Investigating the Shared and Distinct Mechanisms Underpinning Perceptual Decision-Making and Metacognition

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Declaration

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Summary

In order to successfully adjust to changes and learn in the sensory environment, humans must be able to detect whether or not decisions are based on reliable sources of information. Because we cannot always depend on the availability of objective feedback regarding the accuracy of our choices, computing a subjective sense of confidence to guide adaptive behavioural strategies is a necessity. Computational neuroscience has made substantial progress in parsing the basis of these metacognitive evaluations, which are reviewed in the introductory chapter of this thesis. Specifically, a set of mathematical models have been devised which hinge on the idea that the same sensory evidence accumulation processes that mediate perceptual decision-making might also govern the emergence of representations of confidence. Support for this prediction comes from invasive recording techniques in both non-human and human animals. However, many questions about exactly how these signals influence metacognitive judgements remain. For instance, it is unclear whether the decision variable is directly read-out to inform confidence, what the precise temporal dynamics of this evidence accumulation process are and what other information sources might influence the emergence of metacognitive representations. By adopting paradigms that allowed for the identification of these distinct neural signatures in non-invasive human brain recordings the current thesis aimed to elucidate the temporal dynamics as well as unique contributions of these different levels of processing along the sensorimotor hierarchy in the construction of confidence.

The experiments presented in Chapter 2 aimed to address two gaps in current explorations of this relationship. Firstly, to extend on previous research by establishing that the sensory evidence accumulation process scales with choice confidence. This was confirmed in two experiments, showing that stronger build-up and higher amplitudes in this signal was associated with higher levels of confidence. This chapter further highlighted important methodological considerations for future work, by demonstrating that domain-general evidence accumulation does not simply continue to build until the choice reports and can be strategically terminated. Secondly, this study aimed to elucidate the role of motor level processes in the construction of confidence. Investigation of effector-specific mu/beta signals showed that, while contralateral motor preparation reached a fixed amplitude prior to response execution, higher activation for the unchosen alternative was associated with lower levels of confidence. These findings were complemented by an analysis of response conflict, which indicated theta band activity was similarly elevated on lower confidence trials. Additionally, the effects occur during a similar time window prior to the response, which provides a tentative indication that motor preparatory signals might indirectly influence metacognitive judgements through the expression of response conflict in theta power.
Chapter 3 built on these findings and examined the temporal dynamics of post-decisional evidence accumulation across these different levels of decision formation and to what extent this process is contingent on external stimulus information. This was investigated through a paradigm where on some trials stimulus presentation continued after an initial perceptual decision. Exploration of domain-general evidence accumulation yielded two key insights. Firstly, post-decisional evidence accumulation occurred regardless of the presence or absence of stimulus presentations. Secondly, its temporal dynamics suggest this signal was comprised of two partially overlapping but qualitatively distinctive phases. Prior to the perceptual choice, sensory evidence accumulation mapped onto the choice alternatives, while the post-decisional evidence accumulation process more closely represented the accuracy of the first-order decision. An interpretation that was further supported by analysis of the differential characteristics of each stage in the emergence of confidence, changes of mind and first-order accuracy. Finally, an examination of effector-specific motor preparation during the post-decision window highlighted an important feature of these signals with respect to confidence. Specifically, a crossover between ipsilateral and contralateral signals was observed on change of mind trials, which reflects a resetting of the decision bound in favour of the final choice alternative. To our knowledge, this is the first demonstration of this behavioural phenomenon at the motor level, which could be further characterised in future research.

A fundamental assumption of neuroscience is that behavioural paradigms tap into the same cognitive processes that govern daily-life decisions. The experiment in Chapter 4 aimed to contribute to the emerging literature exploring this assumption, capitalising on recent advancements in online data collection, and testing procedures. Specifically, behavioural data on a random dot motion task with confidence ratings was self-report measures of daily-life cognition and metacognition collected from a large representative sample, which builds on previous research that has largely focused on psychiatric symptom measures. Behavioural variables were decomposed into the mechanistic underpinnings of perceptual decision formation through computational models. The results from this study indicate that individual differences in multiple self-report measures were associated with metacognitive and perceptual decision formation variables. However, many of the expected relations between the parameters of computational models were not observed. While it is possible this reflects the limited ecological validity of the lab-based metrics and computational models, alternative explanations highlight the challenges of adopting these models in the study of inter-individual differences, which could be addressed in future research.

Finally, Chapter 5 provides an overview of the key contributions of the research in this thesis as well as some avenues for future studies.
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Chapter 2
Rys, R.W., Kelly, S., and O’Connell, R. (In prep). Tracing the Emergence of a Graded Representation of Choice Confidence across Multiple Levels of the Sensorimotor Hierarchy.

