

**Timing the senses and sensing the time:  
Individual differences in subjective duration**

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## **Acknowledgements**

When I finished university, for the first time, I did what any twenty-two year old with a degree in English would do and got a job working in an old house in the middle of the countryside caring for ex-offenders leaving prison (in many cases the “ex” being somewhat aspirational). In working with mental health issues, learning difficulties and an interesting range of addictions and health problems (and that was just the staff – an old joke but also pretty true) I was fascinated by the idea that some people actually, literally, perceive the world in quite different ways on a day-to-day basis. As time went on, and I came to appreciate that most differences seem to be on a spectrum rather than absolute, I started to appreciate that we are probably all walking around constantly experiencing the world slightly differently to the people around us. When you really reflect on this, I find it is one of those bizarre thoughts that, if delved into too much, overwhelms my tiny mind and requires a lie down, or beer, or preferably both. I suspect it was this sort of thinking (and beer) that lead to me taking on a masters in psychology at the University of Essex, and I am endlessly grateful for the opportunities the university has offered me. I only intended to be here a year but have been here six, one way or another, and I can honestly say it’s the best university in Essex.

I suspect that one of the issues in psychology is that we often feel the need, and indeed are required, to explain the value of our research for society. We need to show how our research will change lives for the better, will treat mental ill health or improve politics, healthcare or education. Psychologists have done, and continue to do, all these things, and more. However, if we are honest, in many cases such claims are often rather ambitious, it is the nature of the world we work in. On this occasion I

shall be open and honest; while I hope the work presented here will ultimately lead to some sort of positive effect down the line, if only by advancing the field an infinitesimal amount, it is born first of curiosity, of a simple desire to understand how we experience the world as we do (a goal I suspect I shall never come close to realising fully) and, primarily, it seeks to understand for understandings sake. This is nothing to be ashamed of.

It is however a great luxury and so I must express my sincere gratitude to the whole variety of people and organisations who have facilitated, supported and funded me and the work herein. The first thanks clearly must go to my supervisors Nick, Gethin and Vincenzo. Nick for his (almost entirely unsubstantiated) faith in me, general positivity, and getting me to the point of doing a PhD in the first place. Gethin for his insightful questions and comments (even if they were sometimes the difficult questions I didn't want to be asked) and for his help in learning and using matlab, and Vincenzo for being a driving force at the conception of this work. I have been very grateful to be part of this department and owe much to the inspiration, support, and companionship of my fellow students, at both masters and PhD level, and the academic, technical and administrative staff (in order of increasing importance). While there are too many to name I must acknowledge the people I have shared my office (and music, moaning and meltdowns) with who are as responsible as anyone for me getting to this stage; Abigail, Josh, Jordi, Peter and Dan.

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My final thanks goes to my wife, Joy, who has encouraged and supported me, emotionally, practically and financially, throughout. Without you I would not have started on this path, and definitely would not have finished. Thank you for your endless, unconditional, faith in me. I love you.

“The most important words a man can say are, “I will do better.” These are not the most important words any man can say. I am a man, and they are what I needed to say.

The ancient code of the Knights Radiant says “journey before destination.”

Some may call it a simple platitude, but it is far more. A journey will have pain and failure. It is not only the steps forward that we must accept. It is the stumbles. The trials. The knowledge that we will fail. That we will hurt those around us.

But if we stop, if we accept the person we are when we fall, the journey ends. That failure becomes our destination. To love the journey is to accept no such end. I have found, through painful experience, that the most important step a person can take is always the next one.”

*Brandon Sanderson, Oathbringer*

## General Abstract

Although the experimental investigation of the perception of time dates back to around 1864 (Lejeune & Wearden, 2009) the reasons for variation between individuals are still poorly understood. Advancing in this area has been identified as one of the most important issues for the modern investigation of time perception (Hancock & Block, 2012). Although various individual differences in time perception have been identified, these are usually based on comparisons between different groups depending on characteristics such as age or gender; clinical conditions such as schizophrenia or autism; or induced differences such as temperature or pharmacology. In this thesis we seek to investigate whether, and how, intrinsic individual differences in sensory processing within the general population influence individual timing behaviour. This is accomplished over four experiments. The first seeks a relationship between the EEG alpha rhythm, which is strongly associated with visual and audio-visual temporal integration, and behaviour on four timing tasks; while trends are in the expected directions no significant relationship emerges. The second responds to this null result by seeking a relationship between audio-visual integration and estimated, sub-second, durations in a purely behavioural paradigm, in this case the results show a significant association. The final two experiments are concerned with individual differences in interoceptive accuracy (sensitivity to ones own bodily signals), and how these influence the effect of arousal on time judgement. The first experiment, using supra-second durations, finds no effects, but the second, using shorter durations (under 1200ms) and addressing some methodological concerns, does find a significant moderation, by interoception, of the effect of emotional arousal upon time. We conclude that this provides substantial evidence that exteroceptive and

interoceptive primary sensory processes play a role in individual variation in timing tasks, a finding that provides many further avenues of investigation.



## Overview of chapters

### *Chapter 1: An introduction to individual differences and time*

In this chapter we introduce research into human timing, selectively discussing key methods and theories and outlining some of the questions and challenges that exist in this area of research. In particular we discuss the temporal aspect of multi-sensory integration and the effect of arousal on timing behaviour. Finally we outline some of the existing research into individual differences in time perception and the questions that remain in this regard.

### *Chapter 2: Do individual differences in the EEG alpha rhythm relate to differences in time judgements across tasks?*

In this chapter we present an experiment that primarily aimed to investigate whether a neural temporal marker of audio-visual integration, the EEG occipital alpha peak frequency, relates to timing behaviour. Secondly it also compared timing on four different tasks with the aim of clarifying how different judgements relate and what type of judgements are most likely to relate to this marker of sensory integration. Results trended in the expected direction but generally did not achieve significance. We review some of the limitations that may have contributed to this finding.

### *Chapter 3: Individual differences in sensory integration predict differences in time perception*

This chapter addresses a similar question as chapter 2 but in this case seeks a relationship between a behavioural measure of temporal sensory integration, the simultaneity judgement, and timing performance for empty and filled intervals under

1200ms. In this case a significant positive relationship was found between the window of integration and estimations in the empty condition, such that those with a smaller temporal binding window make longer estimates. We discuss the implications of this finding.

#### *Chapter 4: Interoception, arousal and time*

This chapter, covering two experiments, moves from exteroceptive sensory processing to address how individual differences in interoceptive processing may influence timing, in particular with regard to the established influence of emotional arousal on timing behaviour. We applied a standard measure of interoceptive accuracy and compared this to subjective arousal ratings and timing performance. The first experiment finds no effect of arousal, which may be attributed to methodological issues including the supra-second durations and how the arousing stimulus was presented in relation to the timing task. The second experiment addresses these concerns and replicates the established relationship between time estimations and arousal. Finally the results show that this relationship is moderated by interoceptive accuracy, suggesting arousal related time dilation is driven by embodied emotion.

#### *Chapter 5: General discussion*

We draw together the findings on exteroceptive and interoceptive sensory processing and consider the implications for time research. Limitations and future directions are discussed.

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## Chapter one: General introduction

“Perhaps someday we will discover that space and time are simpler than the human equation ”

*Captain Picard – Star Trek: The Next Generation*

### **The equation for time**

Picard speculates that perhaps time is, in reality, easier to understand than humans. How then may we, as psychologists, write the human equation for the experience of time? One might start by accounting for factors, such as the range of durations (Buhusi & Meck, 2005; Lewis & Miall, 2003a), the way of measuring timing behaviour (Block, Grondin, & Zakay, 2018; Droit-Volet, Wearden, & Zélandi, 2015) and the sensory modality involved (Penney, 2003), all of which are known to influence timing in experiments. Manipulations to influence performance, via, for example, attention (Tse, Intriligator, Rivest, & Cavanagh, 2004; Zakay & Block, 1996), arousal (Cahoon, 1969; Piovesan, Mirams, Poole, Moore, & Ogden, 2018) or variation in the characteristics of the stimuli (Fister, Stevenson, Nidiffer, Barnett, & Wallace, 2016; Goldstone, Lhamon, & Sechzer, 1978; Matthews, Stewart, & Wearden, 2011), must also be accounted for. While these may help to predict time at a group level there are also differences between individuals that may influence time, including age (Espinosa-Fernández, Miró, Cano, & Buela-Casal, 2003; Hancock & Rausch, 2010), gender (Espinosa-Fernández et al., 2003; Hancock, Vercruyssen, & Rodenburg, 1992) and mental health (Foucher, Lacambre, Pham, Giersch, & Elliott,

2007; Lee et al., 2009; Wallace & Happé, 2008). In this thesis, we focus on exploring how individual differences in sensory systems may relate to differences in timing within the general population. Specifically we focus on individual differences in multisensory integration and in the sense for one's internal state - interoception.

### **Why investigate time perception?**

As some form of timing is required for almost all actions, social interactions and most other parts of life, there are many valid reasons to study time perception. In the case of this thesis, time perception is of a particular interest from the perspective of perception and consciousness (Craig, 2009a; Wittmann, 2015). In every conscious moment, we are processing sensory information to create a (mostly) coherent order of events to allow us to function. Timing is an important factor in accurately determining whether information, from one or multiple senses, is combined into one event (Bausenhart, 2014; Mégevand, Molholm, Nayak, & Foxe, 2013; Remijn, Ito, & Nakajima, 2004). It is valuable to add to our understanding of how we generate a sense of duration as this is one of the essential factors in understanding how we perceive the world around us, and how and why the version of the world we consciously experience differs from the objective reality. Consequently, the study of time perception may help to shed light on one aspect of how individuals perceive the world differently, both in clinical populations associated with perceptual differences and within the general population.

### **Types of time**

Before one could even begin writing an equation for time, the type of "time" concerned would have to be defined, as it seems there may be radically different processes and behaviours involved according to how we define this sense (Block &



Zakay, 1997; Ornstein, 1975; Wittmann, 2009). Ornstein (1975) provides particular insight on this point:

“It would therefore be useful to determine which research evidence bears on each different process, instead of lumping them all under the single heading of ‘time sense’. It seems to me that there are four major varieties of time experience, the experience of very short interval – the present, the longer experience of duration, the experience of the future or of a temporal perspective, and the experience of simultaneity” (p.20)

From this classification, our primary interest is in “the present”, which may be thought of, for practical reasons, as durations in the order of hundreds of milliseconds to seconds, most often under ten seconds. We will also touch on the experience of simultaneity in considering whether these categories of time are, in fact, separate.

Ornstein was primarily concerned with the second category he lists; the experience of duration over periods longer than ten seconds, and usually from minutes up to hours. His research focused on the cognitive aspect of how we think about and process elapsed durations of this magnitude and the general finding in this area was that the way the information from that period was stored, and particularly the amount or “size” of that information, determined how long it felt to the individual in retrospect. There are however, parallels with the experience of short durations. For example, a key point in Ornstein’s findings is that more material to encode within a duration, such as more events or more complex stimuli, results in a longer perception of duration (measured retrospectively and subject to some cognitive factors such as how the events are grouped). In very short durations, we can find a similar pattern, in that a duration filled with stimuli is often seen as longer than an empty one (Wearden, Norton, Martin, & Montford-Bebb, 2007); although the complexity of the stimuli can

have the opposite effect by distracting the participant from processing the interval (Palumbo, Ogden, Makin, & Bertamini, 2014).

The category of temporal perspective pertains more to how an individual, or a culture, think about the experience of time and thus it is as much social, philosophical and cultural as psychological. On an individual level temporal perspective may be thought of the nature and extent of cognition about our past, our present, and our future (Lennings & Burns, 1998; Zimbardo & Boyd, 2015). An example of psychological engagement with this type of time is the Zimbardo Time Perspectives Index (Zimbardo & Boyd, 2015) which seeks to classify individuals across 5 factors related to how they think and feel about the past, present and future. For example, the past negative construct includes the item “I think about the good things that I have missed out on in my life” and the present hedonistic includes “Taking risks keeps my life from becoming boring”, all scored on a 5 point Likert scale from “very characteristic” to “uncharacteristic”. This measure has been found to relate to aspects of mindfulness which themselves relate to accuracy in judging duration, both in visual reproduction of durations up to 20s and sub-second auditory duration discrimination tasks (Wittmann et al., 2014) and so it is likely that such measures may relate to the timing of short durations. In a more direct investigation, using a different time perspectives measure, a relationship between time perspective and 30s judgements was found, though only reaching significance when moderated by age (Lennings & Burns, 1998).

The experience of simultaneity is arguably of a slightly different category, as it is concerned not with the direct perception of duration, per se, but the effect of duration on perception. Considering this, we might also include in this category other perceptions that rely on specific temporal characteristics, such as the double flash

illusion (Shams et al., 2002) the moderation of the bounce/stream effect by sound (Shams et al., 2002; Watanabe & Shimojo, 2001) and the wagon wheel illusion (Andrews & Purves, 2005; VanRullen, Reddy, & Koch, 2006). These form something of a grey area as these effects rely on the temporal characteristics of perception but it is unclear to what extent these relate to the other, more direct, types of time perception above; this question forms one of the issues of this thesis.

Returning to short durations, an argument has since developed for further dividing this category into two types of timing, based on duration, both of which appear to produce different behaviours and recruit different systems. Generally, the differentiation is between sub and supra-second intervals, though it is not likely that one system switches off while the other turns on at one second; rather we might expect a shift of influence from one to the other as duration increases. Buhusi and Meck (2005) describe the difference as being between timing in the range of seconds (or minutes), which is involved in, for example, decision making and foraging, while millisecond timing is more orientated around movement and speech. There is also the issue that cognitive strategies might become increasingly important for durations in the range of seconds; in particular, chronometric counting appears to become viable from 1.18s (Grondin, Meilleur-Wells, & Lachance, 1999) and changes some timing behaviour (Grondin, Ouellet, & Roussel, 2004; Rattat & Droit-Volet, 2012; Wearden, 2016).

There is also support for the distinction between sub and supra-second timing in the neuroscientific literature. Lewis and Miall (2003b) compared 0.6s and 3s in a visual temporal discrimination task. While certain areas were activated for both durations, including the dorsolateral prefrontal cortex, bilateral insula cortex, right pre-supplementary motor area, frontal pole and inferior parietal cortex, other areas

were significantly more active for the shorter duration, including the front operculum, left cerebellum and temporal gyri, though there was very little that was more active in the 3s condition. Meta-analyses, while not entirely consistent on the regions involved (though the IFG and SMA are commonly identified) generally support a sub-second - supra-second differentiation (Lewis & Miall, 2003b; Penney & Vaitilingam, 2008; Wiener, Turkeltaub, & Coslett, 2010). It should be noted that these include various studies that have identified slightly different patterns, likely due, to some degree, to different tasks and controls. In particular the results of Livesey, Wall, and Smith (2007) suggest we should be cautious in interpreting fMRI data. Using the discrimination of 1s from 1.5s durations they suggest some areas, including pre-SMA, right inferior parietal lobule and (parts of) the dorsal pre-frontal cortex, are recruited according to task difficulty and not timing specifically. They identify three small regions, the putamen, part of the left supramarginal gyrus and an area where the inferior frontal gyrus meets the insula, that appear to be specifically related to timing regardless of difficulty.

The above shows that while broad categories of time experience can be suggested based on duration, and this is a useful distinction, they are often not entirely distinct or clearly delineated. In the course of this thesis, we present one experiment that utilizes a variety of tasks, mostly concerned with durations of 1 second or longer, one that focuses on durations under 1200ms, in relation to sensory integration, and a pair of experiments about arousal and time judgments where the first uses durations from 5 to 10s and the second durations up to 1s.

## Theories of time perception

The idea that time perception relies on some sort of internal clock has been around for some time, for example Hoagland (1933) posited a chemical clock based on the observation that increases in temperature influenced timing behaviour. In the 60s Treisman originated an information-processing model of the temporal system (Treisman, 1963, 2013) lead to a more formal model of time perception that introduced two key elements; the pacemaker and the counter. Firstly the pacemaker produces regular beats or pulses, which is open to the influence of arousal. Secondly the counter records pulses allowing storage and comparison. This model has been the basis of more complex cognitive timing models such as the scalar timing model (SET; Gibbon, Church, & Meck, 1984) and the attentional gate model (Zakay & Block, 1996).

Taking the attentional gate model as our example (see figure 1.2), the pacemaker and accumulator (analogous to Treisman's counter) remain but an attentional gate and switch have been added, as well as a more detailed account of memory and comparison. Although there was significant debate about whether the attentional gate was necessary in addition to the switch (Lejeune, 1998, 2000; Zakay, 2000) it is useful conceptually in terms of considering different types of variance in timing behaviour. In pacemaker-accumulator models the action of the switch (the initiation of which has been characterised both as opening, to allow pulses through, and closing, after the manner of completing a circuit, depending on the theorist) allows pulses to flow from the pacemaker to the accumulator and as such it dictates the onset and offset of timing (Zakay & Block, 1996). The switch can be a source of variation in that there may be a latency between the signal that starts or ends the interval and the action of the switch. In theory switch latency, occurring only at the

beginning or end of the duration, should change the timing of a duration by a fixed amount regardless of the to-be timed duration; it is purely additive (Lejeune, 1998; Meck & Benson, 2002). Manipulations can influence this element by effecting how attention is applied to the start/stop signals. For example it has been found in rats that applying a warning signal in a different modality to the timed stimulus resulted in underestimation, which is interpreted as being due to a delay in initiating the switch due to the need to orient attention from one modality to the other (Meck, 1984).

By contrast the attentional gate is proposed to account for the allocation of attention during the timed duration. In a dual task paradigm results show that the same duration is judged to be longer when attention is directed towards the timing task compared to a secondary, non-temporal, task and distracting attention from timing results in a comparatively short duration (Block, Hancock, & Zakay, 2010; Zakay, 1998; Zakay & Block, 1996). This process is conceptualised as the attentional gate being fully open to allow the flow of pulses when attention is fully orientated towards timing but partially closing and thus restricting the accumulation of pulses where attention is required elsewhere (Block et al., 2018; Zakay, 1998). As mentioned above it has been debated as to whether the addition of the gate is requisite to account for such findings or whether it is more parsimonious to attribute this to the switch closing briefly when distraction occurs (Lejeune, 1998, 2000; Zakay, 2000) however in terms of the effect on timing behaviour both models make similar predictions. Thus there are two potential sources of variance in timing from attention; the initial delay in commencing timing (or in ending it) and the degree of application of attention during the timed period.

A further source of variance within pacemaker based models is the rate of the pacemaker itself. As noted above Triesman's (1963) original model includes an

influence of arousal upon the pacemaker and this can still be seen in the attentional gate model (figure 1.2). The term arousal is used in the broadest sense, operationally defined as anything that increases the rate of the internal clock (Droit-Volet & Meck, 2007), and has sometimes been described alternatively as activation (Burle & Casini, 2001). Conceptually anything that speeds up the pacemaker should produce a scalar increase in duration perception as more pulses are accumulated over time.

Behavioural evidence has suggested the pacemaker can be increased by factors including emotional arousal (Droit-Volet, Fayolle, & Gil, 2011; Droit-Volet, Brunot, & Niedenthal, 2004; Gil & Droit-Volet, 2012; Ogden, Moore, Redfern, & McGlone, 2015), exercise (Verduyn, Hancock, & Mihaly, 1989), click trains (Penton-Voak, Edwards, Percival, & Wearden, 1996; Wearden, Philpott, & Win, 1999) and psychoactive substances acting on dopamine concentrations (Buhusi & Meck, 2002; Cheng, Ali, & Meck, 2007; Cheng, MacDonald, & Meck, 2006; Matell, King, & Meck, 2004; Sewell et al., 2013). While it is less commonly investigated, slowing the pacemaker should have the inverse effect (Buhusi & Meck, 2002; Wearden, 2008; Wearden et al., 1999).

Finally variance may arise in the final stage of the model where memory and comparison processes occur. Introducing other distractor tasks or events between encoding and reproduction of an interval appears to shorten estimates and thus it has been argued that working memory for time shares resources with attentional and memory resources for context (Buhusi & Meck, 2005). There is also recent evidence that individual variance in executive functions such as updating working memory and access to semantic memory correlates variably with timing performance depending on the design of the task (Ogden, MacKenzie-Phelan, Montgomery, Fisk, & Wearden, 2019).

Pacemaker-accumulator models have become popular because of their heuristic value in describing timing behaviour as observed in many lab experiments (Block & Gruber, 2014; Block & Zakay, 1997) though it has been argued that it applies less well to the application of timing in more ecologically valid circumstances where there is a complex series of events interacting rather than a single interval (Grondin, 2010; Taatgen, Van Rijn, & Anderson, 2007). Treisman's original conceptualisation of the model was that the initial temporal information would originate in the processing of primary sensory information but with common mechanisms for processing that information (Treisman, 1963, 2013) but attempts to identify reliable and consistent biological pacemaker were not successful (Treisman, 1984).

The Striatal Beat Frequency model (Matell & Meck, 2000, 2004) is a more neurobiologically viable model of time perception that has some conceptual similarities with Treisman's (1963) model, in that the temporal information is derived from cortical oscillatory inputs and is centrally processed, while theorising a much more complex interaction of these factors. SBF posits that timing can be accomplished by coincidence-detection which is facilitated by a cortico-thalamic-striatal loop. Initially the oscillatory cortical neurons are synchronised by the release of dopamine at the onset of timing (Kononowicz, 2015) but as they have intrinsically different rates of oscillation they then fall out of synchronisation. This creates a pattern of activation that is monitored by medium spiny neurons (MSNs) in the dorsal striatum that each receives thousands of inputs from the cortical oscillatory neurons. Through reinforcement, via dopamine, MSNs become specialised for a particular pattern of activation and thus fire when that pattern is detected. As the neurons are initially synchronised a pattern should occur at roughly the same point after onset



each time and thus the MSNs essentially code for time. The thalamus, which can modulate both cortical and striatal activity, receives the output from the striatum and relays this temporal information to other areas controlling behaviour (Matell & Meck, 2000).

In essence this system “learns” duration by identifying the pattern at the point of reward and then can arrive at the same point again when the activation coincides with the previously identified pattern. While dopamine release is responsible for synchronising the start of oscillations, dopamine release is also thought to produce the effects of arousal on time by modulating cortical oscillation frequencies (Droit-Volet and Meck 2007). As with pacemaker-accumulator models this model accounts well for much behavioural data on timing and additionally has significant support from neurophysiological and pharmacological data, though some of the processes within the model still require empirical support (Lake, 2016).

The cortical areas primarily associated with the SBF model are frontal (Matell & Meck, 2004; Meck & Benson, 2002), however Hashimoto and Yotsumoto (2015) propose an addition to this model to allow for sensory entrainment. In particular they performed a series of experiments where visual flicker dilates supra-second time judgements. Their findings indicated that both the peak frequency and frequency distribution influence the degree of dilation, including the finding that flicker distributed in the 8-12 Hz range cause dilation while flicker in the range of 12-16 Hz does not. Hashimoto and Yotsumoto (2015) produced a model that adds entrainment to the SBF model and successfully predicts the pattern of dilation found in their experiments. Theoretically this suggests that the cortical oscillations involved in the SBF model may be modulated by the entrainment of oscillations in the visual cortex.

This may be a point of intersection between SBF and the evidence for distributed timing discussed below.

A second theory of time based in neurophysiology is Craig's theory of Global Emotional Moments (GEMs), sometimes also known as the Homeostatic Model of Timing (Craig, 2009a). This theory characterises awareness itself as a series of 'global emotional moments' which are built up in the insula cortex. This theory originated with the discovery of the lamina I spino-thalamocortical pathway that essentially projects a representation of the body's state directly to the posterior insula cortex (Craig, 2002). The physiological information provided by this homeostatic afferent pathway is the template for the GEM. From the posterior to the anterior of the insula cortex salient homeostatic, environmental, hedonic, motivational, social and cognitive factors are incorporated (in that order), producing a representation of the self for that particular moment in the anterior insula cortex, with the awareness of self in time arising from a stream of such moments. These moments are of a finite capacity, which means that they fill relatively quickly when there is information that is salient for survival (e.g. in arousing contexts) resulting in time dilation.

It has been suggested that this stream of moments could effectively function as the pacemaker in the attentional gate model (Wittmann, 2015). Support for this theory primarily arises from imaging studies that identify AIC activation in relation to various aspects of consciousness (Craig, 2002, 2009a, 2009b) including interoception (Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004; Henderson, Gandevia, & Macefield, 2007) and time perception (Lewis & Miall, 2003a; Livesey et al., 2007; Rao, Mayer, & Harrington, 2001). In particular in Livesey et al.'s (2007) experiment the AIC was one of the few areas where activation was consistently and primarily

associated with timing (in the range of milliseconds to seconds) once they controlled for task difficulty.

A final consideration with regards to theories of time is the suggestion that time perception may be modular or distributed in nature, rather than utilising a single central mechanism. The most extreme theory in this regard is arguably the state-dependant network model (Buonomano & Maass, 2009) which argues that it is possible that duration can be processed within individual sensory cortices themselves, as with other basic features of a stimulus. This is an intrinsic model, meaning timing has not a dedicated structure or process but is an emergent property of neural processing, which is proposed to vary depending on the state of the relevant network at onset, thus being influenced by context. Studies aiming to test this model have suggested that it is only reflected in behavioural results for durations under approximately 300ms (Buonomano, Bramen, & Khodadadifar, 2009; Spencer, Karmarkar, & Ivry, 2009) and thus is quite limited.

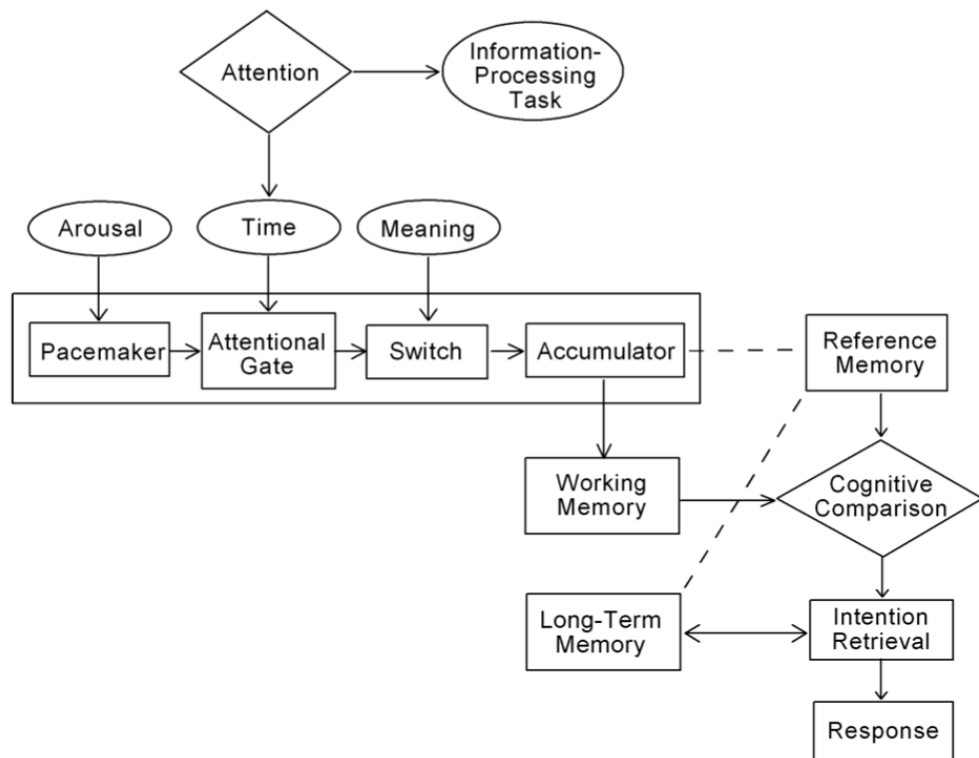
On the other hand, specific models aside, there is substantial evidence that timing relies on a network that is at least partially distributed, with involvement from sensory cortices depending on modality. In particular there is neuroscientific evidence of sensory cortex, including visual cortex, involvement in timing from a number of sources (Bueti, 2011; Bueti, Bahrami, & Walsh, 2008; Bueti & Macaluso, 2010; Bueti, Walsh, Frith, & Rees, 2008; Ghose & Maunsell, 2002; Shuler & Bear, 2006). The work of Bueti and Macaluso (2010) is a notable example. They asked participants to respond as quickly as they could to sounds that were presented after an interval. Participants were trained so that some delays were more expected than others. During the anticipation of the stimulus there was increasing activation in a number of areas including those relevant to auditory stimuli, and motor response, but also in the

occipital visual cortex. This activity was consistent with individual performances on the behavioural task. This suggests not only that timing is distributed but that it also can be cross-modal and that individual performance varies in accordance with sensory cortex activation. In a subsequent study, using both functional and structural MRI, neurophysiological changes were observed in areas including the cerebellum and occipital, parietal and insular cortices. These were associated with the learning of a set duration in the millisecond range and these changes were predictive of performance accuracy (Buetti, Lasaponara, Cercignani, & Macaluso, 2012).

These findings are not necessarily contradictory to the other models previously discussed in this section. It has already been noted that a modification to SBF has been proposed that models modulation of timing by oscillatory entrainment from primary sensory information (Hashimoto & Yotsumoto, 2015). In the GEMs model the integration of information in the insula cortex includes salient sensory information, and indeed the AIC is implicated in cross-modal sensory integration (Bushara, Grafman, & Hallett, 2001; Craig, 2009b). As the model proposes a limited capacity for GEMs then primary sensory information should contribute to filling this. We might expect that changes in primary sensory processing, such as entrainment, may change the characteristics and ultimately size, of the sensory information thus encoded, hence having some effect on the rate of GEMs as a pacemaker.

Notably, Buetti (2011) manipulated the characteristics of sub-second visual and auditory temporal stimuli, via speed and pitch respectively, to distort reproductions. The degree of distortion (e.g. subjective time) correlated with activity in the putamen, mid-insula and mid-temporal cortex, which is interpreted as evidence for these areas acting as a temporal accumulator. The involvement of the insula cortex would be consistent with the GEMs model, but this evidence could also be interpreted

as integration within the SBF model. Finally this finding could fit with theories that propose a more distributed, modality specific type of timing, especially as the accumulation finding was specific for the visual modality in this study. This experiment is a good example of how findings in time perception often can fit with more than one of the theoretical frameworks on offer, partly due to the commonalities between the models. In this thesis we focus on two elements that are common to the models above; firstly the role of processing of primary sensory information in influencing timing and secondly the role of arousal.



*Figure 1.2: A version of the attentional gate model. Taken from Block and Zakay (2006)*

### **Effects of task**

It is well established that the type of task utilised influences outcomes in timing investigations. To exhaustively cover the variations by task would be a considerable work in itself (see Block et al., 2018; Grondin, 2010; Zakay & Block, 1997). Instead, here we highlight some of the key aspects regarding the choices of tasks for this thesis.

