asmundson, 2007). Similarly, Freeston and Komes (2023) suggest that the aversive response exhibited by people with high IU is linked to the felt sense of uncertainty independent of the valence of any triggers, outcomes, and contexts. They argue that IU exists independent of threat, but the threat and uncertainty of a situation can be confounded. Replication of the study that explores the full spectrum of valence, from pleasant to unpleasant stimuli, could be invaluable in understanding how IU varies with sensory uncertainty that is not necessarily tied to potentially aversive outcomes.

The responses used in these experiments could result from differences in methodology. The use of a subjective sense of surprise in response to changing stimulus statistics under sensory uncertainty may be insufficient to capture differences in intolerance of uncertainty. The responses used in Experiments 5 and 6, the anticipation of, and subsequent perception of the aversity of stimuli, are tied to the valence of the stimuli. However, these responses capture something distinct from surprise in response of stimulus change, e.g. the idea that people with high IU are in some way impaired in their ability to accurately anticipate a future event was explored in Experiment 7.

5.4. ‘Intolerance of Uncertainty’ vs ‘Sensitivity to Uncertainty’

In Experiments 6 and 7 I noticed a pattern of results emerging that suggested that under specific conditions of uncertainty, people with high IU demonstrated more nuanced,

and stimulus or condition appropriate, responses. In Experiment 7, the high IU participants seemed to show distinct time courses of physiological markers of vigilance in the different precision conditions, in keeping with more specific targeting of vigilance to the period in the high precision condition where stimulus change was most likely to occur. This could indicate that people with high IU in fact show more precise temporal expectations than people with low IU. This pattern suggests that people with high IU may be more efficient in applying attentional resources to these tasks involving temporal uncertainty, attending more selectively to periods of time where attention is necessary. Although this more selective attention shown by the high IU group did not necessarily result in better performance than low IU participants.

In Experiment 6, during conditions of high precision, with an absent visual cue, and a low mean change size, the low IU aversity perception responses seem unaffected by mean start value (See Figure 16), which is surprising as the start value directly affected the probe intensity. This relationship was unexpected but also found in the unease and anticipation response. The high IU group did correctly incorporate the start value into their aversity perception response. As such, the high IU group's responses do more accurately reflect the stimuli. With this same combination of variables except in the high, rather than low, mean change condition, the low IU group were similarly less affected by starting value, but in this case the high IU group seem over-reactive, giving high mean aversity ratings. When considering both of these findings together, I could infer that, under certain conditions of uncertainty, high IU is associated with a tendency to make full use of multiple sources of predictive and stimulus information (such as correctly using the starting mean size) when making perceptual judgements. But this also leads to a tendency to exaggerate unexpectedly aversive stimuli.