Chapter 3

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Published Abstracts


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Chapter One

Literature Review

1.1 Introduction

Imagine yourself cycling on a nice sunny day. You go along a road you have never been on before, successfully managing to swerve with the winding street as you go along. This apparently effortless task requires the interpretation of a huge variety of sensory cues, such as the visual and auditory information about contours of the road, the presence of other vehicles and somatosensory cues indicative of your posture and the angle of the bicycle. Thus, our ability to engage in even the simplest goal-directed behaviours relies heavily on our brain’s ability to rapidly and accurately translate relevant sensory evidence into appropriate action commands – a process known as perceptual decision-making (Kiani & Shadlen, 2013). In recent years, neuroscience has devoted a considerable amount of effort in the computational and neurophysiological underpinnings of how these sensorimotor transformations occur, since this ubiquitous process underlies many facets of real-world behaviour.

In recent decades, formal computational models have proven to be a powerful tool that allows researchers to parse behaviour into the latent structure of decision formation. In particular, the domain of perceptual decision-making has greatly benefitted from the sequential-sampling class of models, which all share the assumption that decision-making involves the accumulation of sensory evidence up to and action-triggering threshold (Smith & Ratcliff, 2004; Forstmann, Ratcliff & Wagenmakers, 2016). Crucially, these models provide detailed testable hypothesis about the neural mechanism that govern the perceptual decision-making process. This has aided researchers in the identification of effector-specific and domain-general neural signatures of decision formation across species that exhibit the key predicted accumulation-to-bound dynamics (Gold & Shadlen, 2007; Walton, Bannerman & Rushworth, 2002; Kelly & O’Connell, 2015; Siegel, Engel & Donner, 2011). Moreover, the combined application of mathematical models and neural methodologies has greatly improved understanding of the computational adjustments and mechanisms underlying many behavioural phenomena in perceptual decision-making (for recent reviews see, Forstmann, Ratcliff & Wagenmakers, 2016; Ratcliff, Smith, Brown & McKoon, 2016).

Now envision the same cycling journey but after a certain amount of time a dense fog starts to form that impedes your visibility on the road. You still have to make a decision about the oncoming traffic based on the same source of evidence, but the accompanying sense of certainty or confidence you experience in these decisions might be substantially different. Moreover, while some drivers might
choose to adjust their speed in this new weather others might not, which creates additional uncertainty in the availability and duration of information that you might be able to sample to discern vehicles. While confidence is a seemingly pervasive quantity accompanying many daily-life decisions, comparatively little is known about the precise mechanisms that produce these metacognitive experiences.

In recent times, extended versions of the sequential-sampling models have been developed that elucidate the mechanisms governing metacognitive decision formation (Resulaj et al., 2009; Pleskac & Busemeyer, 2011; Moran et al., 2015; Kiani, Corthell & Shadlen, 2014). Specifically, these models have suggested that the same evidence accumulation processes underpinning perceptual decision formation inform metacognitive representation (see, Moran et al., 2015). This prediction has received some support from neurophysiological experiments in monkeys (Kiani & Shadlen, 2008; Zylberberg et al., 2016) and more recently humans (Tagliabue et al., 2019; Desender et al., 2016; Murphy et al., 2015; Bolt & Yeung, 2015). Although many questions about the functional role of decision-making signals in metacognitive judgements remain unclear. The present thesis aims to capitalize on the recent advancements that have made it possible to parse different stages of decision-making in human EEG (Kelly & O’Connell, 2015; O’Connell et al., 2012). This will further our understanding of the functional relationship of the multiple levels of processing in decision-making and how these contribute to the emergence of metacognitive experiences.

The aim of the introductory chapter is to clarify the key empirical and theoretical concepts surrounding perceptual decision-making and metacognition. A first section of the introduction will focus on the computational models as well as the research on the neural basis of perceptual decision-making across species. Afterwards, a detailed overview of the current computational models of metacognitive decision formation is provided, which will highlight how these models have shaped experimental studies on the neural underpinning of metacognitive judgements. A summary of the key findings in this domain is given subsequently, which will also highlight some of the gaps in the current literature that explores the neural basis of metacognition. The next section of the introduction will shift the focus from the neural investigations and instead discuss the validity of the traditional behavioural paradigms of perceptual decision-making and metacognition to measure real-world cognitive function. A brief overview of the challenges of these studies will be given, followed by general summary of some of the current support for this relationship. Lastly, the final portion of the introduction will give a general summary and outline of the main objectives of the current thesis.
1.2 Theoretical Framework - Perceptual Decision-Making