In the first instance, there is a distinct difference between retrospective judgements (where the participant is unexpectedly asked to provide a judgement on an interval that has already passed) and prospective judgements (where the nature of the judgement required is known in advance). Retrospective judgements tend to be shorter than prospective ones, with more inter-subject variability. They are also differently moderated by processing difficulty, in that increasing cognitive load increases retrospective judgements but reduces prospective ones. This is believed to be because higher load distracts attention from prospective timing but in the memory processes underlying retrospective judgements more content is interpreted as a longer interval (Block et al., 2018; Block et al., 2010; Block & Zakay, 1997). In this context, retrospective judgements are initially attractive for studying inter-individual variation. However, there are two key issues with this as a paradigm. Firstly, as above, memory is necessarily central in retrospective judgements and so it is difficult to ascertain whether individual differences are attributable to timing per se or to differences in recall or the way the information is encoded (Ornstein, 1975). Secondly, these paradigms are difficult to implement, as only a single trial can be truly retrospective. Therefore, in this thesis, we focus on prospective timing.

Within prospective timing, there are three main considerations with regards to the effect of task: the time scale concerned (which is addressed above), the modality

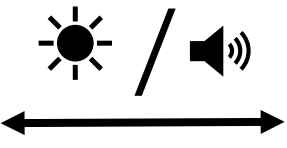

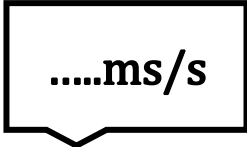

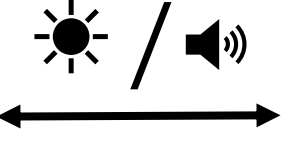

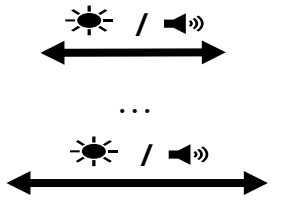
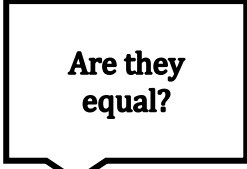
of the input and the manner of the response. There are four broad classes of prospective time judgement (Block et al., 2018; Grondin, 2010). Firstly, the verbal estimate (which may be verbal but often is given via computer input) requires the participant to state how long elapsed during the interval, generally in seconds or milliseconds. Secondly, a production task is where a target duration is set, for example by stipulating a number of seconds. The participant is required to produce that duration to the best of their ability, which might be accomplished by holding a button or pressing for onset and offset. Thirdly, reproduction combines the above two methods as a stimulus is presented for the target duration and the participant then attempts to produce the same duration. Finally, there are interval comparison tasks, which are a variety of procedures that involve making a judgement that compares two or more durations. For example, in the temporal bisection task, the participant is generally given two standard durations, one longer and one shorter. They make judgements about comparison durations, generally in a range between the standards, determining to which standard the comparison duration is closest. From this a bisection point, where the participant is equally likely to respond long or short, can be calculated (Kopeck & Brody, 2010). Temporal generalisation is similar but uses a single standard and participants make judgements as to whether comparators are the same as the standard (see box 1.1 for a breakdown of task types).

Though all putatively measuring the same thing, these tasks recruit different cognitive processes and so may vary in terms of behaviour. For example, verbal estimations are typically more variable than other methods (Zakay & Block, 1997). fMRI evidence, while often showing some areas such as the basal ganglia (in sub-second tasks) to be consistently activated across timing tasks, has also shown some distinctions, with reproduction activating a wider system (including premotor, parietal

and extrastriate visual cortex) than an estimation task with identical stimuli (Buetti, Walsh, et al., 2008). This highlights one consideration, in that production and reproduction tasks generally involve a motor component, which may result in an over-representation of motor areas in studies using these measures. Nonetheless a meta-analysis by (Wiener et al., 2010) suggests that the supplementary motor area (SMA) might be one of the most consistently activated areas across timing experiments, including both motor and perceptual tasks, although it should be noted that the perceptual studies selected largely utilise varieties of temporal discrimination and so some tasks, such as estimation, may be underrepresented.

Interestingly, a behavioural meta-analysis comparing prospective and retrospective timing found no behavioural difference between reproduction and estimation (Block & Zakay, 1997), although a later meta-analysis did find these tasks, and production, to be differently influenced by cognitive load (Block et al., 2010), suggesting that there are differences in how duration is processed in these tasks. In another example, using a reproduction task using relatively long intervals (8,14 and 20s), it was found that individual performance was predicted by a combination of cardiac slowing, primarily during encoding, and heart beat sensitivity (Meissner & Wittmann, 2011) suggesting the (presumably unconscious) use of a strategy that is not universally available in supra-second timing tasks where there is not an encoding phase.



Method	Stimulus	Response
Estimation		
Production		
Reproduction		
Comparison (generalisation)		

*Box 1.1: A non-exhaustive illustration of some common timing paradigms. Double ended arrows represent a stimulus of a set duration. The speech bubble represents a written or verbal instruction or response. The hand icon represents pressing or holding a button.*

With regards to the question of how time perception is influenced by the sensory modality in which the stimulus to be timed is presented, the majority of research has focussed on the differences between auditory and visual stimuli. Auditory intervals tend to be perceived as longer, and show less variability, than those presented visually (Grondin, 2010; Walker & Scott, 1981; Wearden, Edwards, Fakhri, & Percival, 1998). Bringing task and modality together, Merchant et al. (2007) used a

variety of interval timing tasks, including producing intervals via tapping a button and perceptual judgements comparing intervals to standards, these being between 299 and 1300ms. These tasks also varied between auditory and visual stimuli. Their findings show that whether the task is production or perceptual is the most important factor for performance (with the exception of duration) although this is somewhat clouded by the additional finding that individual variability appears to correlate between some perceptual and production tasks. This is interpreted as support for overlapping elements in different timing processes subtending perception and production. Concurring with other studies they find that visual tasks are generally more variable, though otherwise the performance of a participant is usually consistent across modalities within the task. This does interact with the perceptual/production differentiation such that the modality difference is more pronounced in perceptual tasks. These findings emphasise the important differences that experimental design can produce in results but also provide some reassurance, for our purposes, that differences in individual performance may be relatively stable across task and modality.

Some recent studies have investigated how individual differences in established measures of different executive functions relate to differences in timing behaviour. Updating working memory, switching attention, inhibition (ability to inhibit a dominant response) and semantic memory access all relate to performance on different timing tasks. These show significant differences in the executive resources recruited by tasks. For example temporal generalisation correlates with semantic memory access and updating and bisection generally correlates with inhibition and sometimes access, depending on the parameters (Droit-Volet et al., 2015; Ogden, MacKenzie-Phelan, et al., 2019; Ogden, Wearden, & Montgomery,

2014). Reproduction relates to updating, access and switching while estimation is only associated with access to semantic memory; presumably due to the need to retrieve internal standards of duration, and otherwise appears not to be related to executive capacity (Ogden et al., 2014). While questions remain in this area this research suggests that some tasks may engage more executive resources than theoretically expected and so this becomes an additional consideration for task selection.

In this thesis, we use both visual and auditory timing, as appropriate. While a variety of tasks are used, especially in our first experiment, we focus on tasks such as estimation and production that do not require a comparison duration. As we focus on individual differences it is hoped that this minimises the sort of unconscious process used for encoding and reproduction that is found in Meissner and Wittmann (2011) and minimises confounds that may arise from differences in executive functions (Droit-Volet et al., 2015; Ogden, MacKenzie-Phelan, et al., 2019; Ogden et al., 2014). There is also the possible concern that reproduction or comparison judgements require, in a sense, two timing performances; timing the standard and then the reproduction or comparator. From the perspective of attempting to measure individual differences, that may be constant over both stages, it is hard to say whether the differences may be represented in the first timing, the second timing, or the comparison of the two. The downside of making this argument is that it may also be applied to tasks such as we use; in that for estimation or production the participant must still have a standard timing of some sort in mind, it is just not one that we have given them. Modelling estimation tasks (in the range of hundreds of milliseconds) has suggested that changes in the representation of a duration should be fairly reflected in changes to the response (Wearden, 2015), providing some reassurance. Inevitably

there are some limitations to any timing task and though we aim to make the best choices it is to be expected, and desired, that work building on our findings will use different and varied tasks.

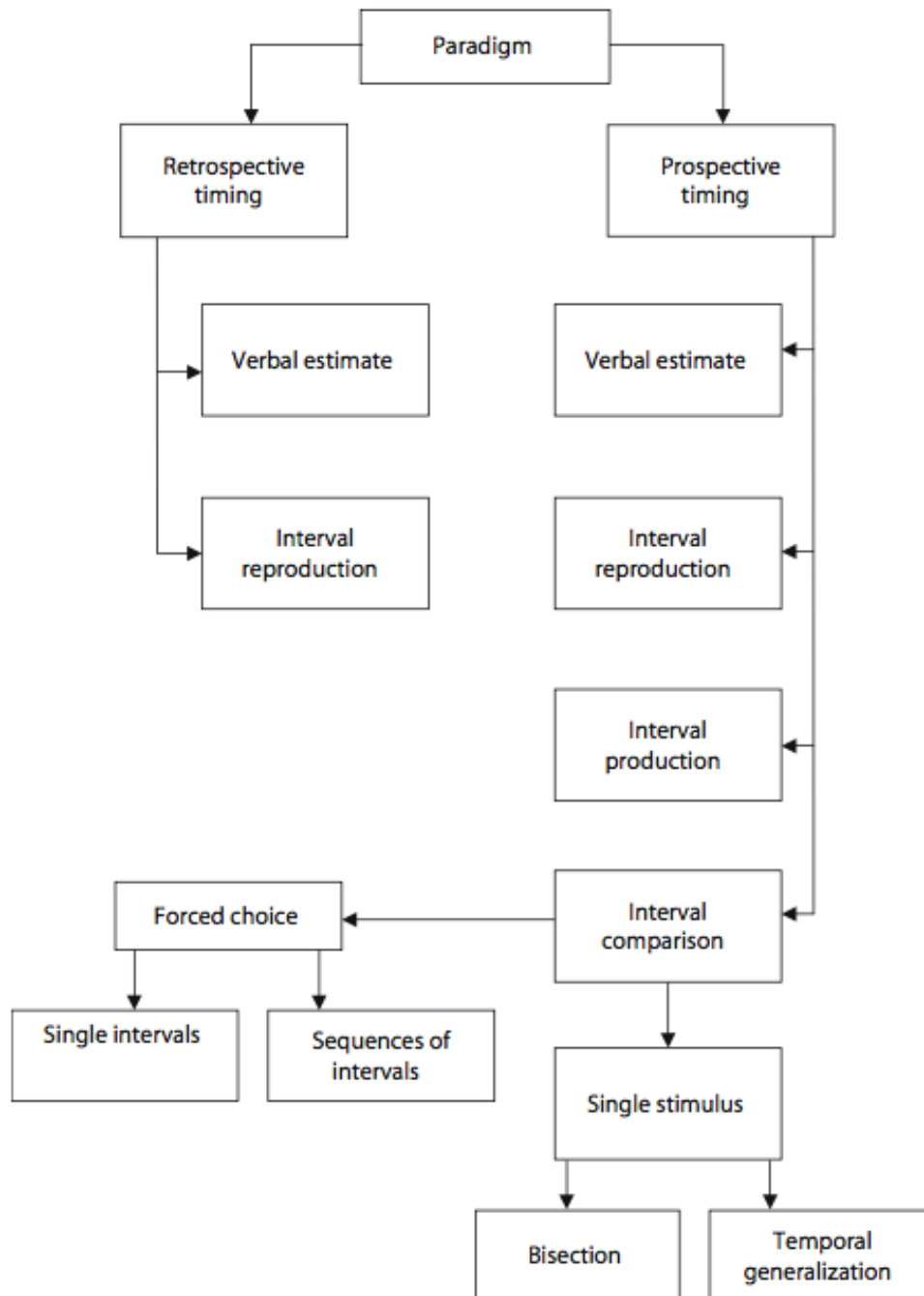


Figure 1.1: Schematic showing the methods commonly used in investigating time perception. Taken from Grondin (2010).

## Manipulations

There is considerable evidence showing that manipulating the amount of attention a participant applies to timing, substantially influences behavioural outcomes (Block et al., 2010). Adding a distractor task before (Wearden, O'Rourke, Matchwick, Min, & Maeers, 2010) or during (Macar, Grondin, & Casini, 1994) a timing task produces relatively shorter time estimates, compared to a non-distracting condition (the relationship to veridical time is dependent on duration), with greater distraction producing a larger change in timing. Attention is a key component in one of the more prominent models of timing, Scalar Expectancy Theory (SET; Gibbon et al., 1984). SET posits a pacemaker producing regular pulses and an accumulator that tracks them. The role of attention is represented by the attentional gate (Zakay & Block, 1996) which varies dependant on the allocation of resources. The more attentional resources are allocated to timing the more pulses may pass through the gate. The switch activates when the beginning of the to-be-timed interval is detected and allows pulses to flow to the accumulator until the end of the duration is detected. These elements are useful in considering two different ways in which attention can influence timing; where a distraction delays the detection of the onset or where attentional resources are allocated elsewhere, in both cases relatively reducing the perceived duration. Once the interval has been timed memory and comparison processes are called upon to produce a judgement according to the task. While it is difficult to find a direct analogue of the model in the brain this model has often been found to be coherent with research findings (Block & Gruber, 2014; Block & Zakay, 1997) though it has been argued that it applies less well to the application of timing in more ecologically valid circumstances where there is a complex series of events interacting rather than a single interval (Grondin, 2010; Taatgen et al., 2007).

Aside from attention and arousal (which is addressed separately below), there are several other factors concerning timing tasks that have been found to influence judgements. It has been found, for example, that moving stimuli are experienced as longer lasting than still ones (Brown, 1995) and larger visual stimuli are judged to be presented for longer than smaller ones (Mo & Michalski, 1972; Xuan, Zhang, He, & Chen, 2007), an effect that is moderated by duration (Rammsayer & Verner, 2014). Varying the complexity of stimuli (“complexity” generally referring to factors such as the number and nature of elements and their layout) has produced mixed results. Schiffman and Bobko (1974) found, using reproduction for intervals up to 23s, that the duration of more complex stimuli are overestimated compared with less complex. Cardaci, Di Gesù, Petrou, and Tabacchi (2005) found that viewing time for more complex paintings (actual time 90s) is underestimated for more complex paintings, while Folta-Schoofs, Wolf, Treue, and Schoofs (2014), using a reproduction paradigm, where the stimulus is a distractor during production, found over-reproductions for more complex stimuli. Finally Palumbo et al. (2014) when varying black and white abstract patterns in an estimation task between 250 and 1500ms, found no effect of complexity. Clearly results are mixed in this area and Palumbo et al. (2014) suggest that complexity only has an effect when it distracts from timing, and as such is a question of attention. This would be consistent with the above findings varying by paradigm and stimulus.

The filled duration illusion is a well-known and robust example in a similar vein: intervals that are filled with a stimulus (for instance a continuous tone) are robustly judged as longer than an empty duration with only onset and offset signalled (Thomas & Brown, 1974; Wearden et al., 2007). Additionally, other work has shown that stimulus intensity (e.g. loudness, luminance) also impacts time perception

(Goldstone et al., 1978; Xuan et al., 2007) although some care must be taken with this as it appears to be relative rather than absolute intensity that is important (Matthews et al., 2011). It seems to be a general trend, though not without exceptions, that more content within an interval is seen as being longer, unless it serves to distract attention from time, in which case it has the opposite effect (Zakay & Block, 1997).

It is little investigated how individual differences may moderate these effects on timing judgements and this forms the central question of this thesis, with the aim of adding to our understanding of both timing mechanisms and the ways individual differences can influence perception.

### **Emotional arousal**

As discussed above models of time generally include an effect of arousal on duration judgements (Craig, 2009a; Matell & Meck, 2004; Treisman, 1963, 2013). Arousal in this context is a general term, operationally defined as anything that can increase the pacemaker, and thus can include stimuli such as click trains (Penton-Voak et al., 1996; Wearden et al., 1999) or psychoactive substances (Buhusi & Meck, 2002; Cheng et al., 2007; Cheng et al., 2006; Matell et al., 2004). Here we focus on the moderation of timing by emotion. In the first instance we will consider the evidence for the effect of emotion on judgements of duration. We will then discuss some of the issues with interpreting these effects and outline how considering individual differences, and in particular interoception, may help to address this.

There is a long standing anecdotal association between emotion and the subjective experience of duration, encapsulated in phrases such as “time stood still” or “time flies when you’re having fun”. In relatively early experiments emotion related time dilation was observed in a variety of manipulations including applying electric

shocks at the end of an interval (Hare, 1963), moving the participant close to a drop into a stairwell (Langer, Wapner, & Werner, 1961), in phobics, relative to non-phobics, observing spiders (Waits & Sharrock, 1984) or when exposed to angry facial expressions (Thayer & Schiff, 1975). While these experiments were not necessarily well controlled by modern standards (Lake, LaBar, & Meck, 2016) similar effects have been further supported over time (Basanovic, Dean, Riskind, & MacLeod, 2019; Gil & Droit-Volet, 2011; Ogden et al., 2015; Stetson, Fiesta, & Eagleman, 2007).

In a more modern example Gil and Droit-Volet (2012) demonstrated a similar time dilation using images from the International Affective Picture System (IAPS, (Bradley & Lang, 1994; Lang, Bradley, & Cuthbert, 1997). They selected sets of three pictures to stimulate high and low arousal disgust and sadness, high arousal fear and neutral images for control. Pictures were presented for short durations (either within 200-800ms or 400-1600ms) and participants were asked to provide estimations of duration in ms. The general results indicated time dilation (longer estimates) for emotional stimuli, with the effect being stronger for high arousal stimuli. The results also showed some variations depending on emotional content, in particular disgust-inducing images produced a stronger effect than fear inducing images, though as this was based on only three images per condition it is possible that variations depended on these specific pictures rather than being intrinsic the emotion they conveyed.

Angrilli, Cherubini, Pavese, and Manfredini (1997) also used IAPS images, in this case five groups of three slides; high arousal unpleasant, low arousal unpleasant, high arousal pleasant, low arousal pleasant and neutral (which had four images). They employed both estimation (on an analogue scale) and reproduction tasks at durations of 2,4 and 6 seconds. Results show the expected relative time dilation for high arousal negative pictures but also for low arousal positive pictures, while both low arousal



negative emotional stimuli and high arousal positive pictures produce relatively short estimates. A nuance to this is that both high arousal conditions show overestimation in the 2s condition. The authors argue that the unexpected results are attributable to attention. In particular that high arousal stimuli activate an emotional mechanism which results in a short dilation, before giving way to a second mechanism; the effect of attention over time. By contrast low arousal stimuli are entirely dependent on attention; the low arousal pleasant pictures require less processing, relative to the negative low arousal pictures, and so the observer dedicates more resources to timing.

A potential issue with studies utilising IAPS pictures is that some evidence suggests that judgements of IAPS images on a bipolar scale (noting that such a scale was originally used to establish scores for the IAPS) can show the same level of emotional intensity while a different ratings system shows significant differences (McGraw, Larsen, Kahneman, & Schkade, 2010). Similarly neutrally valenced images may reflect mixed feelings, rather than true neutrality, with the level of ambivalence predictive of arousal (Schneider, Veenstra, van Harreveld, Schwarz, & Koole, 2016). Another concern is that physiological arousal has sometimes been found to vary with valence when not varying arousal, for example in terms of scalp potential (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Pastor et al., 2008). Finally the relationship between arousal and valence is not entirely consistent. Lang et al. (1997) originally reported a quadratic relationship, with high arousal being associated with both high and low valence and low arousal scores with middling valence and this has been replicated in some samples (e.g. Ito, Cacioppo, & Lang, 1998). However other studies have shown a relationship that is essentially linear with low valence being associated with high arousal (Grühn & Scheibe, 2008; Ribeiro, Pompéia, & Bueno, 2005); this may be attributable to sampling and or cultural

differences but suggests that caution is required as in some samples, at least, arousal and valance may be poorly differentiated.

The findings of Angrilli et al. (1997) raise the question of how attention and arousal interact in timing. This relationship can be expressed quite simply within the pacemaker-accumulator framework as attention is theorised to influence the onset of timing, and thus is additive, and arousal influences the pacemaker, and is thus cumulative. This lends itself to analysis as fitting a slope to timing data allows the calculation of the intercept, which is additive, thus representing attention, and the slope, which is cumulative, thus represents the pacemaker (Droit-Volet & Meck, 2007). However Lake et al. (2016) suggest that this differentiation is not clear cut. One concern is that pacemaker-accumulator models often include an effect of attention on the slope of timing estimates, either by the switch opening and closing during timing (Lejeune, 1998, 2000) or the effect of an attentional gate (Zakay & Block, 1996) which is not accounted for in this sort of analysis. Thus truly differentiating arousal and attention is problematic as theoretically either can have proportional effects on timing, and either can increase or decrease overall temporal estimates.

Lake (2016) suggests an alternative approach that moves away from considering attention and arousal as separate unitary concepts and rather argues that they are multifaceted and strongly interact. They propose that the initial orientation to the emotional stimuli is driven by attention modulated by the emotional salience, thus being an interaction. This is followed by a transitory period of up to a few seconds where dilation is primarily driven by physiological arousal. As the duration increases estimates may become further influenced by the degree to which attention and working memory is sustained, which again may be modulated by physiological

arousal. A further challenge arises as it is further possible that timing behaviour modulates emotional experience as well as the other way around (Pomares, Creac'h, Faillenot, Convers, & Peyron, 2011).

The issues describe above make the isolation of arousal and attention effects very difficult, especially where they are deeply interrelated. One way to address this issue is to consider “arousal” as a construct made up of different elements and thus investigate further as to the mechanisms through which physiological arousal interacts with timing behaviour. Recent timing studies have distinguished between the effects of two branches of the autonomic nervous system; the Sympathetic Nervous System (SNS), responsible for flight or fight responses, and the Parasympathetic Nervous System (PSNS), which helps to maintain homeostasis and facilitates rest and relaxation. Results have shown some relationship between SNS activity and time judgements but indicate that the relationship is more complicated than models such as SET or SBF would predict (Ogden, Henderson, Slade, McGlone, & Richter, 2019; Piovesan et al., 2018; van Hedger, Necka, Barakzai, & Norman, 2017).

In particular van Hedger et al. (2017), using reproductions, only found evidence for a relationship between SNS activity (measured by the pre-ejection period in the ECG) and timing performance at the shortest duration (400ms) for negatively valenced stimuli only. Distortions in estimations (between 200ms and 1300ms) caused by pain also related only to SNS activity (as measured via skin conductance response) but not where the to-be-timed stimulus was separate from the pain itself, suggesting the arousal must be task relevant, although it could also be that orienting attention away from the source of the arousal reduces the effect of the arousal itself (Piovesan et al., 2018). Finally Ogden, Henderson, Slade, et al. (2019), using IAPS

images, presents evidence that SNS activity only predicts estimations (in a sub-second range) where the image is high arousal and negatively valenced.

Considering the evidence above it appears to be generally the case that physiological arousal does influence timing, but also that this is subject to substantial limitations. One avenue for further clarifying the role of arousal is to pursue an individual differences approach. Studies have already shown that significant differences in timing may emerge for the same stimuli, for example in the case of phobics (Basanovic et al., 2019; Buetti & Lleras, 2012) or those with higher generalised anxiety (Bar-Haim, Kerem, Lamy, & Zakay, 2010). Assessing the effect of individual differences in interoception may be particularly beneficial in further breaking down the unitary concept of arousal. While many arousal studies assume a direct relationship between physiological arousal and timing judgements there is evidence that interoception moderates the relationship between physiological and subjective arousal (Dunn et al., 2010) and that subjective arousal relates to temporal distortions (Schwarz, Winkler, & Sedlmeier, 2013). Including interoception in timing studies may help to clarify whether physiological arousal, sensitivity to that arousal, subjective arousal or a combination of these factors best predicts the relationship between arousal and duration judgements.

### **The timing of perception: Temporal Binding**

Thus far, the focus has been on timing in the milliseconds to seconds range. However, also of interest is what Ornstein (1975) described as the experience of simultaneity, but we would expand to include other cases where the percept changes based upon temporal characteristics (focussing on phenomena in the milliseconds to hundreds of milliseconds range). A neat example of this is the bounce-stream illusion

whereby two identical moving objects briefly share the same space on a screen and may then be perceived as passing, or “streaming”, through one another or bouncing off to continue the original trajectory of the other object. Typically, the streaming percept is reported, but including a sound in proximity to the collision (at most about 250ms before to 150ms after) increases the chance of perceiving objects as “bouncing” (Watanabe & Shimojo, 2001).

In another example, the double flash illusion is created when two beeps are presented with a single flash, which may then be wrongly perceived as two flashes. Varying the time delay of the second beep with the first, which is always simultaneous with the flash, shows a window of approximately 100ms for the illusion (Shams et al., 2002). This is of particular interest as subsequent research has found an association between this effect and individual differences in EEG alpha peak frequency in the occipital cortex, to the extent that modulation of alpha also modulates the window of the illusion (Cecere, Rees, & Romei, 2015). Supporting this, it has also been shown that occipital alpha relates to the window in which two visual stimuli are seen as one (Samaha & Postle, 2015) suggesting this rhythm may represent the temporal resolution of the visual system.

The above are examples of the Temporal Binding Window (TBW), which is the epoch of time within which different sensory inputs are likely to be bound into a single entity. The simplest way to assess the TBW is to present a single beep and single flash at varying offsets and ask the participant whether or not these were simultaneous (Zampini, Guest, Shore, & Spence, 2005). This simultaneity judgement task appears related to the flash-beep judgement (Stevenson, Zemtsov, & Wallace, 2012) as well as to schizophrenia (Foucher et al., 2007; Thoenes & Oberfeld, 2017; Zhou et al., 2018), schizotypy (Ferri et al., 2017; Ferri, Venskus, Fotia, Cooke, &

Romei, 2018), autism (Foss-Feig et al., 2010; Kwakye, Foss-Feig, Cascio, Stone, & Wallace, 2011; Zhou et al., 2018) and obesity (Scarpina et al., 2016), suggesting that it has some validity in relating to on-going perpetual differences.

To bridge the gap between very short windows of integration and on-going perception, we might consider the rubber hand illusion. It is well known that hiding someone's hand and placing a fake hand in its place, then stroking both in synchrony, results in the perception of ownership over the false hand (Botvinick & Cohen, 1998). The stroking must be within a certain temporal window of synchrony to be effective, this varying in accordance with individual sensitivity to visual-tactile synchrony. As with simultaneity judgements, the rubber hand illusion seems to be experienced more strongly by people with schizophrenia and those scoring highly for schizotypy (Kállai et al., 2015; Thakkar, Nichols, McIntosh, & Park, 2011).

Collectively this evidence suggests that the perceptual system has intrinsic temporal characteristics that relate to differences in experience. These differences can be identified in effects that are on a similar timescale to the experience of simultaneity but also appear to exist in on-going perception and long-term individual differences. It remains unclear how individual differences in temporal integration relate to other differences in temporal performance.

### **Alpha, integration and duration**

As touched on above there appears to be some relationship between the temporal binding window and the alpha frequency. Cecere et al. (2015) provide evidence not only that these two co-vary between participants but also that this relationship appears to be causal, at the least in the case of the flash-beep illusion. The first was achieved by comparing Individual Alpha Frequency (IAF) peak with an estimate of each individual's window for the illusion (derived by fitting a sigmoid

function to the plot of the incidence of the illusion against the inter-beep delay and calculating the inflection point). A correlation was identified with the most significant relationship being at occipital electrodes. Secondly, occipital transcranial alternating current stimulation (tACS) was applied to modulate IAF while performing the task. The temporal window of the task was shrunk and enlarged corresponding to the direction of modulation, such that increasing alpha frequency (meaning each cycle is shorter) reduces the size of the window.

Cecere's (2015) interpretation of this finding is that the excitation/inhibition cycle of the alpha rhythm functionally gates perception; as auditory stimuli have been shown to reset the phase of oscillations in the visual cortex (Mercier et al., 2015), the double (or repeated) beeps create a double (or multiple) excitatory peak in activity in the visual cortex, essentially 'resetting' the perception of the flash, which thereby erroneously enters conscious perception as two (or more) flashes. This finding is consistent with the illusion generally being limited to two to three flashes as this roughly corresponds to the maximum duration of the cycle. This finding is further corroborated by evidence that an individual's occipital alpha rhythm relates to the temporal resolution of visual perception in a unimodal paradigm; Samaha and Postle (2015) also recorded occipital IAF and found a significant relationship with individual differences in flash fusion thresholds (the offset at which two flashes are perceived as one).

Cecere et al. (2015) propose that this finding may support a role for the alpha rhythm in visual, and possibly multisensory, timing. There is some, though limited, direct evidence for a role of alpha rhythms in supra-second timing. Cahoon (1969), in investigating arousal, used a paradigm where participants were asked to produce a verbal estimate of the interval between two tones presented 36 seconds apart. EEG

was recorded at two occipital electrodes and the alpha frequency calculated. Although the effect of arousal generally seemed negligible, he did find that these two measures, estimation and alpha frequency, significantly positively correlated in both low and high arousal conditions. He also found that tap rate significantly correlated with alpha frequency but only in the high arousal condition. Finally, a production task was employed where participants had to hold down a button for 22 seconds but results were not significant. To minimise timing strategies, such as chronometric counting, Cahoon only used a single trial of each task per condition. It may be doubted how effective this was as this still means there were four timing trials per participant and, arguably, only a single trial can be truly naïve and thus retrospective (Block & Zakay, 1997).

While estimation would seem to be the task most clearly associated with alpha, in Cahoon (1969) results, it is of interest that a correlation was also found (in one condition) between tap rate and alpha. There is evidence that in faster cued tapping (3-4 Hz) the motor system is continually engaged whereas it is engaged and disengaged for each tap in the 0.5-1Hz range (Toma et al., 2002). Where participants are asked to tap freely (e.g. at a self determined rate without pacer stimuli) the distribution of preferred rates is bimodal with peaks at 272ms and 450ms (Collyer, Broadbent, & Church, 1994). Cued tapping and free tapping seem likely to differentially engage systems. For example, when preferred rates are used as cued rates, produced rates tend to be somewhat slower than the cues. This would seem to suggest that faster tapping may represent increased motor timing compared to slower rates that may draw more on other systems (Collyer et al., 1994). Cahoon's instruction to participants to tap a rate of one per second lay somewhere between cued and free tapping (as the rate is specified but not cued) but would fall into the category



of a 'slower' rate. It is difficult to say why the relationship with alpha was significant only in high arousal conditions; possibly participants under threat of shock, if they did not respond quickly to the cue that ended the response period (no shocks were actually given), were naturally concentrating more on that task, meaning their responses were less constrained and better reflected unconscious mechanisms.

Glicksohn et al. (2009) provide another example where at least partial support for alpha as a timing mechanism was found. They asked participants to produce target intervals of 4, 8, 16 and 32 seconds and extracted peak alpha frequency at locations P3 and P4. Time productions were log transformed and compared to alpha frequency by hemisphere producing non-significant correlations. However, multiple-regression analysis showed the joint contribution of the hemispheres to be significant, in that the asymmetry between left and right IAF predicted productions; although why this should be the case requires further exploration.

It is fair to say that support for alpha in timing is by no means universal, or even consistent. Treisman (1984) employed a production task where the participant, with their eyes closed throughout, was given an example (or two) of a four second duration aurally. They were then asked to terminate the tone after four seconds each time with a button press. This was repeated with intervals of between three and eight seconds for anywhere between 35 and 55 minutes. This was analysed by correlating productions and IAF within each participant; of five subjects, three subjects produced a significant negative correlation between timing performance and Alpha frequency, while two produced a significant correlation in the other direction, prompting the conclusion that "the common pacemaker hypothesis cannot be sustained" (p.563).