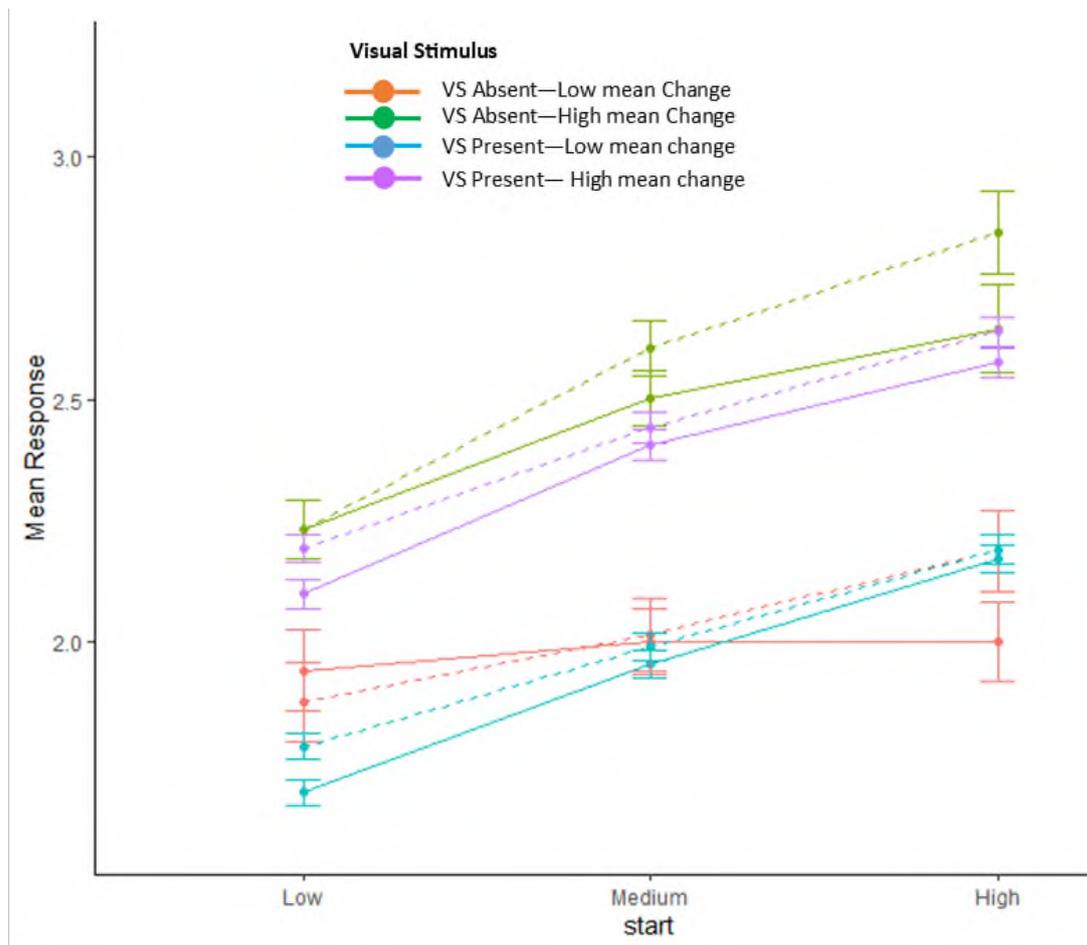


Figure 16. Subfigure of Figure 10 indicating mean aversity perception under low precision conditions from Experiment 6. A subfigure of Figure 10 indicating mean aversity perception response in the high precision condition, across different levels of starting mean, mean change size, and the presence/absence of the visual stimulus. The y axis indicates mean aversity perception response given in response to the relevant stimuli in a 1-4 scale. The x axis indicates the starting mean of the context stimuli, which indicates how likely stimuli were to exceed the ULL. Colour indicates the state of the visual stimulus and level of mean change: orange = the visual stimulus was missing and mean change was low, green = the visual stimulus was missing and the mean change was high, blue = visual stimulus was present and indicated low mean change, magenta = visual stimulus was present and indicated high mean change. Solid lines and dashed lines indicated how these results varied across participants with high IU (dashed lines) and low IU (solid lines).

These patterns could imply that people with high IU experience uncertainty with greater sensitivity, which can lead to both advantageous and deleterious consequences. For example, high IU participants were able to detect and respond to stimulus conditions that were either undetected or otherwise ignored by low IU participants in Experiment 6. This was shown as a potential benefit through more accurate responses to subtle cues in low aversity conditions, but also shown to have a cost when giving higher perceived aversity responses

under high aversity conditions. This should come with heavy caveats that this focusses on small patterns of findings in tasks that require replication and establishment of generalisability before conclusions can be drawn. But this does raise the question of whether IU relates to an overall trait of sensitivity to uncertainty, which is not simply maladaptive.

The majority of the literature exploring IU focuses on the negative associations with the trait, such as its associations with various psychiatric disorders, and its inhibitory effect on behaviour in uncertain situations. There is a dearth of research that investigates any potential positives aspects of intolerance of uncertainty that could explain why high IU has remained such a common trait. It seems likely that if high IU is, or has been in previous contexts, solely a negative trait, adaptive selection pressure would have prevented it from being as widespread as it is. However, if intolerance of uncertainty relates to a general sensitivity to uncertainty, this could go some way in explaining how such a trait has been preserved across populations.