Over the past decades, neuroscience has greatly benefited from computational models of decision-making, which allow for thorough investigation into the underlying mechanism of decision formation in a variety of research domains (Ratcliff, Smith, Brown & McKoon, 2016). One of the first computational descriptions of the process of perceptual decision-making was provided by Signal Detection Theory (SDT; Tanner & Swets, 1954). SDT is a psychophysical model that proposes categorical decisions are formed by converting single pieces of noisy information into a decision variable (DV). This DV is evaluated with respect to a decision rule or criterion, which allows SDT to capture different response strategies (Mueller & Widemann, 2008). In binary choices, the DV relates to the ratio of likelihoods of the two possible outcomes and reflects the evidence in favour of one or the other choice alternative. SDT further suggests decision-making is stochastic in nature due to corruption of evidence through a combination of noise in the external environment and at the neural level. This allows SDT to quantify additional properties of decision-making, namely the sensitivity or $d'$, which reflects the level of discriminability between two choices, and response bias, which measures the preference of one choice over the other (Stanislaw & Todorov, 1999; Macmillan & Creelman, 1990). However, a substantial limitation of SDT is that it assumes that decisions are formed based on singular pieces of sensory evidence. This means that, while SDT forms predictions about the optimal level of evidence required for decisions, it does not account for important dynamical aspects of decision making behaviour such RT distributions or the speed-accuracy tradeoff (Pleskac & Busemeyer, 2012; Gold & Shadlen, 2007). For this reason, the development of sequential sampling models, which account for reaction time as well as choice accuracy by invoking a decision process in which multiple evidence samples are accumulated over time, represented an important breakthrough for the field.

1.2.1 Sequential-Sampling Models

A common assumption across all sequential sampling models is that perceptual decision-making requires the accumulation of multiple samples of sensory evidence over time into a decision variable (DV). This accumulation process continues until an action-triggering threshold or decision bound is crossed (Smith & Ratcliff, 2004, Forstmann, Ratcliff & Wagenmakers, 2016). The threshold is analogous to the stopping rule from SDT and determines the quantity of the accumulated evidence that is required for choice commitment (Gold & Shadlen, 2007). A key advantage of the accumulation process is that it serves to minimize the impact of momentary sensory noise (whether emanating from the physical stimulus or neural activity) on the decision making process (Usher et al., 2013; Ratcliff, Smith, Brown & McKoon, 2016).
While sequential-sampling models share the previous description of evidence accumulation as the basis of perceptual decision-making, the sequential-sampling framework remains an umbrella term that encompasses different classes of models, each with varying assumptions about how the accumulation process is implemented. One class of model implements decision making as a race-to-threshold between two competing accumulators that gather evidence favouring each choice alternative (Vickers, 1970; Brown & Heathcote, 2005; Bogacz et al., 2007). These models can accommodate any number of competing accumulators in the decision formation process and as such, can account for choices with more than two alternatives (Churchland, Kiani & Shadlen, 2008; Churchland & Ditterich, 2012). In contrast, in random-walk models the evidence is sampled into a single DV that accumulates the differential evidence towards two possible thresholds, one for each choice alternative. Specifically, the accumulation process can be approximated by the sequential probability ratio test, which provides the most efficient measure for deciding between two hypotheses (Gold & Shadlen, 2007). Crucially, while both classes of models might provide different mechanistic accounts of the perceptual decision formation process, both accumulator and random-walk models make nearly identical predictions at the behavioural level (Remington, 1969; Usher et al., 2013). Finally, further distinctions can be made between models based on the presence or absence of auxiliary parameters. For instance, some models include a ‘leak’ or ‘decay’ parameter, which causes the older samples of evidence in the DV to be discounted from the cumulative total (Bogacz et al., 2007; Usher & McClelland, 2001).

Perhaps the most common version of the sequential-sampling models is the drift-diffusion model (DDM). The DDM is a particular version of the random walk model and assumes evidence accumulation occurs with continuous sampling of sensory evidence across time without any leak of information in the DV (Ratcliff, 1976; Smith, 2000; Ratcliff, Gomez, & McKoon, 2004). The full DDM typically comprises the following parameters (see Figure 1.1): The DV starts out at the starting point \( z \), which varies uniformly across trials \( s \). The strength of the evidence entering the accumulation process is represented in the mean drift rate \( d \), which varies within a normal distribution across trials \( s \). This accumulation continues until the decision bound or threshold for one of the two alternatives (either \( z_b \) or \( -z_b \)) has been crossed. The model also accounts for processing delays unrelated to the decision process (e.g. delays associated with sensory encoding and execution of the decision-reporting action) with the non-decision time parameter \( T_{er} \) which is assumed to be uniformly distributed across trials \( s \).