While this finding is certainly of interest it does not preclude any role for the alpha rhythm in timing because of the limitations of this paradigm. Firstly the EEG

trace was from left parietal and occipital regions and so it likely to exclude any system specific variations, as well as missing any less than straightforward relationship between the hemispheres. Secondly this methodology involved no visual stimuli and required eyes to be closed, which presents a problem in our present discussion that suggests this aspect of timing may be intrinsic to visual and intra-modal processes, as proposed by Cecere et al. (2015).

Thus the question of whether the individual alpha peak frequency may have a role in a distributed timing system still requires further investigation. As discussed above findings on timing behavior vary considerably by task and yet studies investigating this area are often restricted to one type of performance. Therefore one avenue for progressing this research may be to apply a variety of timing judgement tasks and durations, within the same participants, to observe whether these differ in terms of their relationship to IAF.

### **Evidence for distributed timing**

As mentioned above, scalar expectancy theory (figure 2, Gibbon et al., 1984) is often of use in the timing literature, for its heuristic value in relating well to behavioural results, but is not directly analogous to a neural system. Craig's theory of Global Emotional Moments (Craig, 2009a) offers a partial solution. It is based on the observation that the insula receives direct input of bodily information via the spinal cord and brain stem. He posits that within the insula this is progressively combined with other salient information producing sequential "moments" that form consciousness. It has been suggested that this stream of moments could function as the pacemaker in the attentional gate model (Wittmann, 2015).

A more prominent alternative is the Striatal Beat-Frequency (SBF) theory (Buhusi & Meck, 2005) that posits timing can be accomplished by coincidence-

detection, where sensory cortex oscillations are synchronised at the onset of a to-be-timed interval creating a pattern of activation in a thalamo-cortico-striatal network which is monitored by the basal ganglia. This system learns a duration by identifying the pattern at the point of reward and then can arrive at the same point again when the activation coincides with the previously identified pattern.

Specific models aside, there is substantial evidence that timing relies on a network that is at least partially distributed, with involvement from sensory cortices depending on modality. In particular there is neuroscientific evidence of sensory cortex, particularly visual cortex, involvement in timing from a number of sources (Buetti, 2011; Buetti, Bahrami, et al., 2008; Buetti & Macaluso, 2010; Buetti, Walsh, et al., 2008; Ghose & Maunsell, 2002; Shuler & Bear, 2006). The work of Buetti and Macaluso (2010) is a notable example. They asked participants to respond as quickly as they could to sounds that were presented after an interval. Participants were trained so that some delays were more expected than others. During the anticipation of the stimulus there was increasing activation in a number of areas including those relevant to auditory stimuli, and motor response, but also in the occipital visual cortex. This activity was consistent with individual performance on the behavioural task. This suggests not only that timing is distributed but that it also can be cross-modal and that individual performance varies in accordance with sensory cortex activation.

Craig's (2009a) theory may allow for distributed elements in timing, in that exteroceptive information is also included in GEMs, so the characteristics of this information could contribute to the rate at which "moments" fill. SBF involves distribution by its nature and so accounts well for these findings, as it is expected that cortical oscillations feed into the system; although, as it relies on coincidence detection, then theoretically differences in a cortical sensory system should not

influence behaviour unless the change is between learning and performing the interval.

### **Individual Differences**

If we were to attempt to truly predict timing behaviour then it would be necessary to consider not only how the stimuli influences behaviour but also how differences between participants influence timing perception and judgements. Hancock and Block (2012) identified individual differences as one of the key areas for further investigation to advance time research, and our understanding of this area remains relatively limited. Gender and age have naturally been addressed in a variety of research projects. A meta-analysis focussing on gender, by Block, Hancock, and Zakay (2000), found no overall effect of gender on prospective time but did observe significant gender differences by task. Women made shorter productions than men and larger verbal estimates, with women being further from the target duration in both cases. The number of trials in the experiment also had an effect on gender differences with gender difference more evident in experiments with a larger number of trials where male performance becomes poorer. There was also an effect of age, which interacted with gender differences such that girls make relatively short judgements while older women make shorter productions/longer estimates compared to older men. These findings are largely interpreted as a difference in attention to task, with women being more successful in focusing attention. The gender difference in children may be attributable to the difference in tasks used with that age group. The question of why gender, in and of itself, should be expected to make a difference is hard to answer; differences in metabolic rate or body temperature have been suggested as a

mechanism (Hancock & Rausch, 2010) However we are not aware of any research directly testing this explanation.

Meta-analysis also shows a number of differences in development, with children making larger verbal estimates, shorter reproductions and generally more variable judgements (Block, Zakay, & Hancock, 1999). As with gender, physiological explanations may be offered, including temperature/metabolic rate, but it seems there is also likely to be differences in terms of cognitive factors such as attention, memory and how children conceptualise the units of time, particularly as the studies included generally use supra-second durations. It has been suggested that changes in fronto-striatal systems during development relate to attention and other executive functions that influence time judgements, but also relate to general changes in processing speed and thus to putative clock mechanisms (Droit-Volet, 2013).

Other studies have also linked general cognitive capacity, e.g. tests of intelligence, memory, attention or executive function, to temporal judgements. Examples of findings include that bisection relates to memory access, short term memory and inhibition (Ogden, Samuels, Simmons, Wearden, & Montgomery, 2017); serial production (e.g. pressing a button every 5 seconds) appears to share resources with a go/no-go inhibition task and that general intelligence appears to relate to accuracy in a number of temporal tasks (Rammsayer & Brandler, 2007). This last investigation included discrimination, generalisation, rhythm perception and two integration tasks; temporal-order judgement and auditory flutter fusion (essentially identifying the offset at which two sound bursts become perceived as one sound)

As discussed above, in relation to the differences between timing tasks, some recent research (Droit-Volet et al., 2015; Ogden, MacKenzie-Phelan, et al., 2019; Ogden et al., 2014) has investigated how individual differences in performance on

measures of specific executive functions relate differently to performance on a range of timing tasks. To focus on one example, Ogden et al. (2014) included four tests of executive function: updating of working memory, switching attention, inhibition (ability to inhibit a dominant response) and semantic memory, using established tasks for each. Timing tasks were reproduction, generalisation and estimation. Correlations showed a robust positive relationship between temporal generalisation and both updating and access. Reproduction related negatively to the same measures, though only for the variability and not accuracy, accuracy related only to switching. Finally verbal estimation performance did not correlate significantly with any measure of executive function, though further analysis via median split and ANOVA showed a small but significant main effect of access to memory on estimation, such that longer estimates were associated with lesser access to semantic memory, perhaps representing increased difficulty in retrieving internal standard durations. This finding is broadly coherent with similar studies (Droit-Volet et al., 2015; Ogden, MacKenzie-Phelan, et al., 2019) and serves to qualify other studies of individual differences where, in some tasks, it is possible the timing behaviours may reflect differences in executive function. This finding relates somewhat to the relationship between intelligence and timing accuracy above, in that further work is required to separate out how intelligence and executive function contribute in this context.

Differences in time judgements have also been found in clinical conditions. For example, people diagnosed with Parkinson's disease, which is associated with dysfunction of the basal ganglia, have been found to have a variety of differences in timing (Allman & Meck, 2011), although some evidence suggests such differences are small and task dependent, and may be exaggerated when a motor component is involved (Wearden et al., 2008). People with schizophrenia have been found to show

more variable timing in sub and supra-second bisection tasks (Carroll, O'Donnell, Shekhar, & Hetrick, 2009). This appears to be consistent across task and duration, implying a direct deficit in timing as opposed to related cognitive abilities (Ciullo, Spalletta, Caltagirone, Jorge, & Piras, 2015). This population also tends to overproduce and underestimate durations (Thoenes & Oberfeld, 2017). Some evidence suggests that these differences also exist within the general population varying in accordance with traits associated with schizophrenia (Lee, Dixon, Spence, & Woodruff, 2006; Reed & Randell, 2014), which is of particular interest given the focus of this thesis on individual differences in the general population.

Similar research has been carried out in autism producing a range of, sometimes contradictory, results. However there does appear to be a general tendency towards increased variability in timing for autistic individuals (Allman & Falter, 2015) with some studies finding other differences, such as a tendency to under-reproduce intervals (Martin, Poirier, & Bowler, 2010), or difficulty with reproduction (Szelag, Kowalska, Galkowski, & Pöppel, 2004), and a tendency towards making longer judgements in temporal bisection tasks (Allman, DeLeon, & Wearden, 2011), though Wallace and Happé (2008) found little difference between ASD individuals and controls on estimation and production. A consideration with regards to timing and ASD is that people with ASD often also score highly for alexithymia, a sub-clinical construct that relates to difficulty identifying and describing emotions. Alexithymia is, in turn, associated with a poor sense for the activity of one's own body, called interoception (Shah, Hall, Catmur, & Bird, 2016). Emerging research associates interoception with time perception (Meissner & Wittmann, 2011; Pollatos, Laubrock, & Wittmann, 2014; Pollatos, Yeldesbay, Pikovsky, & Rosenblum, 2014) so it is possible that the link between autism and time perception is not direct.

Interoception is also of interest for this thesis because interoceptive ability may be a naturally occurring variation within the general population that influences the sense of time. Meissner and Wittmann (2011) asked participants to reproduce intervals (8, 14 and 20s duration). They observed a progressive, and roughly linear, increase in cardiac periods (calculated as the intervals between r-peaks) during encoding and reproduction and found that slopes fitted to this cardiac slowing correlated positively with timing accuracy. This may support a role for bodily information in performing time judgements. They also estimated interoceptive accuracy by means of the heartbeat perception task (Pollatos, Kirsch, & Schandry, 2005), which is commonly used as an estimate of interoception and simply involves the individual counting their heartbeats for a set period; their count being subsequently compared with the actual number of heartbeats occurring. They found that scores on this task also correlated with the length and accuracy of time reproductions, suggesting that better awareness of bodily signals facilitates timing. There is however a note of caution in interpreting these findings as cardiac slowing is associated with attention (Bradley, 2009) which also influences timing behaviour (as above) and interoception tests (Buldeo, 2015). Wittmann (2015) reviewed a variety of research focusing on altered states of consciousness, including via drugs, meditation and clinical conditions, and found support for the embodiment of time, in particular suggesting that awareness of self and awareness of time are associated.

As touched on above with regards to emotion, both timing (Livesey et al., 2007) and interoception (Craig, 2002) are associated with the insular cortex. Craig's theory of Global Emotional Moments (GEMs), also described above, involves the accumulation of GEMs in the anterior insula cortex (AIC), possibly regulated by the putamen, with the left inferior parietal cortex associated with counting. Crucially



these have a set capacity, which means that moments are filled more quickly when there is a large amount of salient information, such as in high threat situations (Craig, 2009a). This is consistent with the effects of arousal on time discussed above.

Given the above, and that there is good evidence that timing is significantly influenced by embodied emotional state as discussed previously (for review see; Droit-Volet, Fayolle, Lamotte, & Gil, 2013), there is an open question as to the extent to which individual differences in the interoceptive system moderate the relationship between emotion and time judgements. This is one of the core questions of this thesis, being addressed in experiments 3 and 4.

It was noted above that individual differences in the experience of simultaneity, and other very short-term effects, also appear to relate to differences in perception that occur over time and vary by individual, such as schizophrenia and obesity. They also relate to experiences in the lab, in particular the rubber hand illusion, that are not momentary but can persist over seconds and minutes. It is not clear, however whether these individual differences also translate into differences in the judgement of time in the range of milliseconds to seconds. In essence, does the temporal resolution of perception influence the perception of time? There is good reason to expect that this might be the case; as we have discussed above, differences in the timed stimuli lead to differences in time judgements, thus it might be expected that individual differences in the temporal processing of such stimuli should also influence the effect of this information on duration judgements, particularly as there is evidence for sensory specific elements contributing to perception of duration (Buetti, 2011). This forms the other central question of this thesis, being addressed in experiments 1 and 2.

## **Research aims and methodology**

The overall aim of this thesis is to explore to what extent individual differences in primary sensory processing influence individual differences in subjective time judgements. Within this, we focus on two separate types of primary sensory processing: exteroceptive (in particular visual and audio) and interoceptive. The inclusion of interoception as primary sensory processing is because, theoretically, the process is facilitated by the lamina I spinothalamocortical pathway which projects a representation of body state information to the anterior insula cortex (Craig, 2002, 2009b), arguably in a manner somewhat comparable to the projection of primary visual information to the occipital cortex, for example. These two areas were chosen because in each case there is a developing literature regarding individual differences in subjective perception that have been related to subjective timing but not yet explored fully in this regard.

To illustrate how these two areas of research relate to each other we might express them in terms used by pacemaker accumulator models of timing. In examining alpha timing and audio-visual integration, we look for individual differences in the temporal characteristics of these systems. Assuming these are found to relate to duration, this would be seen as reflecting individual differences in the base-rate of timing, and thus in the “pacemaker”; though in line with findings suggesting that time perception is partially distributed (Buetti, 2011; Buetti & Macaluso, 2011; Buetti, Walsh, et al., 2008) this may be a local rather than a global pacemaker. Interoception, in processing bodily arousal, would be part of the arousal aspect of such models and thus something that acts on a pacemaker. On the other hand, the GEMs theory suggests the representation of bodily information as the basis of consciousness and thus subjective time itself (Craig, 2009a), in which case

interoception would be the root of subjective timing which is acted upon by visual processing via the incorporation of salient visual information. We are not yet at a stage where these streams of research could be combined to examine whether, and how, these influences act upon each other, or represent different timing systems, but this may be a future prospect.

In the first experimental chapter, we build on findings that occipital alpha peak frequency appears to relate to subjective differences in multisensory integration (Cecere et al., 2015; Samaha & Postle, 2015). Cecere et al. (2015) argue that their findings suggest that alpha peak frequency may have a role as a visual, or multisensory, “clock”. As there have been mixed findings over time on the relationship, or lack thereof, between alpha and subjective duration (Cahoon, 1969; Glicksohn, Ohana, Dotan, Goldstein, & Donchin, 2009; Treisman, 1984; van Viegen, Charest, Jensen, & Mazaheri, 2017) we aimed to test individual differences across different timing tasks to establish whether any direct relationship can be found and, if so, whether it is task dependant.

The second experiment addresses an assumption raised by the first: that the temporal characteristics of perception relate to subjective time judgements. In this case, we built on previous findings that individual differences in temporal binding relate to a variety of differences in subjective perception over time (Costantini et al., 2016; Lee et al., 2006; Scarpina et al., 2016). Here we recorded individual differences in the temporal binding window and when participants were estimating filled and empty durations, as it was not clear whether TBW differences might be expected to relate to timing “empty” time or processing a relevant stimulus. In this case, we also measured schizotypy as it has been related to both sensory integration (Ferri et al., 2017) and timing (Lee et al., 2006; Reed & Randell, 2014) and thus may help to

establish whether these short-term effects relate, in the same way, to relatively stable long-term individual differences in perception.

As covered above, the second half of this thesis moves on to address a different, though related, question. Craig (2009) suggested that interoceptive processing is central to subjective time and some recent studies have found a relationship between interoception and timing performance (Cellini et al., 2015; Pollatos, Laubrock, et al., 2014; Pollatos, Yeldesbay, et al., 2014). There is also a longstanding, though still developing, literature on how emotional arousal influences subjective time. We combine these approaches to question whether interoception moderates the influence of emotional arousal on time judgements. In two experiments, we measure interoceptive accuracy and relate this to timing in the 5-10s range (experiment 3) and in the 100-1000ms range (experiment 4). In both cases emotional arousal is manipulated via images from the IAPs database (Lang et al., 1997).



## **Chapter two: Do individual differences in the EEG alpha rhythm relate to differences in time judgements across tasks?**

Forever – is composed of Nows –

‘Tis not a different time –

Except for Infiniteness –

And Latitude of Home –

*Emily Dickinson*

### **Abstract**

Recent evidence that occipital alpha plays a key role in multisensory integration and unimodal visual processing, as a temporal gating mechanism (Cecere et al., 2015; Samaha & Postle, 2015), has lead us to re-evaluate the role of this rhythm in the experience of time. This study firstly examines the relations between visual (estimation) and motor (production) timing tasks in the range of 1-11 seconds and two “rate” tasks: one judging the gap between flashes (ranged between 0.5 and 1.5s) and the other being tapping at a self-determined rate. It then relates performance on these tasks to EEG individual alpha peak frequency (IAF) over the visual cortex. Results suggest that participants’ judgement of the passage of a second, in the flash judgement task, is significantly related to their performance in the visual and motor supra-second timing tasks. Preferred motor rhythms, as measured by the tapping task,

relate primarily to performance on the motor production task. There appears to be no significant relation to occipital IAF in any of the timing tasks.

## **Introduction**

### *Why is integration and time important?*

To say that everything we do and perceive exists in time is likely to be considered a statement of the obvious; it is an intrinsic feature of action and perception. Yet how the brain creates and modulates the subjective sense of time passing remains fundamentally unclear. This is not simply a theoretical question but one that relates to our understanding of many factors that may change perception, such as age (Carrasco, Bernal, & Redolat, 2001; Espinosa-Fernández et al., 2003; Gooch, Stern, & Rakitin, 2009; Hancock & Rausch, 2010), mental illness (Carroll et al., 2009; Ciullo et al., 2018; Ciullo et al., 2015; Gil & Droit-Volet, 2009; Thönes & Oberfeld, 2015) and chemical influences (Cheng et al., 2007; Yanakieva et al., 2018). Investigating whether, and how, the intrinsically temporal sensory gating effect of neural oscillations relates to temporal perception, on the scale of tens, hundreds and thousands of cycles, is an approach that has the potential to provide new answers (and pose new questions) in this area.

### *Visual integration and alpha*

Although our experience of perception is continuous there is a strong argument that it is actually based in the processing of discrete samples of sensory information, conceptually somewhat similar to the discrete frames of a film becoming a continuous moving image when shown at the right speed. VanRullen and Koch (2003) argue that the available evidence supports such discrete processing. In one example, the wagon-wheel illusion (Purves, Paydarfar, & Andrews, 1996), the rotation of stimuli appears to be reversed at certain rates; this illusion can be



explained by discrete sampling (e.g. the brain makes an error in how one sample relates to the next) but not by integration periods alone. VanRullen and Koch (2003) also propose EEG alpha as one of the mechanisms involved in defining the frequency of discrete processing; in particular because various evidence supports this rhythm's influence on the experience of simultaneity. Events that occur in temporal proximity are more likely to be integrated into a single percept (Martin, Giersch, Huron, & van Wassenhove, 2013; Powers, Hillock, & Wallace, 2009). A variety of studies have suggested that this is more likely to be the case where both events occur within 100ms of each other; supporting the existence of a temporal window of sensory integration within the range of approximately 100ms, consistent with the usual average wavelength of alpha, which cycles at between 60 and 120ms (8-14Hz), and this evidence suggests some ways in which this window relates to perceptual experience. Here we choose three exemplars to demonstrate this.

In one example, Slutsky and Recanzone (2001) found that the impression that aural and visual stimuli are simultaneous is consistently found at disparities of 50 and 100ms but not at 150ms. Additionally they found that where visual stimuli were presented within this window, relevant to an auditory tone at a different location, this influenced the spatial localisation of that tone (the ventriloquism effect). This suggests that this period is important for perceptual integration in more than a simple temporal sense. It should be noted that there was an asymmetry in the data where the tone being presented following the visual stimuli appeared to lengthen the window relevant to the opposing order. One potential explanation is that, as light travels faster than sound, light more often arrives first and thus the system for perceptual integration is skewed to balance this tendency, which would be consistent with the earlier development of the Visual-Audio TBW than the Audio-Visual (Hillock,

Powers, & Wallace, 2011). Recent evidence has suggested a different explanation, firstly showing that training of the perceptual window does not transfer from one order of integration to the other (Cecere, Gross, & Thut, 2016). secondly mapping ERPs recorded during integration suggests different neural pathways facilitating the integration depending on leading modality (Cecere, Gross, Willis, & Thut, 2017). These findings suggest the existence of multiple binding systems that may be differentially engaged depending on task requirements.

Secondly, there is also evidence that visual judgements of causality, such as in the bounce-stream paradigm (where two objects move towards each other, then can be seen as either streaming past each other or bouncing off), can be influenced by the presentation of a click coinciding with the moment of collision. This effect occurs most often when it is simultaneous with the objects crossing, but is still robust with a 100ms compared with a 150ms or 200ms offset. The reduction in the effect is much more pronounced when the click follows the coincidence rather than preceding it (Remijn et al., 2004; Sekuler, 1997).

Thirdly, Shams et al. (2002) identified an illusion where presenting multiple beeps during a single flash resulted in the illusion that there were multiple flashes. They measured the window of this effect by presenting one beep simultaneously with a flash and a second at variable offsets. While there was still an effect of the second flash at 115ms offset (e.g. the illusion is perceived at a higher rate than in the absence of a flash) this effect was radically reduced from the peak effect found at 25ms and 70ms offsets. Again there was an asymmetry to the findings with a slower drop-off where the beep followed the sound (see Figure 2.1).

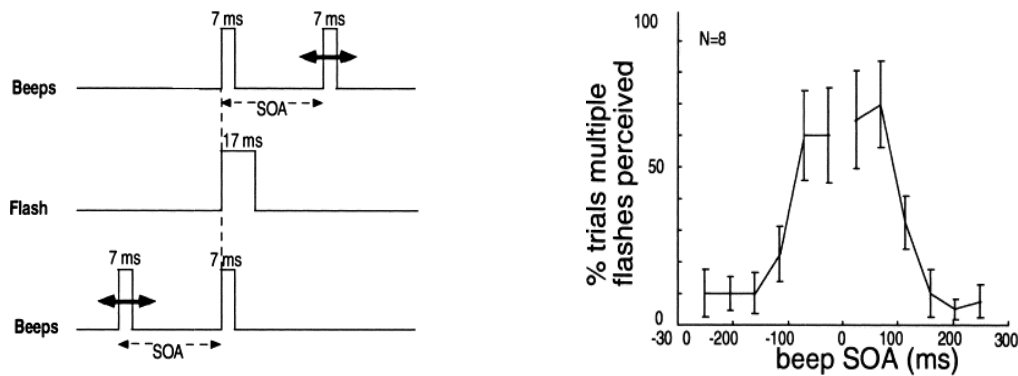


Figure 2.1: The flash beep illusion

Left – The timing of flashes and beeps used to produce the flash-beep illusion

Right – Results showing the incidence of the illusion at stimulus onset asynchronies (SOAs) between -250ms and 250ms.

Figures reproduced from (Samaha & Postle, 2015); Shams, Kamitani, and Shimojo (2002).

Thus far the relationship between these changes in perception and the alpha frequency is postulated based on the similarity of the duration of the window of integration with the frequency of this oscillation. Cecere et al. (2015) provide evidence not only that these two co-vary between participants but also that this relationship appears to be causal, at the least in the case of the flash-beep illusion. The first was achieved by comparing Individual Alpha Frequency (IAF) peak with an estimate of each individual's window for the illusion (derived by fitting a sigmoid function to the plot of the incidence of the illusion against the inter-beep delay and calculating the inflection point). A correlation was identified with the most significant relationship being at occipital electrodes. Secondly, occipital transcranial alternating current stimulation (tACS) was applied to modulate IAF while performing the task. The temporal window of the task was shrunk and enlarged corresponding to the direction of modulation, such that increasing alpha frequency (meaning each cycle is shorter) reduces the size of the window.

Cecere's (2015) interpretation of this finding is that the excitation/inhibition cycle of the alpha rhythm functionally gates perception; as auditory stimuli have been shown to reset the phase of oscillations in the visual cortex (Mercier et al., 2015), the double (or repeated) beeps create a double (or multiple) excitatory peak in activity in the visual cortex, essentially 'resetting' the perception of the flash, which thereby erroneously enters conscious perception as two (or more) flashes. Cecere et al. (2015) note that this finding is consistent with the illusion generally being limited to two to three flashes as this roughly corresponds to the maximum duration of the cycle. This finding is further corroborated by evidence that an individual's occipital alpha rhythm relates to the temporal resolution of visual perception in a unimodal paradigm; Samaha and Postle (2015) also recorded occipital IAF and found a significant relationship with individual differences in flash fusion thresholds (the offset at which two flashes are perceived as one).

The ventriloquism effect and causality judgements described above can be interpreted as consistent with alpha integration as in each case the interaction of a tone with visual stimuli, within a certain window, influences the perception of the event. It was noted that results in all cases showed an asymmetry and this too is consistent with this interpretation, as it would predict a window more directly related to the alpha duration where the sound precedes, or accompanies, the visual stimuli (thus resetting the phase). This is supported by evidence that there are behavioural and neural differences in multisensory processing depending upon the leading modality (Cecere et al., 2016; Cecere et al., 2017).

*Integration and time*

The above supports a relationship between alpha integration and differences in perception for events with very short durations (i.e. around the length of a single cycle). There is also evidence that differences in individual windows of integration relate to long-term differences in perception, such as schizophrenia and schizotypy (Ferri et al., 2017; Ferri et al., 2018; Foucher et al., 2007; Giersch et al., 2008; Lalanne, van Assche, & Giersch, 2010), autism (Baum, Stevenson, & Wallace, 2015; Foss-Feig et al., 2010; Kwakye et al., 2011) and even obesity (Scarpina et al., 2016). (For further information on this, see chapter 1). However there is little research investigating this relationship in durations of hundreds to thousands of milliseconds. This is perhaps partly due to the challenge of designing experiments to address this question. For example, there is evidence that perceptual integration adapts to account for persistent audio-visual offsets (Fujisaki, Shimojo, Kashino, & Nishida, 2004) so in this context measuring individual differences in integration directly may be challenging. An alternative might be to consider individual differences in subjective time. Cecere (2014) argues that their evidence of alpha integration suggests a model of timing where alpha functions as an internal clock in relation to the visual system, possibly extending to other modalities, and is responsive to input from other modalities at a very early stage in processing. Essentially this posits occipital alpha as a pacemaker-like mechanism that operates through the continuous temporal processing of visual information. That the timing system involves distributed, somewhat modality-specific, elements, and particularly a primarily visual timing element in the visual cortex, is supported by further evidence including behavioural (Burr, Tozzi, & Morrone, 2007; Gamache & Grondin, 2010; Kanai, Paffen, Hogendoorn, & Verstraten, 2006), fMRI (Buetti, Walsh, et al., 2008) and TMS (Buetti,

Bahrami, et al., 2008) studies, though the latter also suggests that parietal cortex is involved in both audio and visual timing.

### *Alpha and time*

There is some, though limited, direct evidence for a role of alpha rhythms in supra-second timing. Cahoon (1969), in investigating arousal, used a paradigm where participants were asked to produce a verbal estimate of the interval between two tones presented 36 seconds apart. EEG was recorded at two occipital electrodes and the alpha frequency calculated. Although the effect of arousal generally seemed negligible, he did find that these two measures, estimation and alpha frequency, significantly positively correlated in both low and high arousal conditions. He also found that tap rate significantly correlated with alpha frequency but only in the high arousal condition. Finally, a production task was employed where participants had to hold down a button for 22 seconds but results were not significant. To minimise timing strategies, such as chronometric counting, Cahoon only used a single trial of each task per condition. It may be doubted how effective this was as this still means there were four timing trials per participant and, arguably, only a single trial can be truly naïve and thus retrospective (Block & Zakay, 1997).

While estimation would seem to be the task most clearly associated with alpha, in Cahoon (1969) results, it is of interest that a correlation was also found (in one condition) between tap rate and alpha. There is evidence that in faster cued tapping (3-4 Hz) the motor system is continually engaged whereas it is engaged and disengaged for each tap in the 0.5-1Hz range (Toma et al., 2002). Where participants are asked to tap freely (e.g. at a self determined rate without pacer stimuli) the distribution of preferred rates is bimodal with peaks at 272ms and 450ms (Collyer et

al., 1994). Cued tapping and free tapping seem likely to differentially engage systems. For example, when preferred rates are used as cued rates, produced rates tend to be somewhat slower than the cues. This would seem to suggest that faster tapping may represent increased motor timing compared to slower rates that may draw more on other systems (Collyer et al., 1994). Cahoon's instruction to participants to tap a rate of one per second lay somewhere between cued and free tapping (as the rate is specified but not cued) but would fall into the category of a 'slower' rate. It is difficult to say why the relationship with alpha was significant only in high arousal conditions; possibly participants under threat of shock, if they did not respond quickly to the cue that ended the response period (no shocks were actually given), were naturally concentrating more on that task, meaning their responses were less constrained and better reflected unconscious mechanisms.

Glicksohn et al. (2009) provide another example where at least partial support for alpha as a timing mechanism was found. They asked participants to produce target intervals of 4, 8, 16 and 32 seconds and extracted peak alpha frequency at locations P3 and P4. Time productions were log transformed and compared to alpha frequency by hemisphere producing non-significant correlations. However, multiple-regression analysis showed the joint contribution of the hemispheres to be significant, in that the asymmetry between left and right IAF predicted productions; although why this should be the case requires further exploration.

It is fair to say that support for alpha in timing is by no means universal, or even consistent. Treisman (1984) employed a production task where the participant, with their eyes closed throughout, was given an example (or two) of a four second duration aurally. They were then asked to terminate the tone after four seconds each time with a button press. This was repeated with intervals of between three and eight

seconds for anywhere between 35 and 55 minutes. This was analysed by correlating productions and IAF within each participant; of five subjects, three subjects produced a significant negative correlation between timing performance and Alpha frequency, while two produced a significant correlation in the other direction, prompting the conclusion that “the common pacemaker hypothesis cannot be sustained” (p.563).

While this finding is certainly of interest it does not preclude any role for the alpha rhythm in timing because of the limitations of this paradigm. Firstly the EEG trace was from left parietal and occipital regions and so it likely to exclude any system specific variations, as well as missing any less than straightforward relationship between the hemispheres. Secondly this methodology involved no visual stimuli and required eyes to be closed, which presents a problem in our present discussion that suggests this aspect of timing may be intrinsic to visual and intra-modal processes.

The inherent weakness of the classic ‘biological clock’ models is that they rely on a relatively invariable rhythm providing a simple index of time and so cannot easily account for changes to behaviour as a result of factors such as task, attention, arousal and variations in input (see chapter 1 and Block & Zakay, 1996). Rather than this, we are proposing that the continuous temporal processing of visual information implied by findings on alpha gating (Cecere et al., 2015) may be one element within a distributed timing process, and not a global “clock” in and of itself. The advantage of considering a role for alpha gating in timing, as presented here, is that it may allow for, and even explain, these influences in timing (in the relatively short timeframes described above). In this model, different tasks may differentially engage (or not) the alpha frequency depending on modality and method of response; in particular the distinction between purely motor and purely visual timing may be of interest. fMRI



evidence has suggested that V5 is selectively activated for duration reproduction but not estimation (Buetti, Walsh, et al., 2008) but disruption of this site via TMS does appear to disrupt purely visual temporal discernment, with posterior parietal disruption influencing both visual and auditory timing (Buetti, Bahrami, et al., 2008). So, there remains an open question as to how visual cortex relates to timing tasks involving different modalities in the response.