There is some limited evidence that could indirectly indicate a relationship between IU and sensitivity to uncertainty. Research has shown that the relationship between anxiety and sensory sensitivity, a processing pattern characterised by enhanced sensitivity or reactivity to sensory stimuli, is at least partly mediated by IU (Uljarević, Carrington, and Leekam, 2016; Panchyshyn et al., 2023).

If intolerance of uncertainty can be reframed as a sensitivity to uncertainty, this would encourage a more nuanced approach to understanding people with high IU. The term intolerance implies an inability to cope, whereas sensitivity of uncertainty infers a heightened awareness or response to uncertainty that may or may not have a negative outcome. A person being described as intolerant of uncertainty may lead to pathologizing, and the word 'intolerant' comes with its own negative connotations.

This concept of sensitivity to uncertainty could be analogous to the Highly Sensitive Person scale (developed by Aron & Aron, 1997), a measure of sensory processing sensitivity that indicates awareness and responsiveness to sensory input. The Highly Sensitive Person Scale relates to increased emotional reactivity, in both positive and negative valence, to external stimuli (Lionetti et al., 2018). This construct highlights that the associated differences in stress reactivity with being highly sensitive come with clear benefits as much as downsides,

which are dependent on environmental conditions (Boyce & Ellis, 2005). There is currently a lack of literature exploring the relationship between Highly Sensitive Person Scale and IU scores, however, there may be some overlap as they both involve heightened sensitivity or reactivity to environmental stimuli. Regardless, reframing intolerance of uncertainty as sensitivity of uncertainty could present a more balanced view of how individuals respond to uncertainty by reducing stigma, highlighting the adaptive potential, and recognising associated advantages.

5.5. Conclusions

Over a series of psychophysical and physiological experiments, I have found multiple novel findings that aid in understanding the computations underpinning how people respond to uncertainty. In Experiments 1-4, I found that increasing the precision of stimulus sequences does not necessarily make otherwise equivalent sensory changes more surprising or easier to detect, and in some cases that it has the opposite effect. This paradoxical effect of precision potentially indicates the brain behaving in a non-Bayesian or even counter-Bayesian manner, with inherent biases towards over-inferring small changes in noisy conditions, and towards detecting small increases, mainly in intensity. In Experiments 5 and 6, I found that under uncertain conditions with potentially aversive outcomes, people with high IU anticipate incoming stimuli to be more aversive, and also perceive aversive stimuli as more aversive than people with low IU. I also found that under certain conditions of uncertainty, people with high IU gave more nuanced and appropriate responses to the cues and stimuli presented during the trial compared to the low IU group. However, under similar conditions of uncertainty, but with increased stimulus aversity, the high IU group gave exaggerated responses to the stimuli. In Experiment 7, I found that people with high and low IU demonstrate distinct patterns of attention and arousal in response to uncertainty. Results from physiological measures indicated that under some conditions of uncertainty, people with high IU showed more precise and accurate temporal expectations than people with low IU. This finding suggests that people with high IU may be more efficient in applying attentional resources to tasks involving temporal uncertainty, attending more selectively to periods of time where attention is necessary.

From these findings, a pattern of results emerged that suggest that people with high IU experience uncertainty with greater sensitivity, that might lead to both advantageous and deleterious consequences. This leads me to ask the question of whether intolerance of uncertainty could be reframed as 'sensitivity to uncertainty'. The term intolerance implies an inability to cope, whereas sensitivity of uncertainty infers a heightened awareness or response to uncertainty that may or may not have a negative outcome. Reframing intolerance of uncertainty as sensitivity of uncertainty could present a more balanced view of how individuals respond to uncertainty by reducing stigma, highlighting the adaptive potential, and recognising associated advantages.

6. References

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