Although the DDM has a relatively small number of parameters, it nonetheless captures complex behavioural features from variety perceptual decision-making paradigms in different cognitive domains including lexical memory, response inhibition and numerical discrimination (see Forstmann et al., 2016). The DDM furthermore allows for thorough explorations into the underlying
structure of decision formation process (Ratcliff, 1976, 1979; Smith, 2000; Ratcliff, Gomez, & McKoon, 2004; Diederich & Busemeyer, 2003; Smith & Ratcliff, 2004; Donkin et al., 2011; van Ravenzwaaij et al., 2012). For instance, the DDM provides an intuitive explanation for the occurrence of fast errors in many experiments through the starting point bias ($z$). Specifically, since the starting point varies across trials this means that on some trials the accumulation process starts closer to the incorrect boundary. In these cases, the DV is more likely to cross the incorrect decision bound, which will frequently lead to fast errors choices (Ratcliff & Rouder, 1998; Ratcliff & Smith, 2004). The model also provides an intuitive explanation for the occurrence of the speed-accuracy tradeoff through adjustments of decision bounds. Specifically, emphasizing accuracy increases the decision threshold, which reflects subjects adopting a more cautious response strategy (Ratcliff et al., 2001; Thapar et al., 2003; Rinkenauer et al., 2004; Zhang & Rowe, 2014). For a recent review that highlights the different applications of the DDM in neuroscience and a variety of other domains, see Ratcliff and colleagues (2016) as well as Forstmann et al. (2016).

Figure 1.1 A schematic depiction of the typical drift-diffusion process, which describes all parameters included in the full version of the drift-diffusion model (Figure amended from Wagenmakers, van der Maas & Grasman, 2007).
1.2.2 Limitations of Computational Models of Perceptual Decision-Making

Regardless of the success of sequential-sampling models in the investigation of the latent structure of perceptual decision-formation, the computational modelling approach has substantial limitations. First is the problem of ‘model mimicry’ which refers to the fact that competing model variants that specify functionally distinct mechanisms for the accumulation process can nevertheless make indistinguishable behavioural predictions and provide comparable fits to the behavioural data (Khodadadi & Townsend, 2015; Smith & Ratcliff, 2004). A particularly dramatic demonstration of this is evidence in studies comparing the drift-diffusion model (DDM) to the urgency-gating model, two models that are radically different in terms of the emphasis they place on the accumulation of evidence samples (Thura et al., 2012; Thura, 2016). Although this still under debate (Hawkins et al., 2015; Evans et al., 2017). This is particularly problematic because distinct model can point to very different psychological interpretations of the same behavioural phenomena. For example, a common observation in perceptual decision-making literature is that accuracy decreases with slower reaction times. In the standard version of the DDM, this decline in accuracy is captured by drift rate variability and attributed to fluctuations in the subject’s attention (Ratcliff, Smith, Brown & McKoon, 2016). However, the same behaviour can be explained by alternative models that allow for a ‘collapsing decision bound’, (Drugowitsch et al. 2012), thus attributing slow errors to a strategic adjustment of the decision bound caused by increasing time pressure to respond (Zhang et al., 2014; Tajima, Drugowitsch & Pouget, 2016; Pallestro, Weichart, Zederberg & Turner, 2018).

A second limitation of current modelling approaches is that, in order to fit a computational model to behavioural data, a parameter must be fixed to a single value as a ‘scaling parameter’. This is done to ensure the fitting procedure can settle on a single set of optimal parameters, since otherwise an infinite set of possible solutions exist for the model. In the standard version of the DDM, the within-trial noise is usually used as the scaling parameter and is fixed to an arbitrary value for all participants and conditions (Ratcliff, 2006; Voss, Nagler & Lerche, 2013). While it might be reasonable to assume that the within-trial noise is constant across all levels of an experimental manipulation, there is substantial neural evidence that suggests this assumption is not realistic when contrasting individual and groups. For instance, neurological disorders and ageing have been reported to directly increase the level of noise in the brain (Faisal, Selen, Wolpert, 2008; Park et al., 2017; Ruiz et al., 2019; Gareth et al., 2013). Such differences have to be taken into account during model construction and otherwise effects that are due to noise might be wrongly attributed to other parameters.

Both limitations highlight an important issue in the field of computational neuroscience. Namely, that there is a need in the field of mathematical modelling for clearer guidelines and consensus on the model fitting and contrasting procedures (Dutilh et al., 2018). This need for
consensus becomes even more relevant as the different variants of sequential-sampling models become more readily available in different toolboxes (Ratcliff & Childers, 2015). In this respect, neurophysiological experiments into the underpinnings of perceptual decision-making might be crucial, not only allowing researchers to gain a deeper understanding of decision formation. Importantly, these insights also provide a clear test of the validity of the mechanistic assumptions of models and in this sense can strengthen the ability to distinguish between competing model variants (O’Connell, Shadlen, Wong-Lin & Kelly, 2018).