Additionally, the theory that alpha gating influences duration, may allow for variations in sensory input influencing timing. In the flash-beep illusion, occipital alpha influences the form in which sensory input enters perception and so this may relate to timing judgments where the content of the interval is varied; a shorter alpha cycle encapsulating a lot of information may compare in perception to a longer alpha cycle encoding less. This final point is necessarily speculative and will require empirical support outside of the current study.

#### *The current study*

The arguments and evidence presented above outline the grounds for hypothesising a relationship between Individual Alpha Frequency and time perception. However, the evidence is mixed and inconsistent as to the type of timing task used and, to some extent, the scalp location (i.e. occipital or parietal). This makes testing and quantifying this relationship challenging. In this case we look to address this by using a group of four related timing tasks, both visual and motor, in conjunction with full head EEG, with the aim of exploring the relationships between the tasks and EEG activity to establish the most promising parameters, if any, for future investigations in this area.

The set of tasks employed in the current study are loosely inspired by those used by Cahoon (1969), though different in certain details. As we are interested in the

influence of EEG across durations, and in different modalities, we chose to use common estimation and production tasks, used extensively in time research, with durations between 1 and 11 seconds. Rather than attempting to eliminate chronometric counting, a novel procedure is utilized whereby in a further task participants estimate whether a series of flashes are spaced at more or less than a second; varying the actual duration between flashes produces an estimate of the individual perception of 1s. Assuming any relationship is found this could help to disambiguate as to whether the effect relates to the participant's rate of counting in seconds. Finally, as Cahoon's research found a correlation between tap rates and IAF, a free-tapping task is included as a partial counterpart to the flash task. Similar to the flash task, this may also serve to clarify whether preferred motor rates drive other timing tasks. If, as previously suggested (Cecere et al., 2015), occipital alpha is associated with primarily visual timing we would expect to see a relationship between the IFIE task responses and IAF. If this is found the relationship to ongoing timing can be disambiguated by comparison with the estimation condition, where a slope effect would indicate that alpha relates to the underlying rate of timing and an intercept effect would indicate an effect on timing only found at the onset. If the effect of alpha is purely visual or audio-visual it should be limited to the visual tasks and not found in the tapping or production tasks.

## **Methods**

### *Participants*

23 participants (17-female) were recruited via the University of Essex Sona recruitment system. Ages ranged from 18 to 29 with a mean of 22. All were students at the university and right-handed. One participant was eliminated due to partial data

loss resulting from a technical issue and one due to significant inconsistencies within their behavioural data (suggesting poor engagement with the tasks) resulting in a total of 21 participants being included in the analysis. Participants were rewarded £12 for taking part and, by way of incentive to engage fully with the tasks, a £20 gift voucher was offered for the most accurate results.

*Table 2.1: Summary of tasks, all of which were presented in Matlab<sup>TM</sup> 2014a (TheMathworks, Inc., Natick, MA, USA) using Psychtoolbox 3. There were 15 repetitions of the tapping task and 15 trials of each other task at each target duration.*

	<b>Production (motor)</b>	<b>Estimation (visual)</b>
<b>Duration</b>	<i>Button press for specified duration</i>	<i>Estimation, in seconds, of the duration of a stimulus</i>
<b>Rate</b>	<i>Free tapping</i>	<i>Inter-Flash Interval Estimation</i>

#### *Procedure and tests*

Stimuli were presented on a 17" CRT display (ViewSonic Graphics Series G90FB, refresh rate 85 Hz) in a dimly lit room. Participants sat in a comfortable chair in front of the monitor at a comfortable distance of approximately 60 cm.

Having given informed consent, participants were fitted with the EEG cap. The issue of movement during recording was explained and they were requested to

minimize non-task related movement during tasks and informed that there would be breaks built in to the protocol, where they could move. They were also asked not to close their eyes during tasks.

To begin, EEG was recorded for a 2 minute resting period with eyes closed and a 2 minute resting period with eyes open. They were then presented with an initial screen outlining the structure of the experiment. EEG was then recorded for the duration of the experiment. Tasks were then presented in a set order: tapping, production, IFIE and estimation. These are summarized in table 2.1. Between tasks there was a break where progress was presented and the experimenter checked that the participant remained comfortable and understood the instructions for the next task.

The order of presentation was not varied as this order was selected to minimize interference effects. The tapping task was presented first as we wanted a natural production in this task, which might be affected by the focus on 1 second in the other tasks. The estimation task was presented last because it uses examples of 1s which, should the participant successfully identify this as 1s, could be used as a baseline for subsequent tasks. In addition, all instructions referred to ‘random’ durations to minimize the impression that one task could be carried over to the next.

**Free tapping:** Participants were instructed to ‘repeatedly tap the space key at a comfortable, consistent rate’. Following this, a fixation cross was displayed on screen and persisted while they were tapping. Ten taps per repetition were recorded and this was followed by an un-sigaled variable length of time (1000-3000ms) in which the participant continued tapping but responses were not recorded; thus giving the impression that the duration of the task was random and so rushing would make no difference. As there was some concern from piloting that this task may be susceptible to participants tapping as fast as possible, a lower limit of a mean inter-tap

interval (ITI) of 200ms was imposed. If participants tapped faster than this, they received the message ‘That is too fast, please repeat but with a slower comfortable rate’ and that trial was repeated. There were 15 trials of this task.

**Inter-Flash Interval Estimation (IFIE):** Participants were presented with a fixation cross for 1000ms. This was followed by four flashes, each of 47ms duration. Participants were then asked to indicate whether they believed the interval between flashes was less than (left arrow key) or more than (right arrow key) 1s. The IFIs ranged from 500ms to 1500ms in 100ms increments (11 durations in all) and the order of presentation was pseudo-randomized. As there were 15 blocks, each including 1 repetition of all 11 IFIs, each participant performed the task at each IFI 15 times, meaning there were 165 trials in total.

**Duration tasks:** Target durations in both estimation and production tasks increased by 2s from 1s to 11s giving 6 target durations in total. Each block included one repetition of each target with the order of presentation being pseudo-randomized for each block. Occasional even-numbered intervals (between 2 and 10s, one included per block) were included as one pilot participant reported identifying the inclusion of only odd numbers and basing responses on this in the estimation task. Even numbers were not submitted to analysis in either task. There were 15 blocks of each task, with user-determined breaks every 3 blocks, meaning each participant performed each task at each duration 15 times for a total of 90 trials each for estimation and production.

For production, the initial instruction was: ‘In this block, random numbers will appear on screen one after another. Your task is to hold down the space key for that number of seconds. Speed is not important, so respond to each number as you are comfortable and concentrate on accuracy’. Following this, the target duration was displayed in the center of the screen. This remained until the participant completed

their response at which point the next target appeared immediately.

The estimation task presented a centrally located fixation cross for 1000ms followed by a red square (also central, 200x200 pixels) for the target duration then the fixation cross for a further 500ms. Following this, participants were instructed to enter their estimation in seconds using the keyboard number pad. They had the option to use up to one decimal place and the delete key if they made an error.

#### *Electrophysiological Measurement*

EEG data were recorded with Neuroscan 4.5 acquisition software and Synamps II amplifiers (Compumedics, Melbourne, Australia), using a 64 channel cap (EasyCap) arranged according to the international 10-10 system (Jasper, 1958). 2 facial electrodes above and below the right eye recorded blinks. All data were continuously sampled at 1000 Hz. EEG data were referenced online to an electrode on the right mastoid.

#### *EEG data preparation*

EEG data was analysed in Matlab™ 2014a (TheMathworks, Inc., Natick, MA, USA) using EEGLab (Delorme & Makeig, 2004). The full two minute eyes closed resting period was extracted as a single epoch and, via the `newtimef` function, a fast fourier transform applied, with Hanning tapering and subsampled by a factor of 4 with frequency limits at 1 and 60 Hz, to estimate individual alpha peak frequency for each individual. As Cecere et al. (2015) found that specifically occipital alpha peak frequency gated integration, we took this as an a-priori region of interest and averaged peak alpha frequency across these three electrodes for our initial analysis. Further exploratory analysis utilised topography to map the relationship between timing scores and IAF at each electrode.

## Results

### *Data processing*

For estimation and production tasks, responses were averaged at each target duration for each participant. Additionally, a least squares regression line was fitted to each participant's results providing an estimation of slope and intercept. As a check of goodness of fit,  $R^2$  was calculated in each case; in the majority of cases  $R^2 > .99$ , and the poorest fit was  $R^2 = .87$ . As a measure of individual variation, the coefficient of variation (CoV) was calculated for each duration (standard deviation of estimate / mean estimate) and averaged across durations to give a score for each participant.

For the tap task, the Inter-tap-Interval (ITI) was calculated as the time elapsing between the onset of each tap and averaged for each participant; the first 10 tap trial was not included in the mean as this showed artefacts in some instances where participants required further clarification of the task.

Each participant's responses on the IFIE task were fitted with a sigmoid curve and the inflection point calculated as an estimate of their individual sense of the duration of 1s. The mean  $R^2 = .95$  (SD=.08) with a minimum of  $R^2 = .7$ . One participant was not included in analyses of this task only, due to data loss.

### *Duration tasks*

Figure 2.4 shows mean estimates and productions against target durations. In the first instance time judgements in the estimation and production tasks were compared via repeated measures ANOVA with the six target intervals as a second factor. As Mauchley's test indicates assumptions of sphericity were not met for duration,  $\chi^2(14) = 98.39$ ,  $p < .01$ , or the interaction,  $\chi^2(14) = 187.07$ ,  $p < .01$ , the reported values are Greenhouse-Geisser corrected:  $\epsilon = .39$  and  $\epsilon = .24$  respectively. This showed a significant main effect of duration,  $F_{(1.96)} = 1019.86$ ,  $p < .001$ , which is to be expected,

but no significant effect of task,  $F_{(1)}=2.43$ ,  $p=.14$ . The interaction was also not significant,  $F_{(1,18)}=0.91$ ,  $p=.48$ .

The CoV was also extracted as an index of consistency for each participant. A repeated measures ANOVA, as above, showed a significant effect of duration,  $F_{(1,96)}=11.68$ ,  $p<.001$ ; inspection of the means suggests that this is driven by relatively high variation at 1s, which is particularly pronounced in production (see figure 2.4). There was no significant effect of task  $F_{(1)}=3.36$ ,  $p=.08$ , and the interaction was also not significant,  $F_{(1)}=1.94$ ,  $p=.15$ . As Mauchley's test indicates assumptions of sphericity were not met for duration,  $\chi^2(14)=67.55$ ,  $p<.01$ , or the interaction,  $\chi^2(14)=90.52$ ,  $p<.01$ , the reported values are Greenhouse-Geisser corrected:  $\epsilon=.54$  and  $\epsilon=.45$  respectively.

To compare duration tasks to other measures, a least squares regression slope was calculated for each participant for estimation (mean  $b = 1$  ( $SD=.29$ ), mean  $a = 0.35$  ( $SD=.70$ )) and production (mean  $b = 0.89$  ( $SD=.26$ ), mean  $a = 0.04$  ( $SD=.44$ )). Examining the slopes and intercepts, we find that the average intercept for production is very close to 0 and the average slope is a little under a second, revealing that participants cumulatively under-produced durations. In the case of estimation, the average slope shows that participants were collectively very close to increasing their estimate by 1s for each 1s the target increased, there appears to be a very small overestimation in the intercept. However, coherent with the results of the ANOVA above, there is no significant difference between either the slopes,  $t_{(20)}=0.98$ ,  $p=.34$ , or the intercepts,  $t_{(20)}=1.71$ ,  $p=.10$ , of the lines.



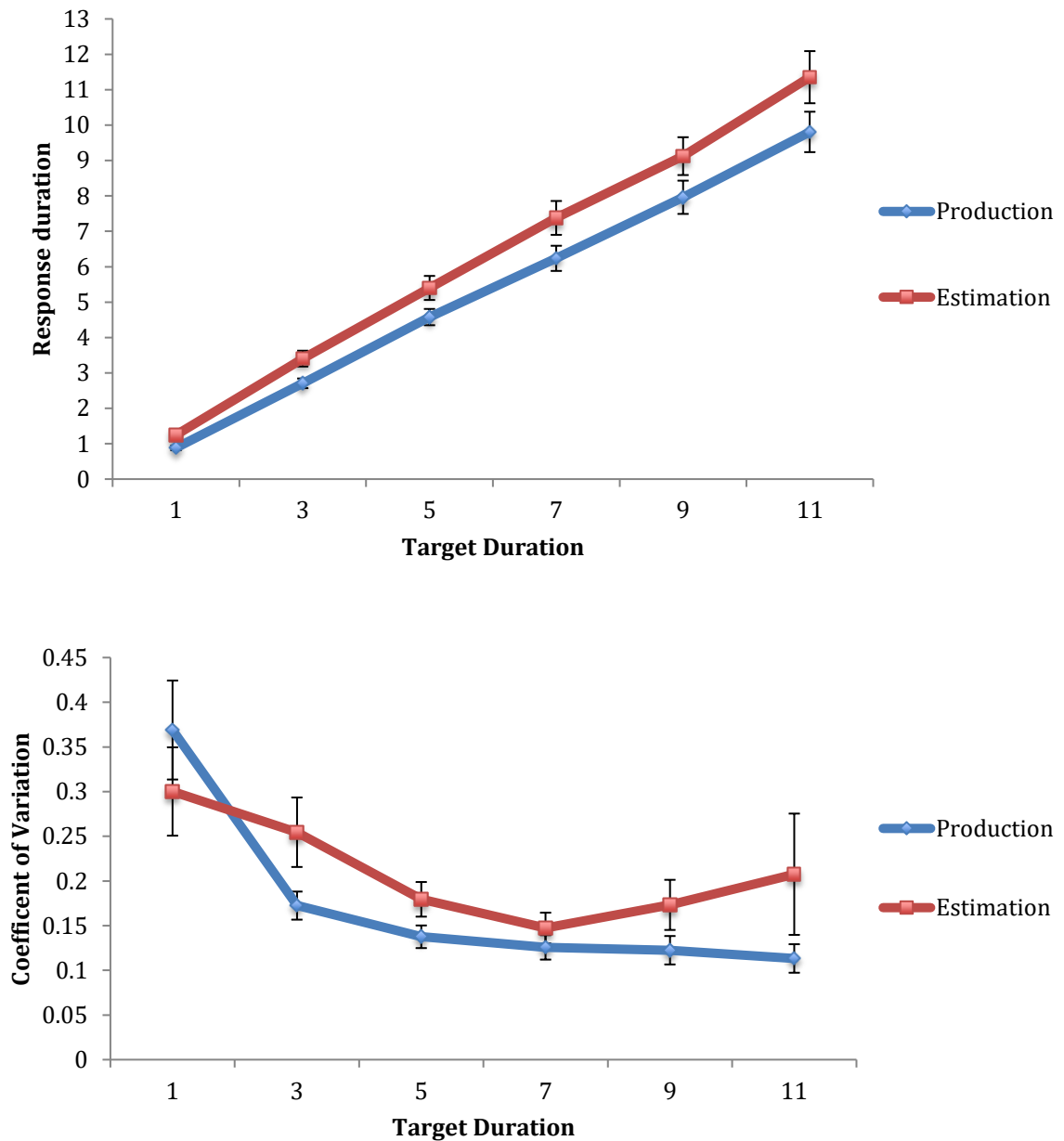


Figure 2.4: Top - mean timing of estimation and production (error bars show SE). Bottom - Mean (and SE) CoV for estimation and production tasks.

#### Correlations between behavioural measures

Slope and intercept values were correlated against both the tapping and IFIE timing tasks and occipital EEG (Table 2.2).

Table 2.2 Means and intercorrelations (Spearman's Rho) among variables

(N=21 / N=20 for IFIE task only)

	1	2	3	4	5	6
1. Estimation slope	-	-.02	-.61**	.61**	-.42	-.38
2. Estimation intercept		-	-.4	.11	-.20	-.07
3. Production slope			-	-.69**	.39	.47*
4. Production intercept				-	-.63**	-.31
5. Tap rate					-	.09
6. IFIE task						-

\*p < .05      \*\*p < .01      \*\*\*p < .001

With regards to the correlations (table 2.2) the primary concern is with the relationships between the duration tasks (production and estimation) and the rate tasks (tapping and IFIE judgment). That both the tap rate and IFIE score relate negatively to the estimation slope and positively to the production slope (although this only reaches significance in the relationship between the IFIE task and production slope) suggests that these two measures relate strongly to the subjective second, in that someone who counts faster (smaller IFIE or inter-tap interval) will have a shorter production and longer estimation. We would have expected the stronger relationships to be between the two motor, and the two visual, tasks, but this is not the case, and these correlations are not significantly different to those between the production slope and the flash task, and the estimation slope and the tap task ( $ps > .05$ ).

*Timing and individual alpha frequency*

To assess the relationship between these two types of timing behaviour and individual differences in occipital alpha activity, both slopes and intercepts were correlated with IAF values (averaged across the three occipital electrodes). As variables were not normally distributed spearman's rho correlations are utilised. While we find weak relationships between some aspects of the timing behaviour and IAF none of these reach significance, thus failing to robustly support a role for alpha integration in subjective time judgements (table 2.3).

*Topography*

Further to the results above, an exploratory analysis was carried out to assess the relationships between measures of subjective time and IAF across the scalp (see figure 2.5) with the question being whether any measure in particular relates specifically to occipital alpha. Scalp topographies were produced representing the relationship between duration timing and IAF, as measured by spearman's rho correlations, at each electrode.

*Table 2.3 Estimation and production slope characteristics correlated*

*(Spearman's Rho) against IAF (mean (SD) =10.09(0.29)). N=21 (N=20 for IFIE task)*

	Mean(SD)	IAF
Estimation slope	1.00 (.29)	-.25
Estimation intercept	.35 (.7)	.29
Estimation CoV	1.27(1.02)	-.33
Production slope	.89 (.26)	.16
Production intercept	.04 (.44)	-.30
Production CoV	.68(.68)	-.17
IFIE	1.03 (.34)	-.19
Tapping	.96 (.48)	.02

\*p < .05

Examining these, the estimation intercept appears to be the measure where a specifically occipital / occipital-parietal effect seems most likely to be found, as the strongest correlations for this condition are in this area, although this does not reach significance (even when not accounting for multiple comparisons) Although the estimation slope and production intercept also appear to have relatively strong relationships with IAF at more central parietal locations the maxima in these cases is in other areas. With regard to the coefficient of variation, the stronger relationships appear fairly widespread in estimation and include some fairly strong relationships at occipital and parietal electrodes. The relationships with CoV for production seem

generally weaker. Overall, these observations do not support a specifically occipital relationship between any aspect of timing and IAF, but does suggest that further investigations in this area may wish to concentrate on estimation.

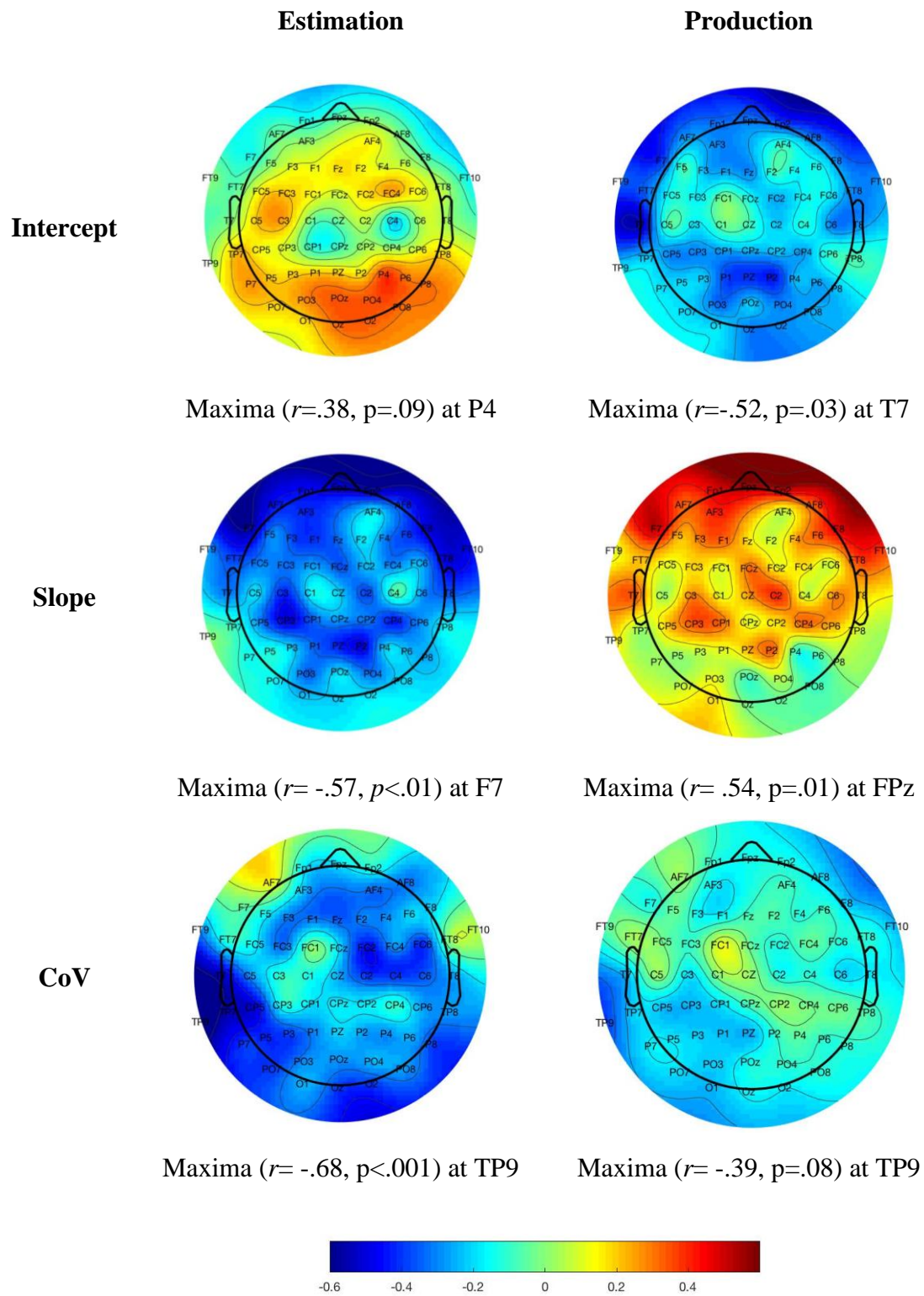
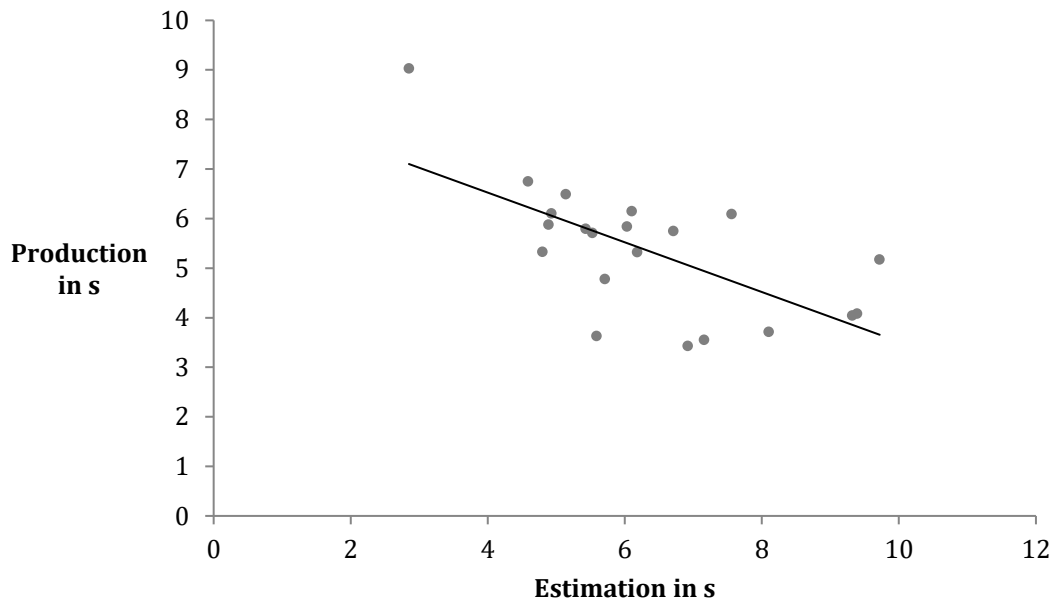


Figure 2.5: Topography plots showing uncorrected correlations (Spearman's Rho) between IAF and measures of subjective time at each scalp location.

## Discussion

This exploratory investigation aimed to examine the relationships between four different timing tasks. These were selected principally for the characteristic that the participant had to generate or estimate the duration for themselves rather than making a comparison between durations. It also aimed to identify timing parameters that may relate to occipital alpha, in its putative role gating sensory integration. Results show a strong relationship between estimation and production tasks, and some relationship between these and the rate tasks, but no significant relationship with occipital IAF.

In analysing the different tasks, it was found that the flash judgement task showed that participants were able to quite accurately judge 1 second. Individual performances in this related to differences over multiple seconds in the production task and estimation task (falling just short of significance in the second instance). This may suggest a common time-base between these tasks but it could also be the case that participants generate a fairly accurate impression of one second and then employ this in counting longer durations, at least in this instance, where chronometric counting is not forbidden. The negative relationship between production and estimation slopes (see figure 2.6) also supports a shared basis, as a relatively fast count, for example, would relate to a shorter production (as they reach the target faster) and a longer estimation (as they count more within that time). The mirroring of results for estimation and production methods is common in the timing literature (Zakay & Block, 1997).



*Figure 2.6: Scatter plot showing the relationship between responses in the Estimation and Production tasks*

The self-generated tapping task shows somewhat surprising results in that the mean tap rate across individuals was just short of 960ms which seems slow given previous studies that suggest an average inter-tap interval in spontaneous tapping of around 400-600ms (Collyer et al., 1994; Drake, Jones, & Baruch, 2000). While about half our participants are within or near this range the rest are distributed fairly evenly between 1000 and 1900ms. A partial explanation for this may be that in previous experiments tapping became quicker over many repeated trials (Collyer et al., 1994) or over a few repetitions interspersed with other, similar tasks (Drake et al., 2000) while in our arrangement it was always the first task and was conducted in relatively short trials, which may have helped preserve the participant's starting rate. It is possible that in previous investigations boredom or a desire to finish increased the tap rate. The answer to this in future investigations may be to sample both starting tap rate and tap rate after tapping for an extended duration, as it is hard to say which of



these rhythms, if not both, might be of interest. Although all participants were instructed to tap at a “comfortable” rate, it is also possible that small differences in the instructions and method of recording tapping between studies may have changed behaviour. Finally, as at least one participant with English as a second language required the meaning of ‘tap’ to be clarified, it is possible that a small number of participants somewhat misconstrued the task in that the word ‘tap’ may not have naturally carried the connotation of relatively fast and rhythmic movement with minimal cognition. Nonetheless the findings on tapping are interesting as they relate to estimation and production slopes in a similar manner to the flash task (albeit less significantly) to which it is unrelated. A possible interpretation of this, requiring further investigation, is that the tapping task shows a natural inclination towards shorter or longer timing, while the flash task relates to their model of one second, and the two may both contribute to duration judgements.

The expectation was that the timing methods would be related by modality, as the flash discernment and estimation tasks are visual, whereas the tapping and production tasks are motor. In actuality, the rate tasks were not significantly different in their relation to both slopes. For the flash task, this is perhaps not surprising as we expect this is mediated by chronometric counting being used in both time tasks. The relationship between the production intercept and tap rate may be evidence of a more modality specific effect and further work on motor time judgements should look to examine the relationships between free tapping, tapping bias at a specified rate and producing or reproducing durations in order to establish whether individuals have systematic innate motor timing biases.

Comparing IAF to time judgements, we found no significant relationships but, as the investigation is exploratory, the moderate correlations found, and the related

topographies, provide some tentative suggestions for future research, which are discussed in the following paragraphs. For example the IFIE task was intended to estimate each participant's concept of 1 second, free of the onset artefacts that may be associated with the production and estimation methods, and thus to allow the disassociation of a relationship with the unit of timing (assuming counting) from a relationship with underlying biases in time judgement. That the IFIE task relates only weakly to IAF suggests that future research addressing this, or related, questions would be wise to minimise chronometric counting. In supra-second tasks, this may be best achieved by simply instructing participants not to count (Rattat & Droit-Volet, 2012). However, the most direct and reliable method would arguably be to use short durations of less than about 1.18s where counting is not useful (Grondin et al., 1999).

Although our correlations were not significant it is notable that the relationships between our duration tasks (in particular the intercepts) and IAF were of a very similar magnitude, approximately  $r=.29$ , as those originally found for the estimation task by Cahoon (1969), even though the tasks used are not directly comparable. This provides some encouragement that there may be a meaningful finding in this area, if future investigations can accurately measure the size and specificity of such a relationship. One factor to address in doing so is power. While our sample size is not unusual in investigations in this area, in this case, there is certainly the consideration that the theorised relationship would have to be relatively strong to attain significance. Assuming a power of 0.8 and a best-case correlation of 0.4, future studies should look to have upwards of 47 participants. It is possible that the general reduction in variation associated with chronometric counting (Rattat & Droit-Volet, 2012) weakened any effect so addressing this may also help to substantiate the relationship, or more conclusively fail to support it.

In our findings, the estimation and production measures have inverse relationships with IAF, for example the estimation intercept is positively related and the production intercept negatively so. This is consistent with the two having a common influence (as with counting above) as a higher IAF (and thus faster cycles) would relate to a longer estimation judgement and shorter production, and thus a faster sense of time passing overall. This pattern is present here, although the two timing methods do not produce significantly different behavioural results. Again, it would be interesting to replicate this while minimising chronometric counting (in which case, we would expect the tasks to vary more significantly) to see if this pattern can be substantiated.

Considering the topography maps, the estimation intercept would appear to be the measure where the relationship with IAF, though not the strongest, is likely to be most occipital. This right parietal-occipital relationship would also be consistent with TMS evidence that the extrastriate visual area V5/MT plays a key role in specifically visual timing (Buetti, Bahrami, et al., 2008) and, to some extent, with the results of Samaha and Postle (2015) that show a relationship between flash fusion thresholds and IAF that is occipital but also somewhat occipital-parietal on the right side. The map showing the relationship between averaged CoV (which represents individual consistency) in estimation and IAF have relatively strong relationships at occipital locations but also in other areas. The moderate negative relationship with deviation, indicating that those who vary less may have faster cycles, suggests that individual variation in IAF is a factor worth considering in relation to consistency as well as absolute duration.

A potential concern in experiments such as these is that participants may be prone to rushing in the motor tasks where they have control over the pace of the

experiment, and some participants reported this tendency during piloting the tasks. There were efforts to control this in the design. In the tapping task there was a lower limit on frequency (no upper limit) at 200ms so that anyone tapping as fast as they can, which would relate to an ITI of 150-200ms (Repp, 2005), would be asked to slow down, as per the instructions to tap at a “comfortable” rate. There was also a variable delay appended to the tap task to give the impression that the task ended after a random period, and thus was not defined by their taps; in other words, to avoid the tenth tap feeling like a goal to be reached. In the production task, participants were specifically instructed that the speed of response was not important and they should concentrate on accuracy. To generally encourage participants to focus on accuracy, a prize was offered for the most accurate participant. Although it is not possible to be certain that rushing did not occur, the significant relationships between production slopes, estimation and the flash task imply a consistency between the tasks that would not be expected if motor tasks were disproportionately fast. Additionally, the production intercept is negatively related to the tap rate, whereas if both were rushed (i.e. as quick as possible) this should result in a smaller intercept and smaller ITI and thus a positive relationship.