1.2.3 Summary

The study of perceptual decision-making has strong roots in the domain of computational modelling and psychology. These models have provided a mechanistic exploration of the underpinning of decision formation, allowing for a deeper understanding of perceptual decision-making compared to the study purely behavioural patterns. The sequential-sampling framework and the drift-diffusion model in particular have proven to be a flexible tool that captures many of the behavioural patterns observed in perceptual decision-making, suggesting decision formation requires the accumulation of multiple pieces of sensory evidence up to an action-triggering threshold. Despite this, issues exist across computational modelling field that highlight the limitations of models to parse the latent structure of decision formation. This suggests a possible role for electrophysiological investigations in helping to guide the construction of the models of perceptual decision-making. The following sections will discuss recent advancements in identification and exploration of the neural signatures of evidence accumulation, providing an overview of the neural support for the sequential-sampling mechanisms in both humans and primates.

1.3 Neural Correlates of Perceptual Decision Formation

One of the main advantages of the sequential-sampling framework is that it provides testable hypotheses about the neural dynamics underpinning perceptual decision formation. Specifically, the hypothesis that sensory evidence accumulates over time into a decision variable (DV) has garnered great interest from neuroscience over the past few decades, leading to the identification of similar neural processes across species (Kiani & Shadlen, 2013; Kelly & O’Connell, 2015). The following sections will review the research from these investigations, focusing on findings from single-cell recordings in primates and non-invasive electrophysiological recordings in humans.
1.3.1 Effector-Selective Decision Formation in Primates

The earliest neural support for the sequential-sampling model comes from studies using invasive single-cell recording techniques in non-human primates (Newsome & Bare, 1988; Britten, et all, 1996; Roitman & Shadlen et al., 2002). These experiments adopted the now well-established random dot motion task (Britten, Newsome & Saunders, 1992; Andersen et al, 1990, for a review see Gold & Shadlen, 2007), in which monkeys were required to discriminate the overall direction of motion of a cloud of randomly moving dots by making a saccade to one of two choice targets (Figure 1.2 A). This perceptual task is well suited for explorations into the evidence accumulation dynamics proposed in the sequential-sampling models for several reasons. Firstly, it affords the experiment precise control over the strength of the decision evidence through manipulation of the number of coherent versus randomly moving. Secondly, because the dots chosen to move coherently is randomly varied on each frame, the task encourage the repeated sampling of sensory motion evidence. Finally, response times can be slowed down substantially by lowering coherence levels, which facilitates detailed tracing of neural dynamics during the period of decision formation.

A first area implicated in the decision formation process from single-cell studies using the dot motion paradigm is the middle temporal of the extrastriate cortex (MT/V5). Neurons in area MT show sensitivity to coherent motion information, displaying neural activity levels contingent on the strength of sensory evidence (Figure 1.2 B insert; Britten et al. 1992; Shadlen et al. 1996). Crucially, these cells do not adhere to the predicted patterns of activity of an evidence accumulation signal, since neural firing rates remain constant throughout the presentation of external evidence and diminish in the absence of sensory evidence (Gold & Shadlen 2001; Gold & Shadlen, 2000; Huk & Shadlen 2005). This suggests that neurons in area MT form a direct representation of the external sensory information that is fed to higher-level brain areas that are responsible for the decision making process itself (for a review, see Gold & Shadlen, 2007).

One such higher-level area appears to be the lateral intraparietal cortex (LIP; see Figure 1.2 B & C). In a series of elegant studies, Shadlen and colleagues (2006) demonstrated that firing rate of neurons in this area closely match the key predictions of sequential-sampling models. Firstly, LIP activity exhibits a gradual evidence-dependent, RT-predictive ramping of activity consistent with an accumulation process (Figure 1.2 B; Hanks, Ditterich & Shadlen, 2006; Heiser et al., 2005; Roitman & Shadlen, 2002; Shadlen & Newsome, 2001; Gold & Shadlen, 2001; Gold & Shadlen, 2000; Ditterich et al., 2003; Salzman et al, 1990, 1992). Secondly, LIP reaches a fixed threshold prior to saccade execution irrespective of evidence strength or RT consistent with the crossing of a decision threshold or bound (Figure 1.2 C). Further studies have demonstrated how the LIP neurons display altered activation patterns consistent with strategic bound adjustments across a variety of different
experimental manipulations including speed-accuracy emphasis (Ditterich et al., 2006; Churchland et al., 2008; Ditterich et al., 2012; Hanks, Kiani & Shadlen, 2014) and prior information (Gold, Law, Conolly & Bennur, 2008; Rao, DeAngelis & Snyder, 2012; Rorie, Gao, McClelland & Newsome, 2010).

Figure 1.2 Example of invasive single-cell recordings from the lateral intraparietal (LIP) and middle-temporal (MT) neurons in the macaque’s brain obtained in a random dot motion task (image adapted from Gold & Shadlen, 2007). A) Example of trial layout in the random dot motion task. In this paradigm, macaques were trained to make saccadic motion judgements based on the overall motion of a patch of dots. Firing rates were obtained for LIP neurons in the target and non-target receptive field (RF) of the response cues. B) Neural firing rates for the LIP across different coherent motion strengths, showing the evidence-dependent build-up in these neurons (solid lines). The dashed lines represent the non-target direction. Insert: firing rates across different coherence levels observed in area MT, which shows the absence of build-up dynamics observed in other areas. C) Response-aligned neural activity in the LIP, displaying the evidence-independent build-to-threshold crossing effect predicted by sequential-sampling models.

While much research has focused on area LIP in particular, evidence accumulation dynamics have actually been observed in multiple cortical and subcortical areas including the frontal eye fields (FEF; Gold & Shadlen, 2000, 2003; Spivey et al., 2005), the dorsolateral prefrontal cortex (dPFC; Barraclough et al. 2004, Sugrue et al. 2004) and superior colliculus (SC; Kim & Shadlen 1999; Shadlen & Newsome 1996). The relative contribution of these distinct areas to the evidence accumulation process remains to be determined. In fact, the domain of non-invasive human brain...
recordings has substantial progressed in parsing some of the key processing levels that allow for the sensorimotor transformation from sensory encoding to action commitment. Research has relied on three main methodologies to further understanding of the neural underpinnings of perceptual decision formation, which are Electroencephalography (EEG), magnetoencephalography (MEG) and functional Magnetic Resonance Imaging (fMRI). EEG and MEG are well suited for the investigations into perceptual decision formation due to the high temporal resolution of these methodologies. This differentiates these methods from other non-invasive recording techniques, such as fMRI, which has far greater spatial precision but measures neural activity in the order of seconds (for a recent review see, Mulder, van Maanen & Forstmann, 2014). In contrast, EEG records neural activity in the order of milliseconds, which allows for a direct tracing of the formation of decisions on the timescale on which they occur (Kelly & O’Connell, 2015). Despite this, imaging studies have sought to identify brain areas involved in the evidence accumulation process, aiming to circumvent the relatively lower temporal precision by making assumptions about how the abstract decision variable would behave across different conditions (for reviews see, Keuken et al., 2014; Heekeren et al., 2008). These studies have identified a number of candidate regions, including the left dorsolateral prefrontal cortex (Heekeren et al., 2006; Philiastides et al., 2011), the pre-supplementary motor areas (Keuken et al., 2014; Forstmann et al., 2008) and the bilateral anterior insula (Caspers et al., 2008, Triarhiou, 2007). However, the following sections will outline the neural support obtained through EEG and MEG for evidence accumulation framework, since these methodologies allow for a direct observation of the evidence accumulation dynamics on the timescale that they occur.

1.3.2 Effector-Specific Decision Formation in Humans

Investigations into the neural correlates of perceptual decision-making have focused on multiple levels of processing along the sensorimotor hierarchy. Initial investigations were guided by the results obtained through animal single-cell recording and focused on analogous neural circuits in humans that might be involved in the reporting of decisions. The following section will provide a brief overview of relevant EEG and MEG studies investigating the role of motor signals in decision formation.

Seminal evidence for the build-to-threshold dynamics at the motor level comes from a study from Donner, Siegel, Fries & Engel (2009). These researchers adopted a random dot motion task in which choice reports were delayed until the appearance of a response cue while measuring motor preparation and sensory encoding at the neural level with MEG. The response preparation dynamics was examined through the desynchronization of mu/beta band activity (12-36Hz), which affords insight into the evolving motor preparation over the premotor regions in both hemispheres
Stimulus encoding of the coherent motion was quantified through gamma band activity (64-100Hz) over the middle-temporal (MT) areas of the visual cortex. The results indicated that lateralized beta band activity desynchronised at a rate proportional to the evidence build-up in gamma power, which shows that evidence accumulation can be traced at the level of the motor response. Follow-up studies further cemented these results, replicating the evidence-dependent build up rate in the lateralization index (Siegel, Engel & Donner, 2011 Wyart, de Gardelle, Scholl & Summerfield, 2012; Kubanek, Snyder, Brunton, Brody & Schalk, 2013; Pape & Siegel, 2016), while also demonstrating a threshold crossing effect in the beta amplitude at response (de Lange, Rahnev, Donner & Lau, 2013; O’Connell et al., 2012; Kelly & O’Connell, 2013; Murphy, Boonstra & Nieuwenhuis, 2016; Fischer et al., 2018).