Another risk in this study’s design is that of interference between the timing tasks. Although the set order of tasks was designed to minimise this, it means it was not possible to analyse any effect of task order, although this would anyway be problematic without a relatively large sample. The estimation task, being last, is at risk of influence from the flash task, which could help to calibrate the participants concept of one second to then be employed in estimates. While this cannot be specifically analysed, the similarity in the relationships between the slopes for production and estimation and the flash task suggests that there was no substantial

change in the underlying mechanism as a result of the order of these three. Future work could consider pseudo-randomising the order in a larger sample to check for order effects.

One other possible limitation of this study is that in analysing the data, we produce several correlation coefficients based on a relatively small sample, which raises concerns about multiple comparisons increasing the risk of false findings. While this should rightly inspire some caution in interpreting the results, there are arguably some mitigating factors. Firstly, this study is exploratory in nature, seeking to both clarify how participants manage supra-second timing and to establish avenues of investigation with regards to how this relates to neural patterns of sensory integration; to investigate individual differences in this manner necessitates a number of correlations. Secondly, we focus on the pattern of relations and aim to avoid ascribing undue emphasis to the significance or not of any one result. Future work should aim to address these questions with more direct and specific primary hypotheses but the need to check for specificity in a number of directions will generally require a large number of comparisons in secondary analysis.

Although this investigation is a priori focussed on occipital alpha, existing evidence describes a number of relationships between aspects of timing tasks and oscillatory activity, including, for example, premotor beta power predicting the duration of motor reproductions (Kononowicz & van Rijn, 2015), fronto-parietal and supplementary motor area ERP components relating to bias caused by the content of intervals (Mitsudo, Gagnon, Takeichi, & Grondin, 2012) and parietal and occipital beta and alpha power predicting the correct discernment of 1s from 1.5s intervals (van Viegen et al., 2017). To some extent this variety of evidence is consistent with the proposal of a timing system including both general and multi-modal elements (Buetti,

2011). It is also important to remember that, though we limit ourselves for reasons of experimental practicality, oscillatory activity tends to harmonise with different frequencies (Klimesch, Sauseng, & Hanslmayr, 2007) and functionally synchronise with different areas (Klimesch, 2012) so it is likely that experiments often isolate one aspect of interrelated oscillatory activity.

In this context, it is important to not only have a clear, a priori theory as to which part of such a system one is investigating but also to start to discern to what extent a finding is specific to the systems and tasks concerned. We aimed to approach this by using a variety of tasks and checking locational specificity via topography. If future investigations robustly establish the relationship we theorise here, a further task will be to test the specificity of occipital alpha in relation to visual time judgement by comparison with other likely oscillatory activity. Additionally, it would also be of interest to investigate occipital alpha during the task to test the consistency of the relationship within the participant and establish whether trial by trial fluctuations relate to timing behaviour; this also may help to discern whether any relationship with occipital alpha is causal or symptomatic of individual differences in the general characteristics of related oscillatory systems.

A final consideration is that the rationale for the current experiment is partially based upon the role of occipital alpha in integrating visual and auditory information (Cecere et al., 2015) and the theory that individual temporal differences in integration may relate to differences in temporal perception. The evident way to progress this avenue of integration (besides the suggestions above) is to seek to establish this relationship on a behavioural level via estimating each individual's window of integration and relating this to an appropriate timing task as we do in chapter 3. Such

an experiment, if successful, would also be likely to assist in establishing a robust methodology to continue researching the question on a neurophysiological level.

This chapter sought to investigate the hypothesised relationship between occipital alpha peak frequency and timing behaviour across tasks. While timing tasks significantly related to each other there were no significant relationships with occipital IAF. While this experiment does not provide robust evidence for the effect of occipital alpha on time perception, it does suggest potential areas, and procedures for further research. In particular, there is potential for a moderate relationship between aspects of subjective time judgement, particularly in estimation, and individual variations in alpha frequency; eliminating chronometric counting and improving power is likely to benefit experiments looking to further pursue this question.





## **Chapter three: Individual differences in sensory integration predict differences in time perception and account for individual levels of schizotypy**

Time is an illusion, lunchtime doubly so.

*Hitchhikers guide to the galaxy*

### **Abstract**

To interact functionally with the world around us our perception must be able to locate events in time, including discerning whether sensory events occur at the same time. There is evidence that individual differences in the Temporal Binding Window (TBW), the time window within which two stimuli are integrated into one event, relates to a variety of individual differences, including in perceptual tasks and schizotypal traits. There is, however, little available evidence as to whether, and how, the TBW relates to individual differences in the perception of duration. We address this issue by comparing individual TBWs with individual differences in the filled duration illusion, which involves the judgement of durations that are either empty or filled with stimuli, being typically perceived as longer in the second instance. As schizotypy has also been associated with timing behaviour this too is measured as a potential link between these tasks and enduring perceptual differences. Findings demonstrate the filled duration illusion and significantly relate the magnitude of the effect, and individual variation in performance, to the size of the TBW. The two measures relate to different schizotypy subscales suggesting that temporal binding is associated with differences in sensory experience while timing judgements may be

influenced by impulsivity. This provides evidence that the individual rate of sensory integration relates to both perception of duration and schizotypy.

### **Introduction**

In everyday life it is sometimes easy to assume that the world is as we experience it and that the other people we interact with experience it in the same way. While this is, broadly speaking, a reasonable way to think, otherwise interaction and communication would be greatly challenging, there are a wide variety of ways in which common experiences differ. Thus the challenge for psychologists is not only to understand the commonalities within sensory experience but also the nature and causes of differences between individuals. In considering the perception of time, the ability for collective time perception and synchronisation in time is perhaps most obvious in music, though no doubt it occurs in every facet of life from driving to sport. In this research, we aim to go one step further in the consideration of individual differences, to examine how the natural variances between individual perceptual systems combine with systematic differences in stimuli in producing subjective time estimates.

Both events in the environment, and the neural encoding of those events in our brain are dynamic in nature. Thus, time is a fundamental aspect of the way we perceive the world around us. It is well established that both the nature of the task and the characteristics of the stimuli, such as duration, complexity and intensity, influence experimental timing judgements (Block & Zakay, 1997; Matthews et al., 2011; Zakay & Block, 1997). There is also evidence of individual differences in timing. Mostly, these are related to characteristics such as age (Carrasco et al., 2001; Droit-Volet, 2008), gender (Block et al., 2000; Espinosa-Fernández et al., 2003) or conditions such

as Schizophrenia (Lee et al., 2006) or Autism (Allman & Falter, 2015; Falter, Noreika, Wearden, & Bailey, 2012). Research has also linked interoception (sensitivity to internal signals from the body) to timing (Meissner & Wittmann, 2011), showing that individual variation in other types of perception can influence subjective timing. Craig's (2009a) model associates timing with the processing of interoception in the insula cortex, however there is also evidence that some aspects of timing are embedded within other sensory systems (Buetti, Bahrami, et al., 2008; Gamache & Grondin, 2010). In the previous chapter we tested the possibility of a direct relationship between occipital individual alpha peak frequency, a neural marker of sensory integration, and duration judgments, with inconclusive results. Here we address a similar question but aim to establish whether there is a relationship between behavioural tests of sensory integration and duration judgments, something that was postulated in the previous chapter. Hence the aim of the current study is to test the possibility that our judgments of duration are also influenced by the rate at which we sample the world through our senses.

Previous research has shown that the window within which individuals classify two stimuli from different sensory modalities (in this case tactile and auditory) as occurring synchronously, positively relates to the degree to which they are susceptible to the rubber hand illusion (Costantini et al., 2016).

A wider temporal binding window has also been associated with clinical conditions such as autism (Baum et al., 2015; Foss-Feig et al., 2010; Kwakye et al., 2011) obesity (Scarpina et al., 2016) and schizophrenia (Foucher et al., 2007; Giersch et al., 2008; Thakkar et al., 2011) or its non-clinical counterpart schizotypy (Ferri et al., 2017; Ferri et al., 2018). Collectively, these findings suggest that individual differences in temporal integration relate to a number of differences in wider

perception and behaviour that persist over time. Notably Reed and Randell (2014) found the individuals scoring highly on the Unusual Experiences subscale of the O-LIFE schizotypy scale, which relates to positive aspects of schizotypy, showed significant differences in a bisection task, where their estimation of the mid-point of the stimulus range was longer than it was for low scorers.

Changes in perception related to multisensory integration have been associated with the frequency of occipital alpha rhythms in the human EEG, varying both by individual and from neuromodulation (Cecere et al., 2015; Samaha & Postle, 2015) demonstrating directly how neural timing relates to perceptual differences. In particular Cecere et al. (2015) used the flash-beep illusion, wherein a single flash can be perceived as two flashes when presented with two beeps, one simultaneous and one closely following, as a measure of the TBW. They found that this measure correlated with IAF and was modulated by tACS. Occipital and parietal alpha rhythms have also been associated both historically (Cahoon, 1969) and more recently (Glicksohn et al., 2009) with timing. While the idea of alpha as a “biological clock” has not been supported by the evidence, this does not discount the possibility of alpha having a role in modal sensory timing. For example, one of the key studies debunking alpha as a clock (Treisman, 1984) required participants to keep their eyes closed, while recording online alpha, and so comprised no visual element at all. The associations that have been found may suggest that occipital alpha has an indirect relation to the timing of visual stimuli; this gives reason to posit a possible link, common underlying neural mechanisms, between the size of an individual’s temporal binding window, and their judgements of duration. This study looks to test this putative relationship behaviourally with a view to facilitating future neuroscientific investigation.

Considering the above we use the temporal binding window as a measure of individual differences in integration that, in relating to a variety of other conditions and measures, appears to be indicative of wider and more enduring differences in perceptual experience. As there is reason to think of human perception as being derived from a stream of discrete, temporally bounded, sensory samples (VanRullen & Koch, 2003) then differences in the TBW may be indicative of individual differences in the fundamental timing of perception.

This investigation uses a variation on the Simultaneity Judgement (SJ) task (Zampini et al., 2005) to provide an estimate of the TBW. Typically this task presents a brief visual stimulus with an auditory beep at a range of offsets; it can then be estimated, via fitting two sigmoid functions, at what point the individual perceives simultaneity and at what point the visual and auditory stimuli are no longer perceived as simultaneous the majority of the time. However asymmetries in data from this task are common and evidence has suggested that the two sides of the curve (by convention the right side is visual leading and the left auditory leading) differ in both behavioural and neural terms (Cecere et al., 2016; Cecere et al., 2017) and that the right side specifically relates to other illusions (that are in themselves used to measure the TBW) such as the McGurk effect and flash-beep illusion (Stevenson et al., 2012). In this case we only measure the temporal binding window for the right (visual leading) side, allowing more trials and smaller differences between the offsets.

To compare the TBW to timing judgements this study uses a novel measure in exploiting the filled duration illusion as an indicator of individual differences. The filled duration illusion is a robust and well supported effect whereby intervals “filled” with stimuli (often sound) are routinely estimated as longer than those where only the beginning and the end of the target duration are signalled (Thomas & Brown, 1974;

Wearden et al., 2007). Filled durations have also been found to be less variable than unfilled ones in some experiments (Rammsayer & Lima, 1991; Wearden et al., 2007). While filled intervals can be filled by a continuous tone (e.g. Wearden et al., 2007) the effect is also found when the interval is filled with a series of tones, or events in other modalities, and the size of the effect varies in accordance with the number and distribution of these (Buffardi, 1971; Foley, Michaluk, & Thomas, 2004; Horr & Di Luca, 2015; Schiffman & Bobko, 1977). It has also been found that applying a click train prior to the timed stimulus, putatively speeding up the pacemaker, increases estimates in both conditions (Wearden et al., 2007). Plourde, Gamache, and Grondin (2008) found that the effect is still found even when they split the filled and unfilled durations over separate sessions, so there is no direct comparison. Notably some results seem to show that the effect is not reliable when the two conditions are split between groups (Droit-Volet, 2008; Robertson & Gomez, 1980). From this we might suggest that the effect is relatively stable within individuals but not necessarily between them, and so might be a good indicator of individual differences.

We propose to use the filled duration illusion as a novel measure of individual difference where a participant's timing score is based on the comparison of their estimate of the duration of a stimulus to their own timing of an empty duration of the same length. An additional advantage of this method is that it allows further analysis as to whether any relationship identified is driven by the empty duration, which might be more indicative of an individual's baseline timing (e.g. timing that is relatively uninfluenced by stimulus characteristics), or the filled duration which would suggest the relationship is more specific to how a stimulus is processed (given that typically this condition varies depending on the timed stimulus). Systematic individual

differences in both conditions (rather than in the difference between them) would indicate a general difference in the pacemaker between individuals.

As noted above, schizophrenia and schizotypy have been associated with altered temporal binding (Ferri et al., 2017; Foucher et al., 2007; Giersch et al., 2008; Thakkar et al., 2011). As altered timing (including perceived duration and variability), on temporal bisection tasks, has also been associated with schizophrenia (Lee et al., 2009) and schizotypy (Lee et al., 2006; Reed & Randell, 2014), schizotypy was measured via the O-life scale (Mason, Linney, & Claridge, 2005), as used by Reed and Randell (2014), as a way of potentially relating these measures to more enduring individual differences in perception in behaviour. In particular, and in line with the above findings, a relationship is expected with the Unusual Experiences subscale, which represents positive schizotypal traits including differences in perception. Measuring schizotypy also helps to begin to disassociate whether any relationship between the measures is direct or mediated by schizotypy.

The priority is to test whether any relationship exists between integration and timing. As people with wider TBWs appear to be more susceptible to sensory illusions we expect that TBW width will relate positively to the size of the filled duration illusion. This corresponds with developmental studies where separate findings show that children have a wider TBW (Hillock - Dunn & Wallace, 2012; Wang, Datta, & Sussman, 2005) and a larger filled duration effect (Droit-Volet, 2008) compared to adults. If this is driven by changes in the filled slope, this suggests differences in how the stimulus is processed, while if driven by changes in the empty slope, this implies baseline differences associated with rate of integration. Further to this schizotypy scores have been previously associated with both timing (Lee et al., 2006; Reed & Randell, 2014) and temporal integration (Ferri et al., 2017) and so we

include this measure. It is hypothesised that schizotypy scores will relate to both of the primary measures (time estimations and simultaneity judgement) thus associating these measures with long term perceptual differences as well as transitory ones.

## **Methods**

### *Participants*

102 participants were tested in groups (separate individual booths). All participants were paid volunteers. Two were removed prior to any analysis due to missing data (due to a technical issue and a non-completion). Of the remaining 100, 63 were female (1 unspecified), 92 were right-handed and the mean age was 23 years (SD=7.89).

### *Procedure*

Participants performed all tasks in batches of up to 30 individuals. Each was in an individual booth within a larger room and wore sound cancelling headphones. They were instructed to sit upright, facing the screen. The experimental protocol was presented using psychophysics toolbox (Brainard & Vision, 1997; Kleiner et al., 2007; Pelli, 1997) in Matlab™ 2014a (TheMathworks, Inc., Natick, MA, USA).

The experiment consisted of a timing task and the simultaneity judgement task, which were counterbalanced in terms of order and separated in each case by completion of the O-Life Schizotypy questionnaire (Mason et al., 2005), which also served as a buffer to minimise any effect of one task upon the other. For both the simultaneity and timing tasks, the order of stimuli was pseudo-randomised via a random permutation function seeded to the participant number. The procedure lasted approximately 40 minutes, depending on the individual.



*Simultaneity judgement*

Participants were presented with two-alternative, forced-choice simultaneity-judgment tasks where they were presented first with a fixation cross (8x8mm / 30pixels) for 664ms (40 frames). The visual stimulus was a white ring (50 pixels / 132mm diameter) circumscribing the fixation cross for 30ms and this was simultaneous with, or preceding, a tone of 3520 Hz for 30ms duration; the following Stimulus Onset Asynchronies (SOAs) were used: 25, 50, 75, 100, 125, 150, 175, 200, 225, 250, 275, 300, 325, 350, 375, 400. The options “simultaneous” and “non-simultaneous” (these terms having been clarified in on-screen instructions) were continually on the screen at the bottom left and right corners (the sides counter-balanced between blocks); participants selected one of these via the left and right ctrl keys (having been instructed to use one index finger for each). The next trial was initiated once a response was given. Regular breaks were incorporated into the task which consisted in total of 1 block of 1 set of 8 intervals (25,75,125,175,225,275,325,375) for training, followed 2 blocks each of 16 sets of 17 intervals; resulting in 32 repetitions at each level and 544 trials in total.

Each participant’s simultaneity judgement responses were calculated as the percentage that were simultaneous. For each participant, these percentage scores were fitted with a psychometric Gaussian function (using *cftool* in Matlab) and the value for the window was taken as the point on the x axis corresponding to 50% simultaneity. Where participant’s response curves were at a value greater than 50% simultaneity at 400ms their score was set at 400ms as a proxy. The  $R^2$  for each curve was recorded as an indicator of goodness of fit. For the initial analysis a strict inclusion criteria was applied (only those participants with an  $R^2$  of above 0.6 who

achieved less than 50% simultaneity by 400ms were included; 55 participants) however as this eliminated 45 of 100 participants, the analysis was repeated including all participants to verify the findings.

#### *Filled duration illusion*

Two types of timing trial were used: “filled”, a single (494hz) tone presented for the duration of the target interval, and “unfilled”, two (1046.5Hz) tones of 10ms presented at the beginning and end of the target interval. The 10 target intervals were (in ms) 77, 203, 348, 461, 582, 707, 834, 958, 1065 and 1181. Participants completed 5 blocks, each consisting of the 20 stimuli (10 filled and 10 unfilled) in random order for a total of 100 trials. Each trial was commenced by the participant pressing any button. The fixation cross was displayed for between 500 and 1500ms (delay pseudo-randomly generated) followed by the auditory stimulus, during which the fixation cross remained on the screen. Participants were then asked to estimate the duration of the tone, or the gap between tones, in milliseconds using the keyboard number pad. In instructions they were reminded of how milliseconds relate to seconds (0.5 seconds = 500ms, etc.) and at each response they were reminded that responses should be within 50-1500ms. Where responses were beyond this range they were discounted and the participant reminded of this range before the next trial.

Participants’ estimates were regressed against stimulus duration giving a slope and intercept value for filled and unfilled conditions for each participant.

Theoretically the intercept relates to delays in the onset of timing, while changes in the slope indicate changes in the “pacemaker” or underlying substrate of timing (Gil & Droit-Volet, 2012) which is primarily of interest for our purposes. The differential of the two slopes is taken as a score representing the size of the filled duration illusion for that individual. Mean scores and the Coefficient of Variation (CoV; standard

deviation of estimate / mean estimate), which essentially represents variation adjusted for individual timing performance, were also calculated for each condition and duration.

*Oxford Liverpool Inventory of Feelings and Experiences*

All participants completed the short O-Life schizotypy scale (Mason et al., 2005) which consists of 43 items. This scale measures schizotypal traits occurring in the general population and comprises of four subscales: Unusual Experiences, Cognitive Disorganization, Introvertive Anhedonia, and Impulsive Nonconformity. Questions were presented singly on screen and the participant responded with the Y or N key (Yes or No respectively) which automatically initiated the next question. O-life scale scores were calculated in the standard manner for both the overall survey and the four subscales.

## **Results**

*Time estimation*

An ANOVA was carried out on the time task data (all participants included). This showed a significant main effect of stimulus type,  $F_{(1,99)} = 228.04, p < .001$ ; and stimulus duration,  $F_{(9,891)} = 479.21, p < .001$ ; and a significant type X duration interaction,  $F_{(9,891)} = 228.04, p < .001$ . The filled-duration illusion was observed as filled durations were longer than empty ones, this difference being greater for longer durations, with a significant differences in means (averaged across target durations),  $t_{(99)} = -15.10, p < .001$  (see figure 3.1).

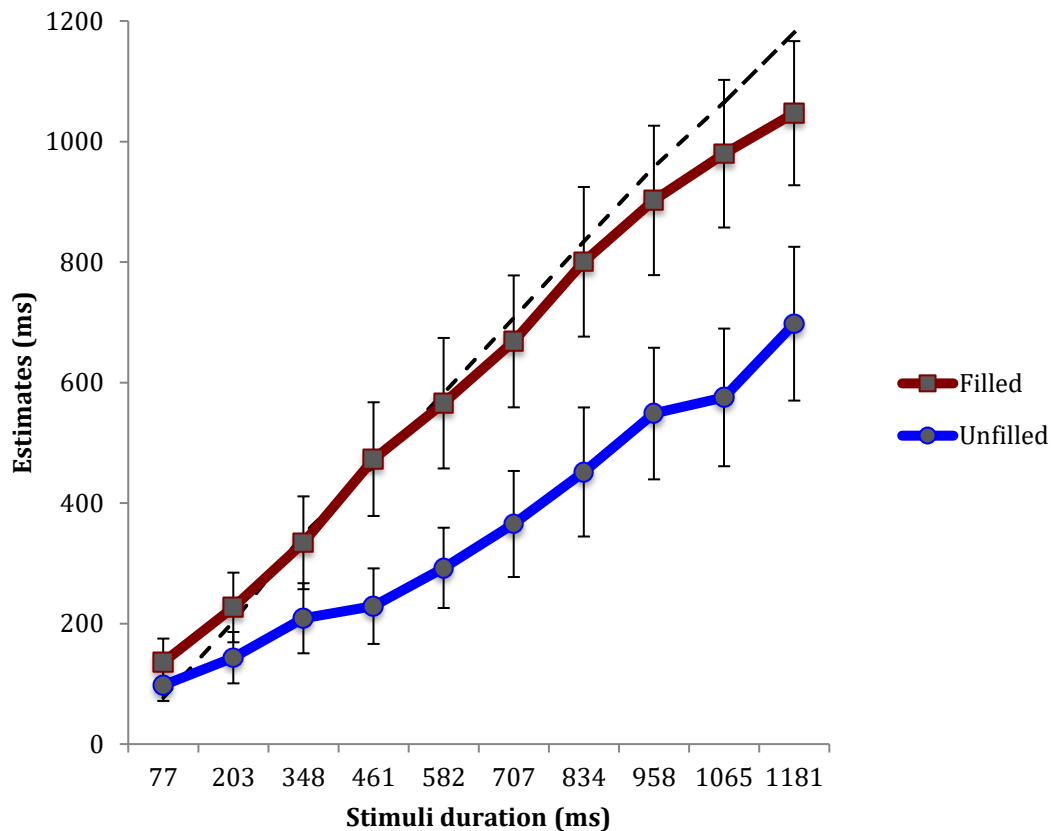


Figure 3.1; Mean estimates of duration for filled and unfilled intervals plotted against stimulus duration. Error bars show standard error of the mean. Dashed line shows a 1:1 relationship.

Slopes and intercepts were calculated for each participant for filled (M slope=.86,  $SD=.26$ , M intercept=62.29,  $SD=151.66$ ) and unfilled (M slope=.54,  $SD=.32$ , M intercept=17.72,  $SD=127.88$ ) intervals. Wilcoxon tests show that the filled condition slope is significantly steeper than the unfilled slope ( $Z=7.83$ ,  $p<.001$ ) and the filled intercept is also higher ( $Z=2.60$ ,  $p<.01$ ). Simple examination of the slopes shows that the filled condition is closer to 1, 1 being a perfect relationship between increases in duration and increases in estimate, while the unfilled slope shows a general tendency to underestimate compared with real time. The size of the filled

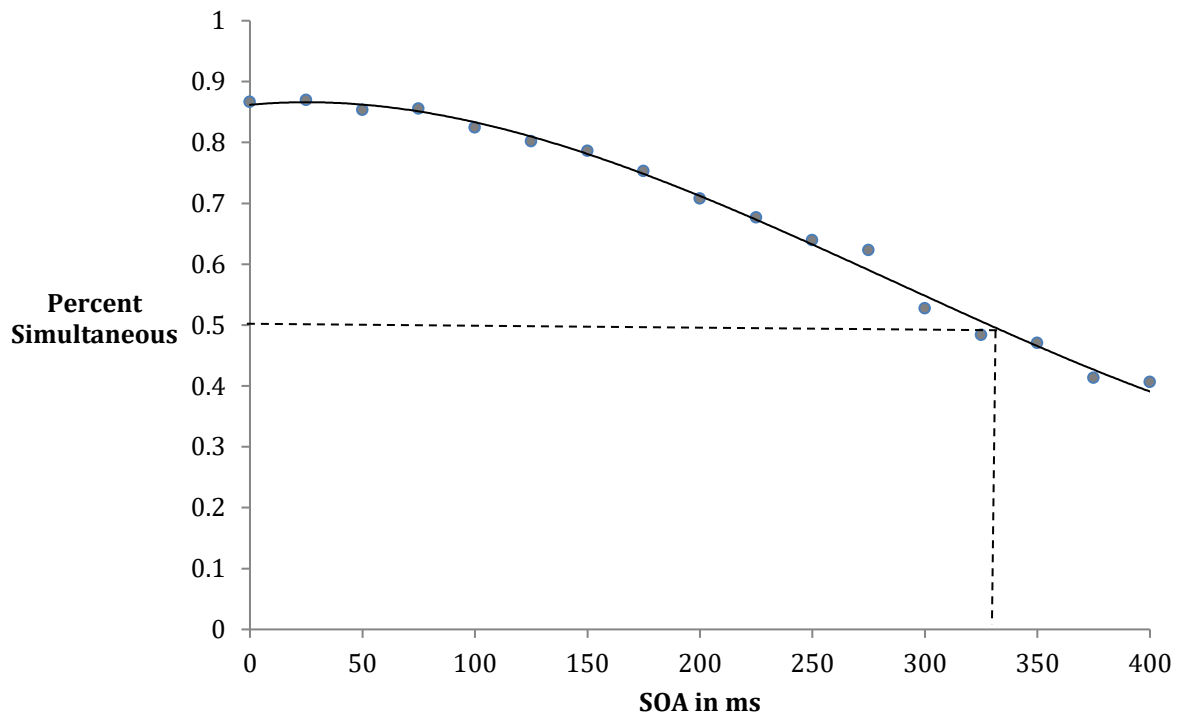
duration effect was estimated as the difference between the filled and unfilled slopes for each participant.

The CoV was collapsed across durations and compared between conditions, this showed that performance in the unfilled condition ( $M=52$ ,  $SD=.18$ ) was significantly more variable than that in the filled condition ( $M=.43$ ,  $SD=.16$ );  $t_{(99)}=-4.9$ ,  $p < .001$ , coherent with previous research using this task.

*The relationship between TBW and timing slopes*

To test the primary hypothesis that the TBW and duration estimates are related the relationship between the filled duration effect and the point of 50% simultaneity was assessed via Pearson correlation coefficient;  $r=.36$ ,  $n=55$ ,  $p<.01$  (figure 3.2). Conservatively, only participants who had a good fit ( $R^2 > 0.6$ ) and that were not over 50% simultaneity at 400ms SOA were included. As this resulted in excluding a high number of participants, the analysis was repeated without any exclusions and the result is very similar;  $r=.36$ ,  $n=100$ ,  $p<.001$  (see figure 3.2). As such the remaining analysis includes all cases but has also been performed implementing the conservative controls, which does not substantially change the results. The window of integration appears to relate to the difference in the slopes between conditions as predicted, the positive nature of the relationship suggests that a larger window of integration relates to a greater difference between the slopes.

As a check this analysis was repeated using the difference between the intercepts of the slopes, which represent a difference in orientating to the stimuli; the non-significant result,  $r=-.16$ ,  $n=100$ ,  $p=.12$  suggests that the relationship with the TBW is specific to the slopes.



*Figure 3.2: Averaged judgements of simultaneity ( $n=100$ ) for each stimulus onset asynchrony. This is fitted with a Gaussian function. The dashed line represents 50% judged as simultaneous.*

To further analyse this result the individual slopes were correlated against the TBW. The TBW negatively correlated with the slopes for empty intervals,  $r=-.43$ ,  $n=100$ ,  $p<.001$ , while there is no significant relationship between the TBW and the slopes for full intervals,  $r=-.13$ ,  $n=100$ ,  $p=.20$ . This is of interest as it implies that the

unfilled condition drives the difference between slopes, which may suggest the relationship is with an individual's baseline timing rather than in how stimuli are processed.

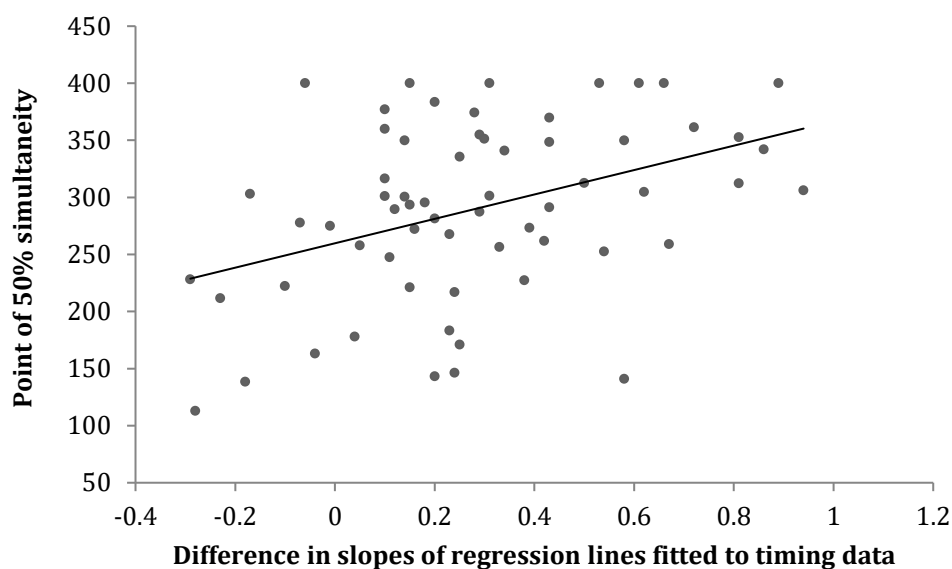
CoVs were also correlated against the TBW. Results showed a significant positive relationship both for the filled,  $r=.27$ ,  $n=100$ ,  $p<.01$ , and unfilled,  $r=.23$ ,  $n=100$ ,  $p=.04$ , conditions, suggesting that a wider TBW relates to more variable timing in both conditions.

### *Schizotypy*

The O-life Schizotypy scores related significantly to the TBW,  $r=.24$ ,  $n=100$ ,  $p=.02$ . In particular, the unusual experiences sub-scale related positively and significantly,  $r=.32$ ,  $n=100$ ,  $p<.01$ , while other scales did not ( $ps>.05$ ). The unusual experiences subscale relates to positive schizotypal traits including hallucinations and perceptual aberrations and so this result supports the relationship between the TBW and the perceptual aspects of schizotypy.

The difference between the timing slopes did not relate to the overall O-life score,  $r=-.001$ ,  $n=100$ ,  $p=.99$ , but did significantly negatively relate to the impulsive non-conformity sub-scale  $r=-.22$ ,  $n=100$ ,  $p=.03$ . The subscale does not correlate significantly with either timing slope but is close to significance in the case of empty durations,  $r=.18$ ,  $n=100$ ,  $p=.07$  but not filled ones  $r=-.02$ ,  $n=100$ ,  $p=.85$ . Impulsive non-conformity includes items relating to eccentric, anti-social or impulsive behaviour and implies a lack of self-control, so this result might imply high scoring individuals have a small tendency to overestimate empty durations out of a sense of boredom or impatience making the trials feel longer.

As some studies have found increased variation in timing behaviour related to schizophrenia, the CoV was correlated against O-life scores. There was no relationship with the overall scores in either case (Unfilled;  $r=.04$ ,  $n=100$ ,  $p=.68$ , filled;  $r=-.02$ ,  $n=100$ ,  $p=.83$ ) but there was something of a relationship between the unusual experiences subscale and the CoV in the filled condition,  $r=.21$ ,  $n=100$ ,  $p=.04$ , though this was n.s. when the stricter selection criteria were applied (this being the only relationship where this was the case) and so may not be robust.



*Figure 3.3: Scatter plot showing the relationship between the window of integration and the difference between slopes in the filled/unfilled timing task*

### **Discussion**

The intention of this study was to establish whether the individual rate of sensory integration relates to individual differences in the perception of time. In



timing we replicate previous research that showed that filled durations are judged longer, and with more variation, than unfilled ones (Wearden et al., 2007). The finding that the point at which a person reports 50% simultaneity in the SJ (their window of integration) is predictive of the difference between the slopes of their reported timings for empty and full intervals supports the hypothesised relationship. In particular, the positive relationship suggests that the larger the window of integration, the greater the difference between filled and unfilled intervals. This finding is coherent with previous evidence that children have a larger filled-unfilled difference (Droit-Volet, 2008) and a wider TBW than adults (Hillock - Dunn & Wallace, 2012; Wang et al., 2005). Notably the TBW also relates significantly and positively, to individual variation in performance in both conditions, suggesting that people with a narrower window of integration may have more consistent timing behaviour.

To understand why the relationship between the filled duration illusion and the TBW is positive, we consider the filled and unfilled slopes individually and observe that the slope of the unfilled interval, and not the filled, correlates significantly, and negatively, with the TBW. This suggests that those making longer estimates in this condition have a smaller TBW. In other words, those with a faster sensory processing cycle estimate the empty duration as longer than those with slower cycles; in this case, this could be considered analogous to having a faster “pacemaker” where more beats elapse within the duration to be timed. In terms of comparison with real time the filled condition is relatively close to real time compared to the underestimation in the unfilled condition.

We might ask why the effect might be seen in only the empty condition rather than in both, as previous evidence shows that click trains, putatively acting upon the

pacemaker, consistently result in longer estimates of both filled and unfilled stimuli (Wearden et al., 2007), though the effect of click trains is small compared to the filled duration effect. The current research was driven by the question of whether there is a common underlying mechanism that influences both sensory integration and the perception of time. One possible explanation for this finding is that this common mechanism is obscured by the dynamics of the stimulus. In other words, with limited external stimulation our sense of time might depend on a ‘pacemaker’, but when stimulation introduces competing temporal dynamics, this relationship becomes decoupled. Existing research does show that performance for the interval varies in accordance with the stimuli that fill it (Buffardi, 1971; Foley et al., 2004; Horr & Di Luca, 2015; Schiffman & Bobko, 1977). Future research should attempt to test this hypothesis in more detail, for instance by changing the dynamics of the stimulation in the filled condition. With regard to click trains we might postulate that it adds the same temporal dynamics to both conditions with the same effect on both.

With regard to variation we find that both conditions show less variation (as measured by the CoV) for individuals who have a narrower window of integration. We interpret this as the narrower TBW representing a more fine-grained sense of time. If we think of temporal binding as representing the frame-rate, or frequency, of sensory processing, then a variation of a few frames between timing judgements would make a comparatively larger difference for someone with longer frames. Alternatively it might be suggested that both a narrower window and more consistent timing may simply relate to better focus on the task, however our findings on variation in filled and empty intervals mirror previous experiments (Wearden et al., 2007) and the effect remains even when we employ conservative controls to which participants we include.

Note that a directly causal relationship is not assumed; both processes (temporal binding and estimation) are clearly part of a wider perceptual system and correspondences between such factors may represent coherence within that system. To address this question, further research should aim to show covariance between the TBW and timing performance. It has been shown that stimulus intensity influences sensory integration (Fister et al., 2016), and time judgements are influenced by contrast in intensity (Matthews et al., 2011), and so this would be a good candidate mechanism for progressing the research. In particular, it would be a logical progression to move from empty vs full intervals to degrees between no stimuli and high intensity stimuli. If those who experience a greater effect of intensity on sensory integration also experience a greater effect on timing then this would strongly support a relationship between the two. To relate this directly to neural processes, one might also consider varying temporal binding via TDCS (Zmigrod & Zmigrod, 2015), tACS (Cecere et al., 2015) or entrainment (Ronconi & Melcher, 2017) and applying the same manipulation during the timing task.

The results find a relationship between the TBW and schizotypy scores, with this being driven by the Unusual Experiences subscale, which relates to positive schizotypal traits such as perceptual differences. This replicates previous findings (Ferri et al., 2017; Ferri et al., 2018) which used scores from the Schizotypal Personality Questionnaire (Raine, 1991) suggesting this finding is robust across measures.

By contrast time judgements did not relate significantly to overall schizotypy scores and related to a different sub-scale, impulsive non-conformity. There is one exception in that the CoV for full conditions showed some relation to Unusual Experiences, but this requires further substantiation as it was not significant when

more robust criteria were applied. This contrasts with previous studies that did find a relationship between timing and positive characteristics of schizotypy using the O-life (Reed & Randell, 2014) and SPQ (Lee et al., 2006), however the results are not directly comparable as both used a temporal bisection task rather than verbal estimation. From this we would suggest that if there is a relationship between positive schizotypy and duration judgements this is likely to be either timing task specific or relatively weak, such that a very large sample or pre-selection for high schizotypal individuals is required. Another consideration is that Lee et al. (2006) only found the relationship at 1000-2000ms, so the durations used here may be below the range in which the effect is robust, though Reed and Randell (2014) found a relationship using sub-second stimuli. The relationship with impulsive non-conformity, in our experiment, was unexpected. The simplest explanation might be to suggest that higher impulsive nonconformity individuals might engage less well overall with task demands and thus show less manipulation effect. However, as multiple comparisons are made, and we did not preselect for high and low schizotypy individuals or use a clinical sample, conclusions from subscales are necessarily tentative.

These results suggest that, though a wider TBW appears to relate both to schizotypy and time judgements, these may be two separate relationships. Future work may look to assess this using different timing tasks, in particular temporal bisection, and by preselecting in relation to schizotypy; assuming that a relationship can be replicated in the right paradigm then it would be possible to test whether these measures account for separate proportions of the variance in the TBW.

While these results are largely consistent with the literature, the average width of the temporal binding window identified in our study may appear larger than usual, as some individuals did not reach 50% simultaneity within a 400ms offset. However,

it should be considered that the paradigm used here is different to the typical temporal binding task in that the typical task analysis first determines a point of subjective similarity (PSS) then considers the window relative to this, while the current variation of the task purely considers the absolute time difference in time between the two stimuli. This means that for a proportion of participants, the PSS will occur within what is here represented as the (right) TBW resulting in a longer window. As there were further differences, such as using smaller differences between SOAs and providing less training than is typical in this task, further research would be required to investigate the discrepancy and ascertain definitively whether the relationship found in this experiment is driven by the position of the PSS or the width of the window around it. As the result is similarly significant regardless of whether those participants not reaching 50% simultaneity are included, the primary finding appears robust. This is especially the case considering the relatively high numbers of participants and given that training and individual supervision, factors that may promote relative conformity, were minimised.

In conclusion, this investigation provides strong support for a relationship between individual differences in the timing of sensory integration and timing behaviour. This finding provides a basis for further work to elucidate the exact nature of this relationship and provides evidence that time, one of the most basic elements of perception, may be experienced a little differently by each of us according to how we process primary sensory information.



## Chapter four: Interoception, arousal and time

I drove into a lamppost with my bike once. Had arms and legs just hanging straight forward almost hugging the post, just like in the cartoons. My bike was already on the ground. It felt like a solid 5-8 seconds. It was probably just one second. I was so confused as to why physics decided to skip on me and let me have this magical painful moment

*Reddit user “Mittinmang” (2019, used with permission)*

### **Abstract**

In this chapter we present two linked experiments exploring the relationship between emotional arousal and time, with particular reference to how individual differences in interoceptive ability (the awareness of one’s physical state) influence this relationship. The first experiment, using supra-second stimuli in a novel paradigm designed to create a sustained state of emotional arousal, finds no influence of arousal on time but is subject to a number of limitations in this finding. The second addresses the same question with a more established sub-second paradigm and finds the expected relationship where those with higher interoceptive sensitivity demonstrate a greater effect of arousal upon time. We discuss what the combined results tell us about time perception and arousal as well as the methodological implications for future research.

## **Introduction**

### *Arousal and time*

In a novel experiment Stetson et al. (2007) dropped participants 36 metres into a net. The participants reported time dilation, in that their estimate of how long they were falling for was significantly longer than that based on seeing someone else do it. Prior to the drop, each participant performed a task where they had to identify a pair of rapidly alternating digits presented via a wrist worn watch-like device. The rate of alternation was increased and a threshold was determined for each person when they could not correctly identify the digits due to the rate of alternation. During the drop digits were presented just faster than this threshold with the hypothesis that, if perceptual rate actually increased, participants would now be able to discern what was presented and report this after the experience. They found no speeding up of actual (visual) perception, which suggests the perceived time dilation relates to how the duration was encoded and is independent from the rate of sensory input. There may, however, be some doubts about the reliability of this particular method. For example, it was reported that all participants, except one who was excluded, “kept their eyes open during at least part of the freefall” (Stetson et al., 2007, p. 2), implying that most closed their eyes at some point. One can easily imagine other differences, for example in terms of attention, when falling in comparison to observing others, or performing in the lab.

Nonetheless, on the surface, this makes the examination of arousal and time an interesting counterpoint to the other experiments reported in this thesis; while they focus on the influence of low-level temporal sensory integration and simple stimuli on



perceived time, this relates to changes in encoding time related to the emotional content of the duration. Although these seem quite different, the two approaches may theoretically have a lot in common. As we will see below, Craig's (2009a) theory of global emotional moments is based on the posterior insula cortex acting as primary sensory cortex for the internal state of the body and as such both avenues of research are concerned with the integration of primary sensory material in creating a subjective sense of time. Beyond this, Craig's theory suggests a possible mechanism for the further integration of both types of information into a unitary momentary percept (see general discussion chapter).

Gil and Droit-Volet (2012) demonstrated a similar time dilation to that of (Stetson et al., 2007), in less dramatic fashion, using images from the International Affective Picture System (Bradley & Lang, 1994; Lang et al., 1997). They selected sets of three pictures to stimulate high and low arousal disgust and sadness, high arousal fear and neutral images for control. Pictures were presented for short durations (either within 200-800ms or 400-1600ms) and participants were asked to provide estimations of duration in ms. The general results indicated time dilation (longer estimates) for emotional stimuli, with the effect being stronger for high arousal stimuli. The results also showed some variations depending on emotional content, in particular disgust-inducing images produced a stronger effect than fear inducing images. Looking at the specifics of their results there are some points where these relationships are less clear. Comparing high and low arousal disgust, and neutral pictures, in the 200-800ms condition, they find that high arousal disgust is greater than low arousal disgust, but there does not appear to be a significant difference between low arousal disgust and neutral timing. In the 400-1600ms condition the pattern is similar but no differences are significant. When they repeat this contrast in

experiment 2 with a 100-400ms range the pattern remains similar with no significant difference between the low arousal and neutral conditions. From this we might suggest that, in the case of disgust, the difference between neutral and high arousal stimuli is established but not a difference between neutral and low arousal.

Higher arousal has also been seen to lengthen timing judgements in a variety of other forms including pain (Ogden et al., 2015), emotional faces (Gil & Droit-Volet, 2011), physical arousal (Vercruyssen et al., 1989), threat of electric shock (Cahoon, 1969), emotive sounds (Mella, Conty, & Pouthas, 2011; Noulhiane, Mella, Samson, Ragot, & Pouthas, 2007), and emotive pictures (Angrilli et al., 1997). While there are various theories of how time is perceived and modulated, the effect of emotion is commonly explained as a speeding up of some underlying factor (e.g. a “clock” or “pacemaker”; (see Droit-Volet & Meck, 2007 for a review) and which may also be modulated by other factors such as click trains (Wearden, Williams, & Jones, 2017) or intensity (Matthews et al., 2011).

It is worth noting that emotional valance also plays a role as low arousal negative emotional stimuli and high arousal positive pictures produce short estimates relative to longer estimates for high arousal negative pictures and low arousal positive pictures (Angrilli et al., 1997; Gil, Rousset, & Droit-Volet, 2009). The authors argue that this is attributable to attention being more important for low arousal stimuli where negative stimuli capture attention more and thus distract from timing. Attention is acknowledged as a key element in timing and is central to the cognitive attentional gate model (Block & Zakay, 2008; Zakay & Block, 1996); wherein typically, diverting attention from the timing task reduces the perceived duration (Block et al., 2018), theoretically by influencing the switch element so that less pulses are recorded. There is also evidence that a delay in the onset of timing (generally because attention

is orientated elsewhere), or ‘closing the switch’, reduces the perceived duration as, again, less pulses are recorded (Droit-Volet, 2003). Onset delay is often disassociated from changes in the putative pacemaker via fitting slopes where the intercept represents the delay in commencing timing and the slope represents the rate of the pacemaker (Gil & Droit-Volet, 2012).

### *Arousal and interoception*

Interoception is the ability to detect subtle changes within one’s own body. Experimentally, this is often measured via tasks where participants in some way detect their own heartbeats but conceptually, interoception also includes sensing systems such as the skin, joints, internal organs and indeed the physiological condition of the whole body (Craig, 2002). With regards to the processing of emotion, interoception is vital to the understanding of the interaction between the cognitive sense of emotion, conscious “feelings”, and our physiological state.

The oldest psychological conception of this relationship is the James-Lange theory (James, 1890) that the conscious perception of emotion is derived from the physiological response to stimuli which the brain interprets as emotion. While this theory has been modified over the intervening years, the essence is still incorporated into modern theory of emotion, in particular Craig’s (2009) theory of ‘emotional moments’. This theory characterises awareness itself as a series of ‘global emotional moments’ which are built up in the insula cortex. These originate in an interoceptive representation of the body in the posterior insula cortex and progressively incorporate salient homeostatic, environmental, hedonic, motivational, social and cognitive factors in sequence progressing from posterior to anterior insula cortex (AIC). This produces a representation of the self for that particular moment in the anterior insula

cortex. This theory originated with the discovery of the lamina I spino-thalamocortical pathway that essentially projects a representation of the body's state directly to the posterior insular cortex (Craig, 2002) and has found significant support, primarily from imaging studies that identify AIC activation in relation to various aspects of consciousness (Craig, 2009b) including heart-beat awareness.

Dunn et al. (2010) provides evidence of the role of interoceptive ability in translating bodily arousal into emotional arousal. They applied the Schandry heartbeat-perception task (Schandry, 1981) as a measure of interoception. The task involves the participant attempting to count their heartbeats over a defined period while their actual heartbeats are recorded; the agreement, or lack thereof, between the two measures putatively indicates the participants' sensitivity to their own bodily signals. They also recorded heart rate deceleration and subjective arousal and valence in participants in response to a series of images from the IAPS database (Lang, Greenwald, Bradley, & Hamm, 1993). The key finding is that those with better interoceptive accuracy had a much stronger relationship between their HR response and their subjective rating of arousal, in particular showing a smaller deceleration for high arousal pictures than other subjects, and a greater deceleration for low arousal pictures. This was true only for arousal and not valence, which suggests that our primary focus in addressing the influence on timing should also be on arousal.

With regards to time perception, Craig (2009a) suggests his global emotional moment as an element of an internal clock, perhaps somewhat analogous to the pacemaker mentioned above. This theory, coherent with fMRI findings that support a role for the AIC in timing behaviour (Lake, 2016; Wittmann, 2009, 2013; Wittmann, Van Wassenhove, Craig, & Paulus, 2010) has the advantage that it corresponds with the data on time perception and arousal in that it is innately subjective and adaptive to

the emotional content of the moment. Considering a GEM as a finite unit of information, Craig describes them as filling more quickly when there is a great deal of information that is salient for survival (e.g. in the context of high arousal) ). From this we could postulate that for those with a higher interoceptive awareness, more salient information would accumulate, comparative to poor interoceptors, meaning GEMs filling and passing more quickly, as if speeding up a pacemaker, thus relatively dilating subjective time.

While interoception has been mostly estimated via variations on heartbeat perception, there is evidence that a sub-clinical condition called Alexithymia, (typically measured by the Toronto Alexithymia scale; TAS), relates to interoception scores (Brewer, Cook, & Bird, 2016), including in non-heartbeat related measures (Murphy, Catmur, & Bird, 2018). There is evidence for a biological association between alexithymia and interoception which is seen in covariance with glutamate concentration in the left insula (Ernst et al., 2013) and where damage to the anterior insula results in acquired alexithymia (Hogeveen, Bird, Chau, Krueger, & Grafman, 2016). Alexithymia is a sub-clinical condition which is characterised by difficulties identifying and describing emotion in the self (Brewer et al., 2016) and despite the evidence above, the direct association with interoception remains contended, particularly in relation to cardiac perception (Murphy, Brewer, Hobson, Catmur, & Bird, 2018; Zamariola, Maurage, Luminet, & Corneille, 2018). If alexithymia should be related to both interoceptive ability and time judgements then this would both support the association between the TAS and interoception and provide a potential new avenue for investigating time judgements and interoception without the need to record biological measures. To this end the TAS is included, in addition to interoception, in experiment three below.

*Time and interoception*

Having discussed the relationship between time and arousal, and arousal and interoception, the question naturally arises as to whether there is any evidence of a relationship between time and interoceptive ability. Meissner and Wittmann (2011) found support for such a relationship in a study where participants reproduced 8, 14 and 20s durations while cardiac, respiratory and skin conductance information was recorded. The accuracy of reproduction correlated with both cardiac slowing during encoding and interoception scores (as measured by the Schandry task). While similar (though less significant) patterns of cardiac slowing were observed during the reproduction phase, it is unclear to what extent this finding generalises to non-reproduction paradigms (i.e., is it a general mechanism or one that is recruited solely when one needs to encode a specific interval?). Given that other work has found that angry faces do not cause time overestimation in generalisation or reproduction tasks (Gil & Droit-Volet, 2011), this is an important consideration. It is also worth noting that Meissner and Wittmann's analysis did not seek an interaction of interoceptive ability with cardiac slowing in predicting timing behaviour. Further evidence relates heart-rate synchronisation and interval reproduction (Pollatos, Yeldesbay, et al., 2014), though this was not consistent across the durations used (which varied from 0.5 to 40s) and interoceptive accuracy was only associated with the level of synchronisation at 2s. Other studies find some relationship between HR and time perception but do not consider interoception directly (e.g. Cellini et al., 2015).

Given much of the above, it would be tempting to relate time perception strongly to heart rate; indeed, Craig proposes heart rate as a possible temporal

regulator for emotional moments. Some caution is required however, as a study designed to independently vary heart rate and experienced arousal, via exercise and the holding of breath, found that experienced arousal related to time dilation whereas heart-rate itself does not (Schwarz et al., 2013), though again interoceptive ability was not measured.

Further evidence comes from two studies that have found relationships between embodied emotion and timing by using novel methods rather than attempting to measure interoception directly. One showed that holding a pen in the mouth, preventing automatic facial mimicry, removed the tendency to overestimate the period of time that emotional faces were presented for (Effron, Niedenthal, Gil, & Droit-Volet, 2006), though one might question the other effects of such a manipulation (on attention for example). Another showed participants emotive film clips and asked participants to focus on either their interoceptive state or details of the clip and found greater time dilation for fear and constriction for amusement, in the interoceptive focus group (Pollatos, Laubrock, et al., 2014).

#### *Hypothesis and experiments*

In summary, the evidence discussed above suggests a strong link between physical arousal, experienced arousal and time-dilation. From anatomical evidence, we know that information about the state of the body is projected directly to the insular cortex, which also appears to be heavily involved with both emotion and time, whilst behavioural evidence supports the idea that individual differences in sensitivity to bodily signals influences both experience of emotion and experience of time. Therefore, the purpose of the current study is to determine whether individual interoceptive ability influences the effect of arousal upon timing. If such an effect is

found, it would support both theories of embodied cognition and emotional arousal, additionally providing evidence that the influence on time is specifically attributable to arousal rather than potentially confounding factors such as attention.

The two experiments presented here both utilise still images from the IAPS database to elicit emotional arousal (as these are proven and scored emotional stimuli) and the Schandry heartbeat perception task (Ehlers & Breuer, 1992; Schandry, 1981) to measure interoceptive accuracy. As in previous studies, we would expect high-arousal stimuli to increase physiological arousal and dilate experienced duration and we hypothesise that this latter effect will be moderated by individual differences in interoception scores. In the first experiment it is anticipated that we will also replicate a relationship between alexithymia and interoception scores (Brewer et al., 2016; Murphy, Brewer, et al., 2018) and, assuming this is successful, will test whether alexithymia also mediates the relationship between arousal and timing.

While both experiments utilise similar materials to address the same hypothesis, there are significant differences. The first utilises a novel method where we attempt to produce a relatively continuous sense of emotional arousal by blocking stimuli into high and low arousal blocks and interspacing them with both time estimation and production tasks (at supra-second durations) and arousal judgements. The Toronto Alexithymia Scale (TAS) is also employed in this experiment as a scale putatively related to interoception. Finally EEG was recorded from a single occipital electrode during this experiment. This was done with the aim of clarifying the inconclusive results from chapter two in a larger sample. The recording of EEG should not influence any of the other tasks used here. The second experiment, addressing potential issues with the design, is limited to only estimations and uses



emotional stimuli as target stimuli (at sub-second durations) in a more conventional pseudo-random order.

### **Experiment 3**

#### **Method**

##### *Participants*

From 56 participants 7 were removed from the analysis due to technical issues / data loss (3), non-completion (1) or extreme scores implying lack of adherence to task demands (3). Of the remaining 49 participants, 33 were female and 45 right-handed with a mean age of 19.5 (SD=2.42). Participants took part for course credit as part of their psychology undergraduate degree.

##### *Procedure and tests*

Prior to commencing, participants were informed as to the nature of the study, in particular the distressing nature of some of the pictures used, and gave informed consent, including the understanding that they could leave at any time without penalty.

Participants first completed the 20 item Toronto Alexithymia Scale (TAS) (Bagby, Taylor, & Parker, 1994). All items are rated on a scale of 1-5 and higher overall scores represent more severe traits. From this was derived an overall alexithymia score and a score for each of the three subscales: difficulty describing feelings, difficulty identifying feelings and externally-orientated thinking.

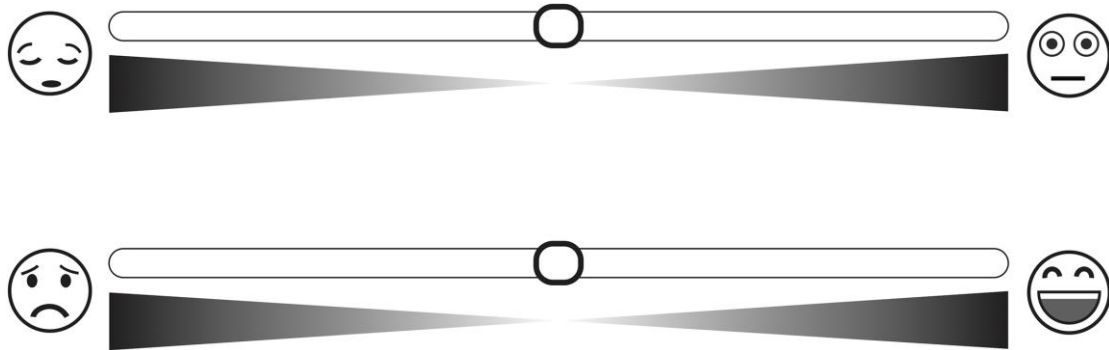
In the body of the experiment participants completed two forms of timing task (estimation and production). In estimation tasks, they were shown an IAPS image for 2 seconds, followed by a fixation cross for 1 second, then a white square (200x200 pixels) for the target duration. The target durations consisted of 5, 6, 7, 8, 9, and 10s. They were asked to estimate in seconds (with up to 2 dp) how long the square had been on the screen by typing in a number. In production tasks, the procedure was identical except that instead of a square, a number followed the fixation cross.

Starting in their own time participants were asked to hold down the spacebar for that many seconds. After releasing the spacebar, the number disappeared and the next iteration began.

High arousal images were selected primarily on the IAPS arousal rating but were also limited to low valance images associated with fear or disgust; these mostly consisted of images including violence or injury. The mean IAPS arousal score for these images was 6.71 (SD=2.14) and valance 2.31 (SD=1.51). Low arousal images were mostly animals and had a mean arousal score of 2.73 (SD=2.17) and a relatively positive valance of 6.63 (SD=2.14). All IAPS scores are scored on a 9-point scale, where 1 is low for that dimension and 9 is high. To avoid repetition effects, no images were seen by participants more than once, so a total of 72 pictures were presented; these were counterbalanced across timing tasks so that no one set of pictures was associated with one task.

Every three timing trials, participants were asked to use two sliders to indicate how the picture made them feel: one representing arousal and the other valance. Affective Sliders (AS) were taken from Betella and Verschure (2016) who established these as an alternative to the Self-Assessment Manikin (SAM). Each slider consisted of a marker on a line that could be slid back and forth using the mouse. An emoticon at each end of each slider indicated the relevant emotional state (see figure 4.1). To ensure participants were clear on each state, training included reading aloud 4 words for each emoticon. These were taken from the word pairs shown to load onto the arousal and valance factors by Bradley and Lang (1994). For example, “stimulated”, “excited”, “jittery” and “wide awake” were chosen for high arousal, and their inverse for low arousal. This was followed by a set of three neutral (landscape) pictures to

check understanding. For each picture this generated a score on a 1000-point scale, where 0 related to entirely negative valance or arousal.



*Figure. 4.1 Affective sliders taken from Betella and Verschure (2016)*

The procedure was structured so that the order was always an estimation block followed by a production block, both within the same arousal condition, followed by a brief break, before another estimation and production block, both within the opposing arousal condition to the first blocks. Therefore, the only counterbalancing was whether participants experienced the high or low arousal condition first. Estimation and production blocks each included 18 trials for a total of 72 trials overall.

Interoceptive ability was assessed via the Schandry heartbeat perception task (Ehlers & Breuer, 1992; Schandry, 1981). This was the last element in each case to try and avoid any influence on how participants performed the timing task.

Participants were given six trials, two each of three durations (25s, 30s and 40s) with onset and offset marked by beeps. They were asked to count their heart beats as accurately as possible during this period. Heart rate was collected using a pulse oximeter via the NeXus 10 system (MindMedia CV, The Netherlands) to allow an

accuracy score to be calculated by comparing actual and estimated numbers of beats ( $1 - (|\text{actual} - \text{estimated}| / \text{actual})$ ).

Following the procedure participants were provided with full information as to the nature of the study and verbally debriefed to check they were not overly affected by the content. While some participants reported some discomfort during viewing some images (which is to be expected) none reported feeling significant distress after the conclusion of the experiment. Information for support services, and contact details for the experimenter, were provided to all participants in case of on-going distress.

## **Results**

### *Arousal*

Mean arousal ratings showed that low arousal stimuli were, on average, rated lower than the neutral starting position of 500 on the slider ( $M=443.50$   $SD=148.03$ ) while the high arousal was rated as more arousing ( $M=673.71$   $SD=168.37$ ). The difference between high and low ratings is significant,  $t(48) = -6.1$ ,  $p < .001$ . Valance scores between the low ( $M=663.03$ ,  $SD=110.86$ ) and high ( $M=218.89$ ,  $SD=105.68$ ) arousal conditions are also significantly different,  $t(48) = 17.25$ ,  $p < .001$ , in the expected direction (high arousal was associated with low valance in the images chosen). This supports the effectiveness of the manipulation in that the high arousal condition was significantly more arousing, with lower valance, than the low arousal condition.

### *Time and Arousal*

Figure 4.2 shows timing performance at each target duration. A three-way repeated measures ANOVA was carried out to assess the effect of arousal (high vs low), task-type (estimation vs production) and target duration (5, 6, 7, 8, 9, 10

seconds) on timing performance. There was a significant main effect of target duration ( $F_{(5,235)}=1651.60, p<.001$ ), as expected, and a significant interaction of task and time ( $F_{(5,235)}=7.33, p<.001$ ) though no main effect of task ( $F_{(1,47)}=2.82, p=0.10$ ).

Inspection of the means suggests that productions were longer than estimations for longer target durations however there is no significant difference between the tasks at 10s target duration when collapsed across arousal levels ( $t_{(48)}=1.49, p=.14$ ). Finally there is no main effect of arousal ( $F_{(1,47)}=2.0, p=.17$ ) and no significant interactions with arousal ( $P_s>.05$ ). This suggests that the arousal manipulation did not have a significant effect on time estimation or production.

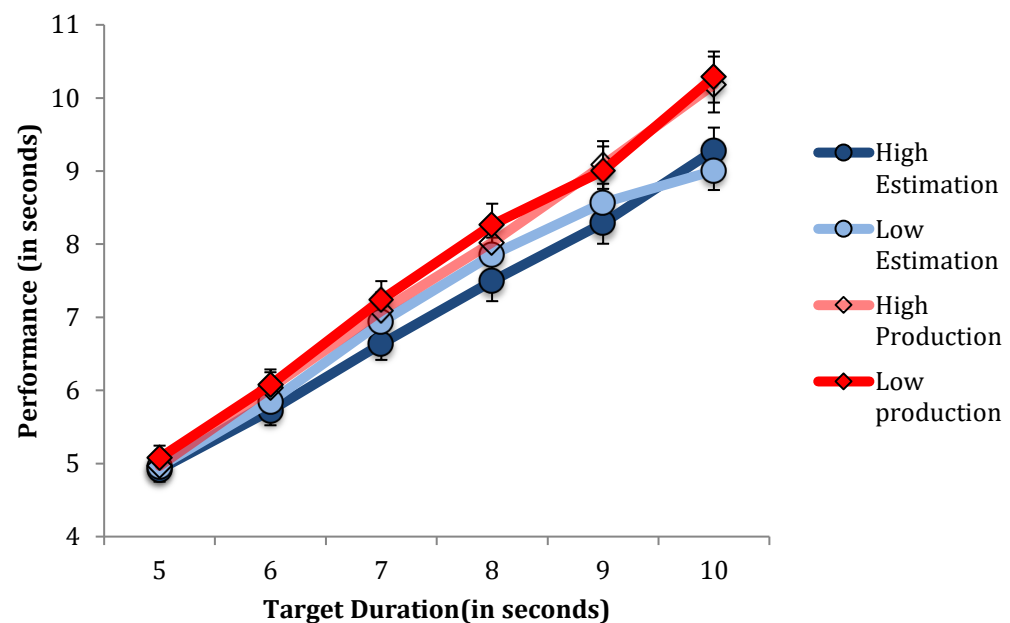


Figure 4.2: Time performance for both tasks (production vs estimation) at both levels of arousal (high vs low) at all target durations. No significant differences were observed.