The traditionally studies utilised beta lateralisation index, which reflects the relative difference in motor preparation for the chosen decision, in order to investigate decision-related motor activation (Siegel, Engel & Donner, 2011 Wyart, de Gardelle, Scholl & Summerfield, 2012; De Lange, Rahnev, Donner & Lau, 2013). However, recent studies have started to investigate effector-specific motor preparation over the premotor areas of each hemisphere separately, which has allowed researchers to gain deeper insight into the dynamics that influence decision formation. For instance, research has shown a threshold crossing effect at response execution was observed in the motor preparation signals over the contralateral hemisphere, while ipsilateral amplitudes have been found to vary at response (Kelly & O’Connell, 2013). Similarly, speed pressure has been found to increase the starting point of effector-specific motor preparation in across hemispheres, pushing the accumulation closer to threshold prior to the onset of decision formation an effect that would not be readily observable in lateralisation indices (Murphy, Boonstra & Nieuwenhuis 2016; Steinemann, O’Connell & Kelly 2018). Taken together, these experiments demonstrate the functional involvement of motor preparation signals in perceptual decision-making. Furthermore, recent studies highlight the importance of investigations of both effector-specific motor preparation and lateralisation indices to gain a full understanding of how these signals are associated with decision formation.

1.3.3 Domain-General Evidence Accumulation Signals in Humans

Recent experiments have succeeded in identifying electrophysiological correlates of perceptual decision-making in humans analogous to the evidence accumulation signals observed through non-human recording techniques (for a review see, Kelly & O’Connell, 2015). In a highly influential study, O’Connell and colleagues (2012) combined a continuous gradual contrast change detection task with non-invasive neural recordings. By having a constant stream of sensory information as well as gradual stimulus changes these researchers were able to exclude stimulus-evoked sensory transients from the
EEG trace and hence obtain a clear view of neural correlates of the decision formation process that would otherwise be obscured due to global signal summation on the scalp (Magliero et al., 1984). Furthermore, the paradigm was designed specifically to parse the different stages of processing at the neural level. The stimuli consisted of a flickering annulus that elicited a steady-state visual evoked potential (SSVEP) over the visual cortex that functions as an index of the sensory encoding during contrast-change decisions. Additionally, participants were asked to respond via manual button presses, which allowed for measurement of effector-specific mu/beta band activity over the premotor areas (Di Russo et al., 2007; Pfurtscheller & da Silva, 1999). The results demonstrated the CPP displayed the key characteristics of the DV signals predicted by sequential sampling models. Firstly, the CPP build-up rate was found to index the cumulative sensory evidence over time measured as the cumulative amplitude of the SSVEP (Figure 1.3 A). Secondly, the CPP was found to reach a fixed amplitude at response execution, analogous to the threshold crossing effect, while the build-up rate and predicted reaction time and target detection probability (Figure 1.3 A). Thirdly, analogous patterns were obtained for the CPP in an auditory detection task, suggesting this signal represents evidence regardless of the sensory modality. Finally, when participants were required to mentally count the number of contrast changes, the CPP was found to significantly build up after each evidence onset, while mu/beta lateralisation disappeared in the absence of overt response requirements. In a follow-up study, Kelly & O’Connell (2013) used the random dot motion discrimination task to establish that the build-up rate of the CPP scales with the strength of the physical stimulus evidence as measured by motion coherence (Figure 1.3 C). An important additional observation in this study was that motor preparation signals (the lateralized readiness potential) also exhibited an evidence-dependent build-up but one that significantly lagged behind that of the CPP. Taken together, these studies suggest the CPP functions as a fully abstract supramodal evidence accumulation signal that acts as an intermediate stage between the sensory encoding and motor preparation level. Moreover, such a decision formation signature is unique to humans, since to date single-cell recordings in primates have yet to identify a similar abstract accumulation signal.
Figure 1.3 Domain-general evidence accumulation signals obtained in two separate experiments (figures amended from O’Connell et al., 2012; O’Connell & Kelly, 2013). A) CPP plotted by response times (RT) in the gradual contrast change detection. Time point 0ms on the left side of the panel, denoted by the black vertical line, indicates evidence onset. Time point 0ms on the right side of the panel indicates response execution. B) Grand average topography prior to response execution, which reveals a positive signal component over centro-parietal areas. C) CPP plotted across the different level of coherence in the random dot motion task. Time point 0ms on the left side of the panel, denoted by the black vertical line, indicates evidence onset. Time point 0ms on the right side of the panel indicates response execution. D) Grand average topography prior to response execution, which reveals a positive signal component over centro-parietal areas.