*Interoception*

The mean score on the Schandry heart beat task was .54 ( $SD=.17$ ), which is low for this test, and only 1 person exceeded .85, which is often used as the criteria for a good interoceptor.

As it is possible an effect of arousal might exist for relatively good interoceptors while not being evident overall, a regression analysis was carried out for each task. The difference between high and low arousal ratings (means centred) was entered as a predictor variable for the difference in timing between low and high arousal conditions, with interoception scores (means centred) as the moderator. Models were not significant for either production,  $F_{(3,45)}=1.41, p=.25$ , or estimation,  $F_{(3,45)}=.54, p=.66$ . suggesting that interoception did not significantly moderate the relationship between arousal and time.

*Interoception and Alexithymia*

The mean TAS score was 46.16 ( $SD=7.62$ ). 1 participant scored equal to or over 61, which indicates alexithymia, while 11 participants scored between 52 and 60, which is considered borderline.

It was expected that the Toronto Alexithymia Scale would relate to interoception scores, however in this case neither the TAS nor its subscales significantly correlated with interoception ( $ps>.05$ ).

**Interim discussion**

The results of the above experiment show that the stimuli were effective in terms of influencing subjective arousal but had no significant effect on either produced or estimated time. Thus, we must conclude that in this paradigm the arousal conditions did not influence subjective time. This may provide evidence for some

limitations on the effects of arousal, however we must also consider that other limitations of this particular experimental procedure may have contributed to this null result.

Firstly, we should consider the limitations of the timing task employed in this study. Participants were asked to estimate and produce durations between 5 and 10 seconds which are substantially longer than the sub-second durations often employed when considering arousal effects (see Droit-Volet et al., 2013). Contributing to this issue is the likelihood that participants used chronometric counting, which reduces variability (Grondin et al., 2004), though it was hoped that, as you would still expect variation in the counted unit to reflect individual rhythms (Glicksohn et al., 2009), there would still be an effect.

A second concern is that arousal effects can be fairly short-lived (Droit-Volet & Meck, 2007) and while Schwarz et al. (2013) found an arousal effect over longer durations they maintained the physical arousal throughout. Although participants were affected by the emotional stimuli it is possible that this did not transfer to the timing task as the emotional stimuli were not the target. Additionally there is a possible issue of attention as there is evidence that applying emotional content before the encoding or reproduction of a duration distracts the participant resulting in shorter, not longer reproductions (Lui, Penney, & Schirmer, 2011), although we did not use reproduction, as reproduction is not typically the best method for finding standard arousal effects (Gil & Droit-Volet, 2011), it is possible that any effect of arousal was diminished as the images distracted from the stimuli.

In relation to this we concentrated on choosing stimuli to maximise the difference in arousal between blocks, however this resulted in a lack of proper control for valance, which was also different between the two blocks. As some studies have



shown an interaction of valence and arousal in timing (Angrilli et al., 1997) this may have been a confound. This is addressed in the second experiment by the inclusion of a properly neutral control condition and using a more restricted choice of images to focus on high and low arousal disgust.

A practical limitation of this experiment was that we were only able to utilise manual triggers with the nexus 10 system meaning that we were not able to extrapolate HR change for each trial. The HR data was also not as clear as would be hoped, this may be partly attributable to a fault that became evident with a pulse oximeter that had to be replaced in the course of testing. This is addressed below by instead using an electrocardiogram to produce clearer data with more accurate triggers.

In this experiment, the sample did appear to be biased towards poor interoceptors, although it is possible that the technical issues mentioned above contributed to this. As such it is possible that the lack of findings may be partially attributable to the majority of our participants being poor interoceptors and thus having a reduced effect of arousal.

Experiment B below is designed, based partially on Gil and Droit-Volet (2012), to test the same hypothesis as above while avoiding the identified limitations. In particular, switching to a shorter set of durations and timing the emotional stimuli itself minimises issues around counting and attention. We also include extra measures, BMI and blood pressure, to control for confounds in the interoception task as per Murphy, Brewer, et al. (2018).

## **Experiment 4**

### **Method**

#### *Participants*

60 participants were recruited from the psychology volunteer pool at the University of Essex. Participants received either 1 course credit or £6 for taking part. Prior to analysis, 5 participants were removed due to hardware issues leading to incomplete data. Of the remaining 55 participants 34 were female and 21 male with a mean age of 21 years ( $SD=2.41$ ), 50 participants were right handed. Participants who had participated in a previous version of this experiment were not eligible to take part.

Informed consent, including the understanding that emotive images were involved, was given prior to commencement. All participants were seated in a quiet laboratory with a screen between them and the experimenter. They were seated comfortably in front of a 24" monitor at a distance of 60cm. All participants wore noise-cancelling headphones throughout the experiment. All stimuli were presented using psychophysics toolbox (Brainard & Vision, 1997; Kleiner et al., 2007; Pelli, 1997) in Matlab™ 2014a (TheMathworks, Inc., Natick, MA, USA)). ECG was recorded throughout via a biopac MP160 using a standard three lead triangle configuration. Height and weight were recorded at the start of the experiment (measured or reported by participant) as was blood pressure (Omron 705-CP2 blood pressure monitor). Rate of progress was user defined and regular breaks were given. A verbal and written debrief was provided.

*Tasks*

**Picture Timing task:** The same 9 pictures from the International Affective Picture Database (Lang et al., 1993) as used in Gil & Droit-Volet (2012) were chosen; this was 3 high arousal disgust pictures (3000, 3110, 9405), 3 low arousal disgust pictures (9290, 9330, 9390) and 3 neutral (7010, 7020, 7175). Each picture was displayed at 5 target durations (200ms increasing by 200 increments up to 1000ms) within each of three blocks, so 15 repetitions of each picture and 135 trials overall. Order was pseudo-randomised within each block (in all cases pseudo-randomisation was via the matlab rng function seeded to participant number).

Each presentation consisted of a central fixation cross for 1s followed by the picture for the target duration. Following this, participants were asked to report their estimate of the picture's duration in ms. They were reminded at each trial of the upper (1500ms) and lower (50ms) limits for their responses; responses outside this window were removed and participants reminded of this limit.

Prior to the main task commencing, each participant had brief training, to familiarise themselves with the task and response mechanism, consisting of 6 trials as above, except with a white square in place of the picture and only using 2 target durations of 100ms and 1100ms.

**Picture Rating Task:** Following the timing task participants were shown the same 9 pictures one more time in a pseudo-randomised order. They were asked to use affective sliders to make arousal and valence judgements for each picture, exactly as in experiment 3 above.

**Interoception task:** Interoceptive ability was assessed after the other trials via the Schandry heartbeat perception task (Ehlers, Breuer, 1992; Schandry, 1982).

Participants were given six trials, each of one of three durations (2 each of 25s, 30s

and 40s) with onset and offset marked by beeps. They were asked to count their heart beats as accurately as possible during this period. Their actual heartbeats were recorded via ECG to allow an accuracy score to be calculated for each ( $1 - (|\text{actual} - \text{estimated}| / \text{actual})$ ). This task was repeated with participants counting seconds instead as a control, a timing accuracy score being calculated in the same way as the interoception score. As interoception has been associated with obesity and differences in blood pressure (Herbert, Blechert, Hautzinger, Matthias, & Herbert, 2013; Herbert & Pollatos, 2014; O'Brien, Reid, & Jones, 1998) both BMI and blood pressure were also recorded for each participant.

**Heartbeat Deflection:** In addition to the interoception task, ECG data was recorded throughout and used to calculate heart beat deflection in relation to each image. A deceleration in heart rate is associated with the onset of picture stimuli and has been found to be more pronounced for unpleasant (high arousal, low valence) images (Pollatos, Herbert, Matthias, & Schandry, 2007). Individual trials were identified and those showing excess noise (more than  $3SD$  from mean) were automatically removed. The ECG baseline was measured from 1 second before the image onset up to the onset and the heart beat reaction from 1.5 to 3 seconds following presentation. This was shown to be appropriate as average heartbeat was mapped from 1s before stimulus to 5s post stimulus and shows the lowest values within the chosen window. Inter-beat intervals were computed for each sample and the HR change (Heartbeat Deflection) estimated as the difference between the baseline and reaction samples. The resulting heartbeat deflection was then averaged for each condition within each individual.

*Analysis*

In this experiment, our primary aim was to look at individual differences in the effect of arousal on duration, and to test whether this relationship is moderated by individual differences in interoceptive accuracy. To facilitate this, it was necessary to produce scores for each participant to represent the effect of arousal on time. This might have been achieved by calculating the differentials of the mean estimated durations for the different emotion conditions but this is a relatively crude measure as the differences between conditions may change as the target duration increases. In our data, we see that there is very little difference at 200ms but most difference at 1000ms, and thus simply averaging across these would minimise individual differences in the data. The solution we adopted was to account for changes in judgement across durations by calculating a timing slope (via least squares regression) for each participant for each of the three arousal levels, which is a common approach in studies of this nature (Gil & Droit-Volet, 2012; Ogden et al., 2015). A benefit of this analysis is that it gives an intercept and slope for each condition; theoretically these are useful in analysing time perception as the intercept relates to delays in the onset of timing, while changes in the slope indicate changes in the “pacemaker” or underlying substrate of timing (Gil & Droit-Volet, 2012), which is primarily of interest for our purposes. Before analysing slopes we performed a repeated measures ANOVA on the averaged estimations to confirm there was a clear effect of arousal present. Then, to parsimoniously estimate the effect of arousal for each individual, we took the differential between the timing slopes. In this case, there were not significant differences between the neutral and low arousal conditions (see results below) and therefore these were collapsed to give a single slope which is subtracted from the high

arousal slope to give each participant a single score representing the effect of arousal on time.

In the case of arousal and valence scores, we first calculated a mean rating for high, low and neutral pictures within each participant which were used to confirm that there was a general effect of arousal on subjective arousal ratings. For the purposes of comparison with other measures, we averaged these to produce one overall score for arousal and one for valence for each participant, after the method of Dunn et al. (2010).

By the above methods, we arrived at three scores for each participant: the difference between the timing slopes, the average arousal rating and interoceptive accuracy. We then entered these into a moderated regression, which allows us to test whether the relationship between arousal ratings and estimations varied depending on interoceptive ability, thus testing our hypothesis.

## Results

*Table 4.1 Mean (SD) arousal ratings, valance ratings, Heart Rate response and timing for each picture condition. Arousal and valence results are on a 1000 point scale with 500 as the neutral midpoint.*

Arousal level	Time Estimate (ms)	Slope	Intercept	Arousal	Valance	HR response
High Arousal Disgust	510 (222)	.92 (.44)	-40.16 (253.64)	735 (204)	137 (130)	-2.67 (1.96)
Low Arousal Disgust	443 (206)	.81 (.35)	-40.7 (160.52)	542 (160)	312 (120)	-2.30 (2.23)
Neutral	451 (196)	.80 (.36)	-29.0 (201.21)	350 (154)	514 (108)	-2.12 (1.87)

*Pictures influence arousal*

High arousal disgust pictures were rated as significantly more arousing than low arousal disgust pictures,  $t_{(54)}=11.30, p<.001$ , which were more arousing than neutral pictures,  $t_{(54)}=6.89, p<.001$ . It should be noted that 500 represents no arousal effect (the middle of the line where the indicator is before movement) so the low arousal score is relatively close to neutral whereas high arousal stimuli were positively arousing and neutral pictures were judged as relatively relaxing.

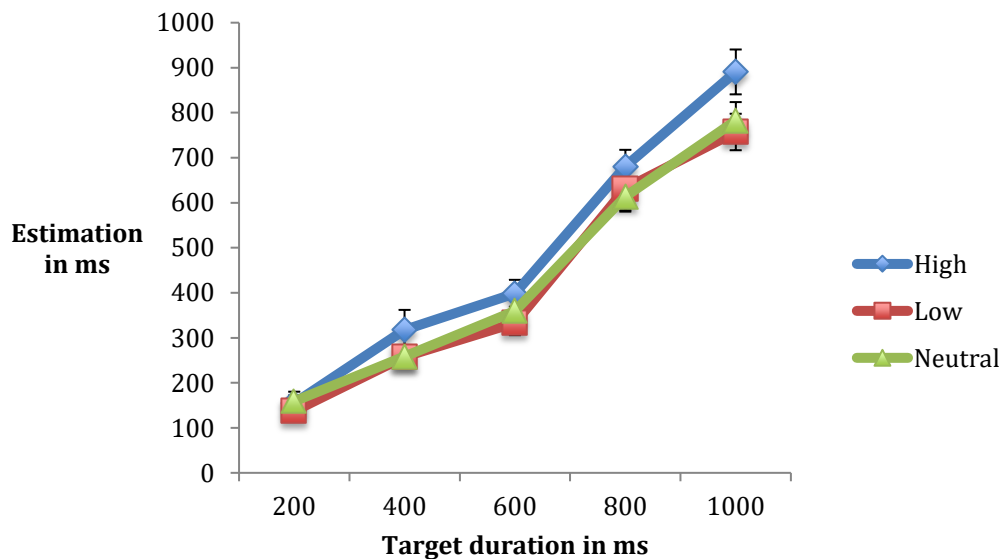
To ensure that the stimuli were producing a genuine physiological response we averaged, across all trial presentations, the change in heart rate for high arousal, low arousal and neutral stimuli (not including the single round of rating trials) and compared these via paired sample t-test. We found that the high arousal stimuli ( $M=-2.67, SD=1.96$ ) produce a significantly greater heart rate deceleration than neutral stimuli ( $M=2.12, SD=1.96$ );  $t_{(54)}=-2.40, p=.02$ . While low arousal stimuli ( $M=-2.30, SD=2.23$ ) produce a lesser deceleration than high arousal, this does not reach significance;  $t_{(54)}=-1.69, p=0.1$ . Collectively this suggests that the pattern of heartbeat change was as expected (high>low>neutral) but is not as clearly differentiated as it might be.

*Effect of arousal on time perception*

A 2-way repeated measures ANOVA shows significant main effects of target duration ( $F_{(4,216)}=252.27, p<.001$ ) and arousal ( $F_{(2,108)}=17.47, p<.001$ ). The interaction does not quite achieve significance ( $F_{(8,432)}= 1.88, p=.06$ ). Examination of the means suggests that the effect of arousal is driven by relatively long time estimates in the high arousal condition (see figure 4.3) while the neutral and low arousal conditions do not appear to be significantly different. This is confirmed by paired-sample t-tests

showing a significant difference between mean high arousal timings ( $M=510$ ,  $SD=222.14$ ) and mean low arousal timings ( $M=443.53$ ,  $SD=206.77$ ),  $t_{(54)}=-4.65$ ,  $p<.001$ , but not mean low arousal timings and mean neutral timings ( $M=451.8$ ,  $SD=196.42$ );  $t_{(54)}=-.96$ ,  $p=.34$ .

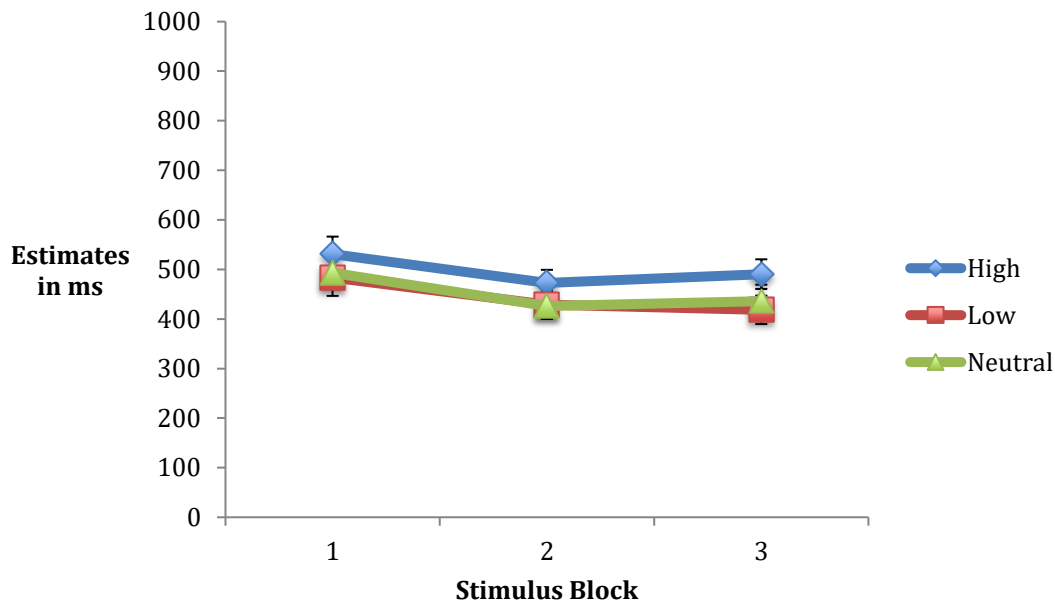
To check that the effect of arousal did not diminish with repetition of the same pictures, we compared (with repeated measures ANOVA) the mean time estimates for each level of arousal (averaged across images) for each of the three blocks. While there was a significant main effect of arousal ( $F_{(2,108)}=12.48$ ,  $p<.001$ ), and a significant main effect of block ( $F_{(2,108)}=6.27$ ,  $p<.01$ ), there was no interaction ( $F_{(2,108)}=.41$ ,  $p=.79$ ), suggesting that although the timing estimates decrease with repetition the effect of arousal is consistent (figure 4.4).



*F*

*Figure 4.3: Mean duration estimations for each target duration for high arousal, low arousal and neutral pictures. Error bars show standard error of the mean.*





*Figure 4.4: Mean duration estimations for each experimental block for high arousal, low arousal and neutral pictures. Error bars show standard error of the mean.*

To facilitate further comparison, timing slopes were calculated for each condition (table 4.1). We tested (with Wilcoxon tests) whether there were significant differences between the timing slopes for different conditions. The slopes for high arousal were significantly different from those of the low arousal condition ( $Z=-2.60$ ,  $p<.01$ ), indicating that high arousal had a larger increase in estimate for each increase in target duration. The low arousal slopes were not significantly different from the neutral condition ( $Z=0.62$ ,  $p=.53$ ). In the case of intercepts, they were very similar for high and low arousal ( $Z=-.24$ ,  $p=.81$ ) and not significantly different between low arousal and neutral ( $Z=-0.68$ ,  $p=.50$ ). This supports the expectation that we would find an arousal effect in the timing slopes and not the intercepts. As they were very

similar, the low arousal disgust and neutral slopes were collapsed and subtracted from the high arousal slope giving each participant a single slope-difference score.

*Interoception, arousal and timing*

The mean interoception score was .77 ( $SD=.20$ ) with a relatively high proportion (24 individuals) above the .85 score associated with being a good interoceptor.

Assessing correlations, we find that average arousal ratings and timing slope difference scores are positively correlated,  $r=.31$ ,  $p=.02$ , but no other comparisons are significant, including, notably, that interoception is unrelated to valance, arousal, timing or ratings ( $ps>.05$ ).

To examine whether the relationship between time estimates (slope difference; the difference in the slope between high and low/neutral arousal conditions) and subjective arousal ratings is moderated by interoceptive ability we ran a moderated regression utilizing PROCESS (model 1) in SPSS (Hayes, 2013). The overall model was significant,  $R^2 = .27$ ,  $F_{(3,51)}=6.27$ ,  $p=.001$ . To avoid multicollinearity issues, the average ratings and interoception scores were means centred. The average arousal rating is a significant predictor of the difference between timing slopes,  $b=.001$ ,  $t_{(51)}=3.14$ ,  $p<.01$ , but interoception is not,  $b=.10$ ,  $t_{(51)}=.52$ ,  $p=.60$ . Including the interaction between interoception and arousal ratings, we find this accounts for significantly more variance,  $\Delta R^2 = .17$ ,  $\Delta F_{(1, 51)} = 12.09$ ,  $p = .001$ ,  $b=.005$ ,  $t_{(51)}=3.477$ ,  $p<.01$ . Considering simple effects (which might also be called simple slopes; the relationship between arousal rating and time estimates at different levels of interoception; see figure 4.5), we find that for poor interoceptors (1SD below the mean) there is essentially no effect of arousal rating on time estimates,  $b=.000$ ,

$t_{(50)}=.017, p=.99$ . There is however a significant effect for average interoceptors ,  $b=.001, t_{(50)}=3.14, p<.01$ , and a stronger effect for interoceptors, one SD above the mean,  $b=.002, t_{(50)}=4.31, p<.001$ . Collectively this represents that for good interoceptors, a higher overall arousal rating relates to a bigger difference in timing between High arousal and low/neutral arousal slopes, thus supporting the hypothesis.

Of our sample, only 4 individuals reported knowing their own resting heart rate. As their interoception scores were .69, .79, .55 and .77, compared to a mean of .77 ( $SD=.20$ ), these do not appear to be particularly anomalous and so this was not considered further in this analysis. BMI score correlates significantly, negatively, with interoception ( $R^2=-.287, p=.03$ ) and positively with systolic blood pressure ( $R^2=.388, p<0.01$ ). This suggests that a higher BMI relates to poorer interoception and higher blood pressure, neither of which is unexpected. There was no direct relationship between either dimension of blood pressure and interoception ( $ps>.05$ ).

As interoception scores correlated with both the control task (accuracy in timing seconds for the same duration;  $r=.29, p=.03$ ) and BMI ( $r=-.29, p=.03$ ), the analysis was repeated including these as covariates. The model remained significant,  $R^2 = .27, F_{(5,49)}=3.70, p<.01$  and the pattern of results was as above, with significant main effects of rating and interoception, and a significant interaction. There was no significant main effects for the covariates.

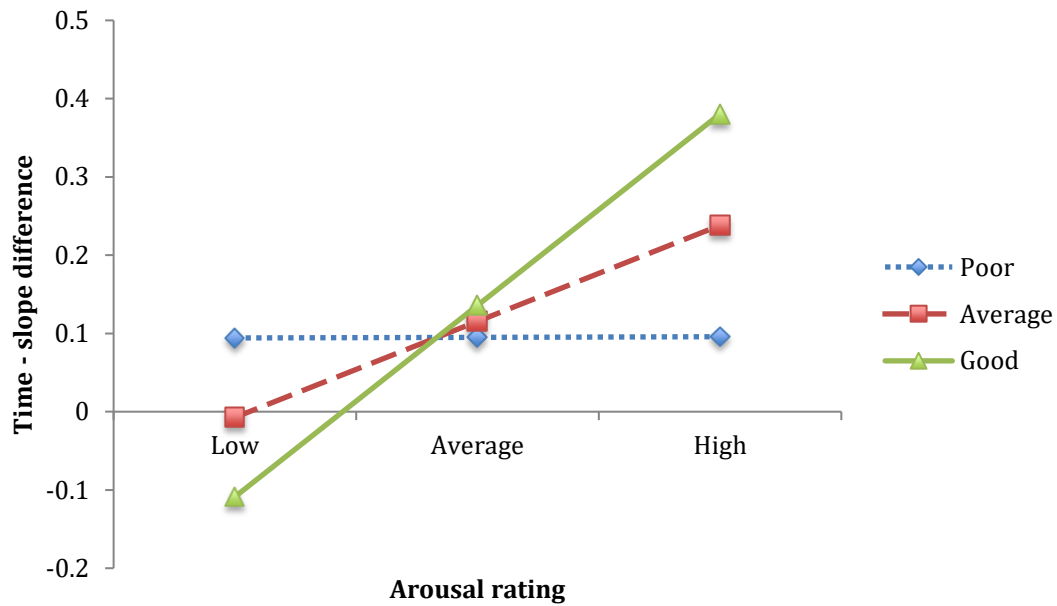
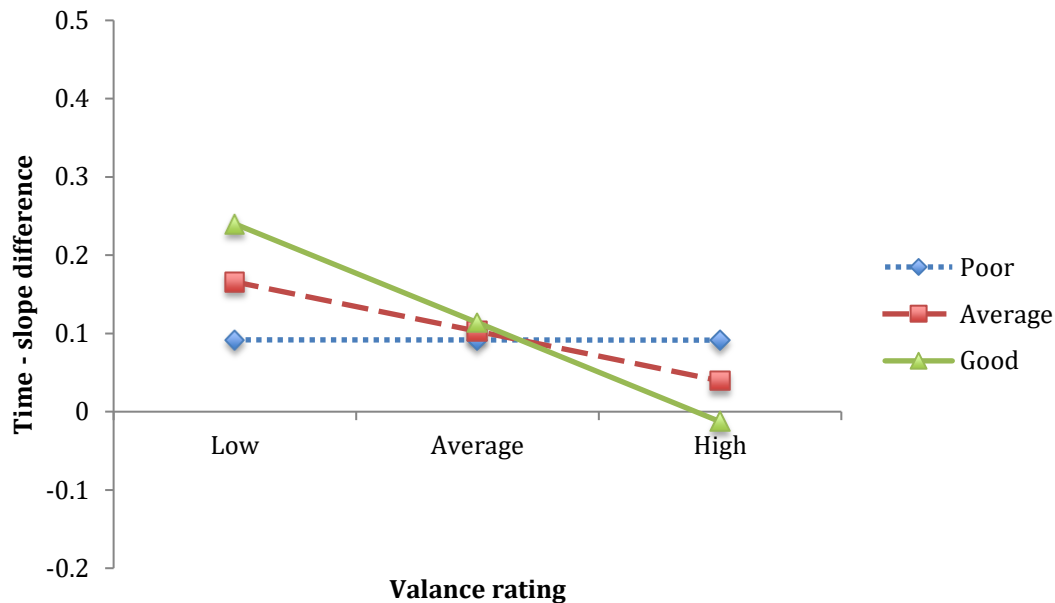


Figure 4.5: The difference between individual timing slopes, for high arousal pictures and low/neutral pictures, as a function of averaged arousal ratings. Lines represent the relationship at different levels of interoceptive accuracy (mean and 1SD above/below).

Repeating the analysis and substituting valence for arousal we find the model does not achieve significance,  $R^2 = .1$ ,  $F_{(3,51)}=1.801$ ,  $p=.16$ , although the pattern of results is similar (noting here that the high arousal images are low valence, and so forth, so the pattern is inverted) see figure 4.6. Repeating this analysis with mean heart rate deceleration (collapsed across conditions) in place of mean arousal is also very much non-significant  $R^2 = .001$ ,  $F_{(3,51)}=.025$ ,  $p=.95$ .



*Figure 4.6: The difference between individual timing slopes, for high valence pictures and low/neutral pictures, as a function of averaged arousal ratings. Lines represent regressions for different levels of interoceptive accuracy (mean and 1SD above/below).*

### **Interim discussion**

This experiment looked to replicate previous findings on arousal and time judgements and test the proposed moderating role of interoceptive sensitivity. It also looked to address some of the methodological concerns with experiment 3, including by changing to sub-second durations and using the arousing stimuli as the target of the timing task. The results show a replication of previous findings (Gil & Droit-Volet, 2012) as high-arousal stimuli produce relatively longer time estimates, although in this case there is not a significant difference in timing between low arousal emotional and neutral images. Additionally we find that the relationship between arousal rating and timing is moderated by interoceptive sensitivity, as hypothesised.

## Discussion

In these studies, we aimed to replicate previous findings that higher arousal stimuli dilate subjective time and to establish whether interoceptive ability influences that relationship. The expectation was that those who are more sensitive to their own bodily signals (i.e. better interoceptors) would show a stronger effect of arousal on estimations of time.

This hypothesis was not supported by the first experiment, however there were clear limitations, which we overcame with the design of the second experiment. The second experiment shows a clear and significant moderation, whereby good interoceptors have a strong relationship between their arousal ratings and time estimations, such that where they reported a relatively high overall arousal rating, they have a larger dilation in timing estimated in the high arousal condition compared to the other conditions. This pattern is diminished for medium interoceptors and absent for poor ones. Essentially, it is only good interoceptors who show an effect of arousal ratings on their time estimations while poor interoceptors may have low or high overall arousal ratings but their timing does not change as a function of this. Arousal is distinguished from valence, as the same analysis with valence does not produce any significant results; the similarity in the pattern of the results is likely driven by the association of high arousal with low valence, and vice-versa, in the stimuli.

This replicates the core finding of Gil and Droit-Volet (2012), who used a very similar picture timing task with a variety of emotional IAPS images, in that estimates of duration are dilated by high arousal disgust stimuli. On the other hand, our result, provides a clarification in that it does not show a differentiation, in timing,

between low arousal disgust and neutral images. While not dissimilar to some of their figures, depending on condition, this is somewhat contrary to their general conclusion that emotive content has a dilation effect. In the case of disgust, it would appear that any dilation is based primarily on the aspect of arousal, though we cannot dismiss possible differences in effect between different emotions.

This does raise the question of why low arousal disgust and neutral images are differentiated in terms of arousal scores but not timing behaviour. One answer to this is that high arousal disgust is the only stimuli that was judged to be positively arousing whereas low arousal disgust pictures were collectively judged to be near neutral in terms of arousal. This being the case, we might postulate that our results represent that stimuli that increase arousal speed up the putative pacemaker while we cannot be certain as to whether stimuli that decrease arousal slow it. As high arousal stimuli theoretically produce a fast autonomic nervous system response, in preparation for motor responses to threat, it is reasonable to assume this response may be better observed at these short durations than other effects that may impact behaviour more slowly (Droit-Volet & Meck, 2007).

Another consideration is that arousal ratings may be subject to desirability or cognitive strategy. For example, if we assume that participants were able to discern that there were three categories of picture, some of which were clearly intended to be different to others in terms of emotive content, they may have tended to differentiate these by category in their responses. It is also worth considering that there were multiple timings of each picture but only one rating (to avoid dividing attention between temporal and arousal judgements). An avenue of further investigation would be to use a wider range of emotional stimuli across the spectrum, rather than groups

of stimuli, with a rating associated to each timing trial. This would allow examination as to whether reported arousal specifically links with duration on a trial-by-trial basis.

Having replicated previous findings on arousal these results also show a novel and timely addition to the field in showing that the relationship between arousal and time judgement is mediated by interoceptive accuracy. This strongly suggests that the effect of arousal is driven by embodied emotion (rather than attention, for example), in that it would appear that those more sensitive to their bodily signals show more of an arousal effect on their timing. In particular, it is coherent with Craig's theory that the sense of time arises from the passing of global emotional moments that are rooted in interoception (Craig, 2009a); we provide support for a close relationship between interoception and time where the subjective sense of duration varies with interoceptive ability. Future research may wish to confirm whether the effect we find here is further related to individual differences in the activation of the insula cortex.

However, the current experiment does not replicate the finding of Dunn et al. (2010) that good interoceptors showed a stronger relationship between heart rate change and arousal rating. This is possibly attributable to differences in experimental design in that, focussing on timing, we used different and fewer images with more repetition and only rated the pictures for arousal once at the end rather than at each occurrence. Dunn and colleagues also presented images for much longer (6s) than was possible in this task and averaged heart rate across that duration, which may have contributed to a clearer effect. In our findings, the heart rate response was not significantly different for low and high disgust images and this lack of clear differentiation may have contributed to the null result. It should be noted that the design of this experiment prioritised measuring timing performance and producing a reliable arousal effect. Nonetheless, the broad findings are somewhat in agreement in



that they found that interoceptive ability moderates the experience of arousal and the current experiment finds that this also influences the subjective experience of time.

Recently new timing research has measured arousal in timing by structuring the stimuli into blocks according to arousal and valence (Ogden, Henderson, McGlone, & Richter, 2019; Piovesan et al., 2018; van Hedger et al., 2017), an approach not dissimilar to our first experiment in this chapter, though in these cases utilising estimations under 1000ms and clearly differentiating arousal and valence. This approach allows for long samples of cardiac activity allowing more sophisticated and reliable analysis of the change from baseline in each condition. In particular this approach allows the differentiation of parasympathetic (PNS) and sympathetic (SNS) nervous system activity via measuring pre-ejection period and high-frequency heart rate variability respectively. Their findings show that only the index of SNS activity related to timing, and this only for high arousal negative stimuli. They interpret this as supporting both bottom-up (physiological arousal) and top-down (threat detection) process in the effect of arousal on time. Theoretically it is only the bottom up, physiological, aspect of this model where we would expect an effect of interoception, which is consistent with our current findings but could be specifically tested by combining our approach with that of (Ogden, Henderson, McGlone, et al., 2019).

While the findings for heart rate deceleration are not entirely conclusive, they do support the validity of the paradigm by showing the stimuli did produce a physiological change. As heart rate is only one aspect of biological arousal, and it has been shown that where heart rate and arousal are independently manipulated, it is subjective arousal that moderates time perception and not heart rate (Schwarz et al., 2013), future studies may benefit from including a wider range of indicators of arousal so as to more clearly link the biological response to subjective perception. In

this case, the effect of interoception remains clear, as good interoceptors do not appear to have significantly different changes in heart rate but do appear to translate arousal into larger changes in perception.

From a methodological perspective, replicating previous findings also further validates the use of affective sliders as an alternative to the self-assessment manikin as a response mechanism in arousal research. While Betella and Verschure (2016) initially validated the slider as producing similar results to the SAM, this finding (that the arousal ratings thus produced significantly relate to other behaviour as predicted) supports the use of this methodology.

Considering together the two experiments reported here, we can conclude that the initial hypothesis that interoception moderates the relationship between subjective duration and subjective arousal is supported but subject to limitations with regards to the method of time estimation and the manner in which time estimation and arousal are combined, particularly considering the role of attention. Further experimentation would be required to precisely establish why the first paradigm was unsuccessful and, for example, whether this finding is constrained to sub-second timing or can be found at longer durations if methodological issues are overcome. There is evidence that emotional arousal (induced with film clips) can dilate time in a subsequent timing task, using durations under two seconds (Droit-Volet et al., 2011), so it is not unreasonable to hypothesise some transfer where the timing task is subsequent to the arousal stimulus, although a long film clip may have had stronger sustained effects in this regard than still images. Subjective arousal can dilate supra-second durations but in these cases, the arousal is sustained though the target duration and either explicit instructions or the direction of attention elsewhere may help to control chronometric counting (Pollatos, Laubrock, et al., 2014; Schwarz et al., 2013). In aggregate, the

evidence suggests interoception is likely to moderate the role of arousal for intervals longer than 2s, and arousal can transfer from a preceding stimulus to a timing task, but practically applying both these elements within the same experiment as attempted here is likely to be challenging.

While the effect of arousal remained consistent over repeated trials, time estimates for all conditions reduced between the first and second block of testing. This is likely to be attributable to participants becoming more comfortable with the task itself (noting that there was little training prior to the first block). It may also represent a generally reduced reaction to repetitions of the same images. This is not a major limitation, as the effect of arousal is preserved, however it is an argument for changing the stimuli regularly, or including a larger range of stimuli, in order to maintain novelty. Ideally, future research should aim to replicate our findings on a trial by trial basis to directly relate physiological arousal, experienced arousal and time perception for each presentation. The challenge might be in producing a reliable index encompassing physiological arousal, as discussed previously, heart-rate can be disassociated from perceived arousal while skin conductance responses (SCR) have a relatively large latency (Angrilli et al., 1997) although including SCR would be a good first step in this regard.

One of the aims in designing the second experiment was to minimise any influence of attention. The lack of significant differences in intercept suggest that there was not an effect of attention orientation, as a delay in orientating to particular stimuli would be expected to shift the intercept (Gil & Droit-Volet, 2012). As the arousal stimuli were the target of the timing task there are no concerns about splitting attention and the relatively short durations employed should avoid any effects from the need to sustain attention (Droit-Volet & Meck, 2007).

The Schandry heart beat detection task has been subject to a fair amount of criticism including that changes to actual heart rate are not necessarily reflected in perceived heart rate and may be modulated by feedback or prior knowledge (Brenner & Ring, 2016). In the case of our experiment, only 4 individuals reported knowledge of their own resting heart rate, though arguably we did not measure general knowledge about heart rate as in Murphy, Brewer, et al. (2018). It is also hard to imagine why prior knowledge regarding heart rate would systematically moderate timing behaviour.

Support for the HBD task includes fMRI evidence of an association between heart rate perception and insula cortex activation (Critchley et al., 2004) and significant correlations between HBD and the water load test measuring gastric interoception (Van Dyck et al., 2016). There is also an increasingly well supported association between heart beat perception and eating habits and obesity (Herbert et al., 2013; Herbert & Pollatos, 2014) providing evidence of long-term impacts on behaviour. Our results support these previous findings in that we find a significant, negative, relationship between BMI and interoceptive accuracy. Although the direction of this relationship cannot be inferred in this case, previous research has shown that interoceptive accuracy mediates the relationship between aspects of intuitive eating (reliance on internal satiety cues and eating for emotional vs physical reasons) and BMI, thus suggesting high BMI is more likely to be a result, rather than a cause, of poor interoception.

As evidence from large sample studies continues to call into question the exact nature of the heartbeat perception task (Zamariola et al., 2018) future investigations may wish to consider including novel measures of interoception such as those described by Murphy, Catmur, et al. (2018). This said, the perception of heart rate is

still of particularly relevant in this case given the proposal by Craig (2009a) that this may play a role in regulating (though not defining) temporal experience.

In the second experiment we did appear to have a sample where interoceptive accuracy was relatively high. A recent finding that interoceptive accuracy is relatively high when wearing ear protectors (Hall, Lopes, & Yu, 2018) may explain this, as our participants wore noise-cancelling headphones. This is not of significant concern in this case as we were not using this as a selection measure and all participants performed the test in the same way, however it should be a consideration for future paradigms.

In summary, these findings replicate previous timing research on emotion and time perception while also providing evidence for a key role of interoception in moderating this relationship. As such, this supports theories of embodied emotion and may have particular relevance to Craig (2009a) theory of emotional moments, given that this specifically relates time perception and interoception. There are clear avenues for further research in terms of relating the effect more directly to physiological changes and investigating the limitations of the role of interoception, for example in perceiving longer durations. We conclude that individual differences in interoceptive accuracy significantly influence the way emotional arousal acts on the perception of time.



## Chapter 5: General discussion

The lives of all people flow through time, and, regardless of how brutal one moment may be, how filled with grief or pain or fear, time flows through all lives equally.

*Orson Scott Card, Children of the Mind*

### Chapter summaries

*Experiment 1. Do individual differences in the EEG alpha rhythm relate to differences in time judgements across tasks?*

The first experiment set out to explore the potential relationship between individual occipital alpha peak frequency across a range of timing tasks including supra-second estimation and production tasks, free tapping and a visual discernment task designed to measure the individual's concept of 1s. Behaviourally, results suggested that variation in the participant's behaviour in the rate tasks, the 1s discrimination task and tapping, also relates to individual variation in the supra-second tasks, primarily production. Relationships between timing tasks and occipital IAFs showed some moderate trends in the expected direction, such that faster oscillations relate to a faster pacemaker, but did not reach significance. Topographic analysis suggests that estimation, in particular the slope of individual results, may be the task most specifically related to occipital alpha. Results are interpreted as failing to support the hypothesised relationship but showing potential for future studies with higher power and more targeted methods.

*Experiment 2. Integration and timing*

This experiment aimed to test behaviourally, and with a large sample, the relationship between sensory integration and timing that was not clearly supported in our first experiment. Methods involved a simple audio-visual simultaneity judgement task and the filled duration illusion, whereby participants estimated the duration of intervals (up to 1181ms) filled, or unfilled, with sound. They also completed the short O-Life schizotypy scale. Previous findings were replicated in that filled durations were judged to be significantly longer than unfilled ones and schizotypy scores correlated with the temporal window of integration. The results showed a significant positive relationship between individual differences in the TBW and individual differences in the filled duration illusion, with this being driven by a negative relationship with the unfilled condition. Schizotypy did not relate to integration. Results support a relationship between the timing of sensory integration and timing judgements, in particular, it appears that this effect applies in the empty condition, perhaps because the characteristics of the stimulus in the filled interval override or mask the intrinsic rhythm.

*Experiments 3 & 4: Arousal and timing*

The final two experiments moved from exteroceptive integration to how interoceptive accuracy moderates the relationship between emotional arousal and time. Both experiments used high arousal and control images from the IAPS database (Lang et al., 1997) to produce emotional arousal, and affective sliders (Betella & Verschure, 2016) to assess subjective arousal. Interoceptive accuracy was measured via a standard heartbeat counting task. In experiment 3, images preceded supra-



second time judgements. Here no arousal-related dilation in timing was found, nor was there any moderation by interoceptive ability. This lack of effect may be attributable to the paradigm and thus the question was implemented differently in the fourth experiment. In this case, sub-second durations were employed and the arousing images were the timed stimuli. Here a significant dilation was found for high-arousal timing judgements, and this was moderated by interoceptive ability. We conclude that the effects of emotion on time are genuinely driven by embodied emotion, rather than attention, and that this is moderated according to individual differences in interoceptive sensitivity.

### **General interpretation of results**

#### *The role of sensory systems*

The primary question of this thesis was whether individual differences in interoceptive and exteroceptive processing relate to differences in timing. The findings of experiment two show that a narrower TBW relates to longer estimations (though only where the timed duration is empty), and less variable timing, consistent with a smaller TBW representing a faster ‘pacemaker’. This is coherent with the trends in experiment one, which are consistent with occipital alpha peak frequency (which putatively gates temporal integration) having a small relationship with timing judgements. In experiment 4, we find that individuals with higher interoceptive sensitivity show a greater influence of arousal stimuli on duration; such that good interoceptors, whose ratings showed the stimuli effectively increased arousal, gave longer estimations. Overall, we would suggest that the evidence presented here supports the hypothesis that individual differences in audio-visual integration and in

interoceptive sensitivity moderate timing judgements, though also demonstrating that such effects are likely to be paradigm-specific and subject to limitations.

*Sub-second vs supra-second timing*

As covered in the introduction to this thesis, there is often a difference drawn between (approximately) sub-second and supra-second intervals (Buhusi & Meck, 2005) with fMRI evidence suggesting that areas of the brain are differentially engaged depending on duration (Lewis & Miall, 2003a; Penney & Vaitilingam, 2008; Wiener et al., 2010). In our findings, the experiments that used supra-second intervals failed to show significant changes in timing related to the individual differences in question. It is tempting to suggest from this that individual differences in sensory processing are primarily to be found for sub-second intervals. This is, however, too simplistic a conclusion. Previous experiments have shown supra-second timing to be moderated by both arousal (Angrilli et al., 1997; Schwarz et al., 2013) and interoception (Meissner & Wittmann, 2011; Pollatos, Yeldesbay, et al., 2014) in the right circumstances, so we can be moderately confident that these effects are not found solely at sub-second durations. Additionally, within our first experiment, it should be noted that the 1s discernment task arguably has a similar range to many tasks in the literature that we might think of as being sub-second, or at least distinct from tasks in the ranges of multiples of seconds, yet this also found no significant relationship.

We would suggest that rather than, or in addition to, these effects being primarily present at very short durations, they are simply harder to consistently identify for longer durations. Durations in the range of seconds to tens of seconds carry additional methodological and theoretical concerns. For example, cognitive

strategies comes into play much more strongly in these ranges. Chronometric counting is perhaps the most obvious issue, and likely one that impacts our experiments by reducing variance (Wearden, 2016). However, even where this tactic is forbidden we would expect that different cognitive processes may be recruited in timing the same duration. In much longer durations, where counting is again of little use, Ornstein (1975) found that the perception of a duration varied according to how individuals thought about the content. It is not clear what the lower limit on this effect is but it seems likely that in most cases of a duration of more than a second or two, the participant has time to think about the task or unrelated things, and this may influence behaviour in ways we are not able to control. Maintaining attention also becomes a more significant issue for supra-second durations, which is of particular concern with regard to individual differences where attention to the task may also be influenced by such differences, for example in schizophrenia (Fioravanti, Carlone, Vitale, Cinti, & Clare, 2005). Related to this is the question of how the stimuli, or a manipulation, relates to the duration in supra-second trials. In the case of arousal, effects are often short-lived and so in most cases the arousing stimuli are timed, though Droit-Volet et al. (2011) provide an exception where the to-be-timed interval takes place after arousing stimuli.

Returning to our investigations, it seems likely that some of these limitations adversely influenced our results, particularly in the case of the supra-second judgements where there was no effect of arousal on estimated or produced time. In our first experiment, looking into the role of occipital alpha, this is less clear as neither tasks around 1s or longer tasks related significantly to individual differences. However, the strongest trends were for the tasks in the range of 1-11s suggesting it

might be possible to confirm such a relationship, despite the limitations noted above, given the right paradigm.

### *Theoretical interpretations*

On a behavioural level our results could be interpreted in line with pacemaker-accumulator models of timing. Cumulative effects on timing are traditionally associated with changes in the rate of the pacemaker while additive effects are interpreted as attentional. In experiment two we find that that a steeper timing slope (e.g. more accumulation in the same interval) is associated with smaller windows of temporal integration. Assuming continuous cyclical discrete perception (Andrews & Purves, 2005; VanRullen & Koch, 2003), this indicates that a faster cycle of perception is associated with longer timings in the same manner as a faster pacemaker. Thus we interpret this evidence as suggesting the TBW is indicative of pacemaker rate.

One element of our integration results (in experiment 2) are somewhat at odds with a pacemaker interpretation. It might be expected that a faster resting pacemaker would be reflected in both slopes, as in Wearden et al. (2007) where the pacemaker is increased before the interval via click trains, however, in contrast, our study showed a significant relationship between the TBW and the empty slope, but not the filled. However, it might also be suggested that the increase in the pacemaker in the filled interval may be more dependent on the qualities of the stimulus than the resting rate, which forms an important suggestion for future research to clarify this finding.

Additionally there was a significant relationship between the coefficient of variance, in both conditions, and the TBW, such that higher accuracy was associated with a smaller window of integration. This suggests that both timing conditions have

some relationship to temporal binding but differentially engage with the shared aspects of the timing system. The (n.s.) trends in our EEG investigation (experiment 1) are coherent with the results in chapter three in that faster oscillations appear to have some relation to a faster pacemaker rate.

A cumulative increase in estimations is also associated with higher arousal in our findings (experiment 4), replicating previous studies (e.g. Gil & Droit-Volet, 2012; Mella et al., 2011; Ogden et al., 2015; Schwarz et al., 2013), and adding that the relationship between subjective arousal and estimations is moderated by interoceptive accuracy.

As addressed in the introduction to this thesis Lake et al. (2016) identifies some issues with traditional pacemaker models for arousal and rather suggests an interaction of attention and arousal where the initial orientation to the emotional stimuli is driven by attention modulated by the emotional salience. This is followed by a transitory period of up to a few seconds where dilation is primarily driven by physiological arousal. As the duration increases estimates may become further influenced by the degree to which attention and working memory is sustained, which again may be modulated by physiological arousal. Our findings on arousal are consistent with this approach as we do not find an effect of arousal on intercepts, suggesting attention orientation to the images was consistent, but do find an effect of arousal in the slope, only where the range of responses is limited to the very short term. Where we measured arousal for durations over 5 seconds there was no effect.

Our finding here suggests a new approach to investigating Lake's model. As interoception should only moderate the physiological arousal aspect it may be possible to use this by mapping the relationship between interoception, arousal and estimation at each time point over a wide range. This should show an initial

cumulative increase in the relationship followed by a reduction for longer durations, over a couple of seconds, as sustained attention becomes more important. Varying the salience of the stimuli would allow proper testing of the theory that arousal interacts with attention to contribute to orientation for high-salience stimuli.

As the pacemaker explains behaviour but not necessarily how this functions in the brain, we may also consider how this finding could relate to popular theories in this area (though noting that the intention, and design, of our research was not to test theoretical models but to advance knowledge with regards to individual differences in timing).

Firstly, we could suggest that sensory integration shares characteristics with the timing system, for example within the context of the striatal beat frequency theory (SBF; Buhusi & Meck, 2005; Matell & Meck, 2004). In this case, the cortical activity associated with multi-sensory integration, probably in the parietal and occipital cortex (Buetti, 2011; Buetti, Bahrami, et al., 2008; Buetti & Macaluso, 2010; Cecere et al., 2015), could also form part of the oscillatory activity that is tracked by the basal ganglia for coincidence detection. As such, integration could not be said to be acting directly upon timing but rather that these are products of common characteristics within connected areas. In this case, arousal acts upon the system via modulation of cortical oscillations by dopamine (Droit-Volet & Meck, 2007). Differences in sensory integration may reflect baseline oscillatory differences for that individual.

Secondly, we could suggest a more causal relationship, where individual differences in how information is processed impact the effect of that information on timing. An adaption of Craig's theory of Global Emotional Moments (Craig, 2009a) can be posited. In this model, primarily interoceptive, but also exteroceptive, information is fed into a system, in the insula cortex, that combines information

moment by moment to produce a series of GEMs which facilitate conscious awareness and, in being sequential, provide a basis for the temporal aspect of perception. These being of a set capacity, greater input means time moves more quickly when more salient information is provided. This would certainly fit with our findings on interoception and arousal. The finding that the relationship between integration and time is primarily in the unfilled condition (in our experiment 2) might be interpreted as this representing the base rate of sensory input into the system while longer estimates, unrelated to integration, in the filled condition are driven by the higher level of salient information.

As our findings provide initial support for the role of interoception in timing, they are compatible with this theory, but further investigation is required to clarify the relationships between physiological arousal, subjective arousal, interoception and estimation. Recent findings differentiating between markers of sympathetic and parasympathetic nervous system activity have found similar results to ours in that only for high arousal negatively valenced stimuli is there an association between SNS activity and time estimations (Ogden, Henderson, McGlone, et al., 2019). This approach may provide a clearer index of relevant physiological arousal that, combined with our approach may allow the mapping of the relationships between physiological arousal and subjective arousal, and how both these factors relate to timing.

Another alternative is that it is possible that duration can be processed within individual sensory cortices themselves, as with other basic features of a stimulus, as proposed by the state-dependant network model (Buonomano & Maass, 2009). This is an intrinsic model, meaning timing has not a dedicated structure or process but is an emergent property of neural processing, which is proposed to vary depending on the

state of the relevant network at onset, thus being influenced by context. This might fit well with our integration results conceptually, as it would make sense that the integration task relates to the dynamics of sensory processing, which are reflected in timing judgements in the absence of stimuli, but changes to process the sound in the filled condition. On the other hand, studies aiming to test this model have suggested that it is only reflected in behavioural results for durations under approximately 300ms (Buonomano et al., 2009; Spencer et al., 2009), which makes it less compatible with our findings.

While this is by no means an exhaustive list of possible theoretical interpretations, it does suggest three ways in which individual characteristics, such as sensory integration, may relate to timing behaviour: by acting directly upon a timing system; by being indirectly related, as characteristics are shared with a timing system; or by being essentially two expressions of the same system. It is worth noting that the above theories are not necessarily fully exclusive. For example, we might suggest that the SBF is most suited to behavioural learning and replication of intervals while GEMs are most relevant to the conscious experience of timing and the state-dependant network model covers the processing of the temporal characteristics of very short sensory events. That our new findings regarding individual differences in timing might conceivably fit several different models illustrates one of the challenges for research in this area. It may be possible to adapt our findings to test how well these reflect different models, for example in the filled duration task, one could increase the intensity of the stimulus in small steps from no stimulus at all. If there is a gradual reduction in the relationship with sensory integration, then this would favour a theory such as the adaption of GEMs mentioned above, as additional information progressively fills the finite moments more quickly.



### **Limitations and methodological implications**

The individual experimental chapters describe the limitations associated with the particular methods we utilised in each case. The primary limitation that spans across this thesis is one of task and stimulus dependency. In our EEG investigation, results varied by both task and by the attribute of behaviour under consideration (represented in our data by the slope and intercept). In experiment two, sensory integration only relates significantly to the unfilled condition. In investigating arousal and interoception we find clear results but only for sub-second durations. This is largely in-line with the observation, made in the introduction to this thesis, that the timing literature often shows effects that vary by duration and paradigm (Block et al., 2018; Block et al., 2010; Block & Zakay, 1997; Buhusi & Meck, 2005; Lui et al., 2011; Matthews & Meck, 2014). For example, arousal effects can be reversed if arousing stimuli are placed so as to distract from timing (Lui et al., 2011) and it is possible to find different results for the filled duration effect, at very short durations, using different methods of time judgement (Hasuo, Nakajima, Tomimatsu, Grondin, & Ueda, 2014).

These differences often have good explanations, for example differences in arousal paradigms appear to demonstrate the effects of attention (Angrilli et al., 1997). However, this limitation does have two general implications for the field. Firstly, it is important that results are not overstated, in that generalisation must be cautious unless the results are replicated with different parameters. Secondly, it would be very informative to have more experiments including multiple types of timing or stimulus. This is exemplified, in this thesis, in experiment two. Had we only included the empty timing condition it might have been concluded simply that the rate of integration influences timing. If we included only the filled condition then we would

have no option but to conclude the measures to be unrelated. In including both, and the difference between the two, we are able to draw a more nuanced and informative conclusion, albeit also one that is less clear-cut and thus produces further questions.

### *Specificity*

With regards to our findings, the generalizability of these experiments is yet to be established and this requires some further investigations. In the case of integration the simultaneity judgement is a well-established measure of the temporal binding window but given that we used an adaption of the task (by only using audio leading trials) and found a slightly different than expected spread of results, it might be wise to replicate this with the usual version of the SJ task and related multi-sensory temporal binding tasks such as temporal order judgement, the flash-beep illusion or the McGurk effect (Stevenson & Wallace, 2013). On the timing side of the relationship, we might consider temporal and task generalisation. With regards to temporal generalisation, we utilised sub-second durations; it might be of interest to extend the range of durations to establish at what point we cease to find differences in timing significantly associated with differences in temporal binding; we would expect this relationship to decline at longer intervals where cognitive strategies may have greater influence.

In terms of timing task, it is desirable to check that the relationship can be generalised beyond verbal estimations, as if it cannot, then this would suggest a bias in responding rather than in the actual experience of duration. It might be appropriate to use temporal generalisation, wherein it is judged whether test durations are the same as a standard duration, as the filled duration illusion has been evidenced using this task (Wearden et al., 2007). A final consideration with regard to this task is that

we only utilised auditory stimuli. It is an important clarification to replicate this, if possible, with visual stimuli; indeed an important question is whether this relationship only applies to multisensory integration or whether it might be better understood by also seeking a correspondence between unimodal integration and timing of stimuli in that modality.

With regards to our arousal experiments, the question of specificity is somewhat different, duration is a consideration but so is whether the relationship can be generalised to other types of emotion and other types of arousal. Given that similar dilation effects have been found for stimuli that elicit fear, (Droit-Volet et al., 2011; Gil & Droit-Volet, 2012) including the anticipation of pain (Ogden et al., 2015), we would expect the moderation by interoceptive ability to generalise to these conditions. Pain in particular would be of interest as Ogden et al. (2015) find an effect of arousal on both the intercept and the slope of timing behaviour. Replicating this with interoception would allow us to test whether the effect of arousal applies to the pacemaker only or also the initial orientation of attention to the stimuli. With regards to other types of arousal, it might be of interest to apply this finding to physical arousal as this has also been shown to increase estimates of duration (Schwarz et al., 2013). These types of arousal may also provide a practical way to test the moderation by interoceptive accuracy at supra second durations as arousal can be sustained through the interval using physical arousal (Schwarz et al., 2013) or may more effectively manipulate a subsequent time judgement when a fear-inducing video is used (Droit-Volet et al., 2011).

### *Causality*

Another limitation of the research presented here is in the difficulty in establishing causal links rather than associations. For example, while a smaller TBW is associated with longer estimations (of an empty duration), we cannot say whether the dilation is caused directly by differences in sensory binding or whether both are influenced by other factors. In arousal there is a clearer pattern of evidence, in that results show both that the stimuli influences heart rate and that those more sensitive to their own heart beats show a greater influence of arousing stimuli on time. Nonetheless, this experiment did not directly show a change in physiological arousal resulting in time dilation mediated by interoception. In both cases, the experiments presented here establish the relationship and create a basis for further experiments to more clearly establish the nature and mechanism of these relationships.

In the case of integration, we would suggest that having established a behavioural relationship it would be appropriate to work to establish a neurobiological basis for this. A logical progression might be to attempt to replicate our behavioural finding of a relationship between temporal binding and timing in combination with replicating the relationship between temporal binding and occipital alpha oscillations found in Cecere et al. (2015). If this can be achieved it would also provide an avenue for causality to be established via neuromodulation of the alpha frequency, which changes the size of the TBW and, if this has a causal influence, should lead to a corresponding change in timing. An alternative would be to build on findings that temporal discrimination is influenced by disruption, via TMS, of the right posterior parietal cortex, for visual and auditory tasks, or visual cortex, for visual tasks only (Buetti, Bahrami, et al., 2008), to establish if disruption of these areas equally inhibits integration and duration judgements.

In the case of arousal, the next step towards confirming the nature of the relationship might be to adapt the paradigm to attempt to replicate the finding that good interoceptors showed a stronger association between heart rate change and arousal rating (Dunn et al., 2010) while further showing the effect of this on time judgements (ideally looking to model this on a trial-by-trial basis to allow for intra-individual variation). On the other hand, we have argued that too strong a focus on heart rate alone should be avoided, as it can be disassociated from the effect of arousal on time (Schwarz et al., 2013) and because the heart beat response is actually relatively slow, often peaking after the sub-second durations in question. Therefore, another avenue would be to confirm the moderation found in our experiment while using non-cardiac methods of estimating interoceptive ability, such as gauging respiratory output or muscular effort, and additional measures of physiological arousal such as pupil dilation and galvanic skin response. Establishing causality is not simple, however one option might be to build on fMRI findings and assess whether insula cortex activation, which relates to interoceptive accuracy (Critchley et al., 2004), shows a pattern of activation corresponding with individual differences in interoception-mediated time dilation by arousing stimuli.

### *Stability*

Another issue we do not test within this thesis, and that may benefit from more investigation in general, is how stable the behaviours measured are within the individual over time. In terms of temporal binding, there is indirect evidence for stability, in that measures relate systematically to on-going individual differences such as schizophrenia and schizotypy (Ferri et al., 2017; Ferri et al., 2018; Foucher et al., 2007; Giersch et al., 2008; Lalanne et al., 2010; Zhou et al., 2018) or obesity

(Scarpina et al., 2016), though of course these characteristics do vary within the individual over time so are not absolutely stable themselves. There is some more direct evidence, for example Mallick, Magnotti, and Beauchamp (2015) found very little difference in the McGurk effect when retesting after an interval of one year and Stone et al. (2001) included two sessions of simultaneity judgement at least 24hrs apart and found results were highly correlated. It should be noted however, that there is some evidence that responses in the SJ can be manipulated by feedback (Powers et al., 2009), perhaps influencing the interpretation of what is simultaneous, and so some caution is required in asserting the stability of this measure. For the purposes of our interest in individual differences, this is not an area of substantial concern as long as participant instructions, training and (lack of) feedback are consistent. In our case, training on the task was minimal with the intention of avoiding any inadvertent adaption.

In the case of interoceptive accuracy, as measured by heartbeat counting, Ferentzi, Drew, Tihanyi, and Köteles (2018) discuss a variety of evidence providing moderate support for the relative stability of interoceptive accuracy, including studies where there appears to be test-retest reliability (Bornemann & Singer, 2017; Fischer, Messner, & Pollatos, 2017; Mussgay, Klinkenberg, & Rüdell, 1999; Parkin et al., 2014) though these were all primarily focussed on assessing clinical samples and so conclusions in this area are limited. Ferentzi's own findings, testing a fairly large sample ( $n=103$ ) with an 8-week delay, shows a reasonable correlation ( $r=.6$ ) between test and retest, and so provides good evidence for this measure being moderately stable.

There appears to be less evidence available when it comes to the stability of timing judgements. Rakitin et al. (1998) repeatedly tested a small sample ( $n=7$ ) over

10 days and reported consistency between sessions with no trends over time, although they did use a version of a supra-second reproduction task, called peak interval procedure, where participants are asked to aim to distribute button presses around the target interval and given feedback on their performance, which could arguably increase the stability of responses. Other studies have also shown stability at the group level when testing in different sessions but have not looked at individual performance (Anderson & Schmitter-Edgecombe, 2011; Gooch et al., 2009). Shammi, Bosman, and Stuss (1998) also test this at the group level with older and younger adults. They used empty intervals, and intervals filled by reading words, for 15s judgements. They found relative stability in the younger group but surprisingly an interaction was found, with the older group's estimates for the filled duration appearing to go from the shortest estimate of all in the initial session to the longest of all in the second. It is not very clear as to why this would be the case but as variability is also a lot higher in the second session it may relate to a developing strategy or cognitive changes, such as boredom, over the course of repetitions of the task.

Anderson, Rueda, and Schmitter-Edgecombe (2014), with the express aim of testing stability using supra-second verbal estimates (range 10-60s), tested 20 healthy older and 20 healthy younger adults with a year's delay between sessions. They found that responses were relatively stable in both groups, although at the shortest duration (10s) there was not a significant correlation between test and retest estimations for the older adults. Sadly, there does not appear to be a correlational analysis for the younger adult group, so it is hard to know whether this is consistent. It would appear that there is a need for further studies designed specifically to establish the within-participant stability of time judgements across a variety of methods, durations and delays. In terms of our studies it is hard to be certain of how stable and enduring the

individual differences are. Thus, a potential avenue of interest for the future would be to look to replicate our findings in a test-retest format over 2 sessions. This would allow one to determine both if the overall relationship remains stable and whether individual behaviour either remains stable or co-varies; it would be substantial evidence for the relationships we find in this thesis if any change between sessions were to be mirrored in the related measures.

### **Conclusions**

Understanding how we process duration is a key element in understanding conscious perception and experience. Despite some limitations, there are two important findings in this thesis that provide a significant addition to the study of how differences in primary sensory processing interact with subjective duration. The results in chapter 3 show that individuals with a smaller TBW produce longer estimates of empty durations and are less variable in both conditions. The results in chapter four show that individuals with better interoceptive accuracy show a stronger effect of arousal on timing. These findings suggest that individual differences in both the processing of audio-visual synchrony, and embodied emotion, appear to relate to individual differences in our sense of time, with experiment 1 providing some evidence as to how this might be further investigated via electrophysiology. While these findings primarily serve to support the existence of relationships between primary sensory processing and timing behaviour, they also provide substantial suggestions for further research on a number of levels, including cognitive, behavioural and neuroscientific. Such research has the potential to inform theories of timing, and consciousness, and to progress our understanding of how individual differences within the general population may influence perception.





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