Similar to neurophysiological work in monkeys, recent studies have aimed to explore the sensitivity of these neural signals to experimental manipulations that influence decision-making behaviour. Twomey and colleagues (2016) explored the impact of the presence of absence of foreknowledge of stimulus-to-response (S-R) mappings on the effector-selective mu/beta and CPP signals. Participants performed coherent motion discriminations but had to withhold indicating their choices until a delayed response cue appeared. In the absence of S-R foreknowledge, effector-specific motor preparation only commenced after the response cue. In contrast, the CPP was not modulated by the foreknowledge of the response mapping, showing an evidence-dependent build-up that peaked at
the same latency and returned to baseline prior to the response cue in both conditions. Secondly, temporal uncertainty in the onset of evidence has also been found to influence neural decision-making signals. In a recent study, Devine and colleagues (2019) adopted two decision-making tasks where the onset of sensory evidence varied randomly between three delays. The CPP was found to commence its build-up around the time of the average onset time of the physical evidence demonstrating that evidence accumulation onset is subject to strategic control. Finally, the effect of the speed-accuracy tradeoff on decision-making signatures revealed functional differences between evidence accumulation dynamics measured through the CPP and mu/beta motor preparation (Steinemann, O’Connell & Kelly, 2018). Under speed emphasis, evidence-independent urgency was found to specifically alter effector-specific mu/beta activity in both hemispheres, pushing the motor preparation closer to threshold prior to evidence onset. However, this manipulation did not affect the amplitude of the CPP prior to the evidence. Additionally, the CPP exhibited a smaller peak amplitude in the speed condition in contrast to a baseline shift. Taken together, these findings suggest the accumulated evidence measured in this signal forms a direct index of the sensory stimulus accrued prior to response execution whereas mu/beta motor preparation reflects the decision threshold and strategic adjustments of the decision policy.

Finally, the CPP shows a great deal of similarities with another traditional centro-parietal component known as the P300 (P3b; Twomey, Murphy, Kelly & O’Connell, 2015). Since its discovery, the P3b has garnered great attention from neuroscience because of its sensitivity to multiple neuropsychological disorders (Verleger et al., 2013; Diner, 1985; Souza, 1995). However, while many theories have been proposed about the nature of the P3b, its functional role has remained unclear (for reviews see, Polich, 2007, 2012; van Dinteren et al., 2014). For instance, some of the dominant theories contend that the P3b reflects context updating (Donchin & Coles, 1988: Polich, 2003), orienting and response preparation (Nieuwenhuis et al., 2011; Yamaguchi et al., 2004) or surprise (Kopp & Lange, 2013). Additionally, evidence did emerge to suggest that the P3b might reflect decision-related processes with some experiments observing a systematic relationship between its peak latency and reaction times and that its amplitude was larger for detected versus undetected stimuli (Hillyard et al., 1971; Squires et al., 1973). However, until recently no formal investigations were conducted into possible role of the P3b as an evidence accumulation signal. Twomey and colleagues (2015) did a formal exploration of this hypothesis, showing that the P3b exhibits accumulation-to-threshold dynamics as predicted by the sequential-sampling models. These results further suggested a functional equivalence between the canonical P3b and the CPP, providing novel insight into the functional role of this well-studied ERP component as a dynamically evolving decision formation signal.
1.3.4 Summary

Neural investigations into the mechanical underpinnings of perceptual decision-making have identified multiple areas that exhibit key features proposed by the sequential-sampling framework. Non-human primate research with the random dot motion task has shown regions downstream from the extrastriate cortex have firing rates that show build-to-threshold dynamics. This sparked a parallel expansion of efforts to identify corresponding neural signatures of decision formation in humans with non-invasive methodologies. Research in this area has focused largely on two neural signatures. Firstly, a domain-general evidence accumulation signal, known as the centroparietal positivity (CPP), was identified that forms a pure index of the sensory evidence over time. Secondly, at the motor level a threshold-crossing effect was observed in the desynchronization of effector specific mu/beta band activity, which was found to be sensitive to strategic adjustments in urgency. One open question is how perceptual decision formation is related to metacognitive experiences of these decisions. This will be the focus of the following sections, which will demonstrate how the domain of metacognition has benefitted from the recent advancements in computational models and the identification neural signatures of perceptual decision-making.

1.4 Theoretical Framework – Metacognition

Perceptual decision-making underlies behaviour in many daily-life scenarios. For instance, imagine you are crossing the street and have to attempt to discriminate whether or not a distant object in traffic is an oncoming car. One potential method to perform this task would involve the repeated sampling of sensory evidence about the distant object, until you successfully recognise it as a vehicle. This type of evidence accumulation process is well described by the sequential-sampling framework and has garnered great interest from neuroscience (for reviews see Navajas, Bahrami & Latham, 2016; Yeung & Summerfield, 2012). However, recent studies also have started to investigate how the decision formation influences the sense of confidence, which seems to be inherent in the decision-making process (Yeung & Summerfield, 2012). In the previous example, imagine the difference between deciding about whether an object is approaching car when the roads are covered in fog. The same discrimination process needs to take place, but you might feel less confidence about your ability to recognize objects in the distance. This sense of confidence is crucial since it allows people to flexible adjust behaviour and learn from changes in the sensory environment particularly when external feedback is ambiguous or absent.

Metacognition in this context is defined as any process that ‘refers to knowledge of one’s own cognitive processes’ (Flavell, 1979). This description is widely adopted in the study of metacognition.
and implies a dual-process structure where metacognitive representations such as error detection, interact with ‘object-level’ representations (Nelson & Narens, 1990; Fleming, Dolan & Frith, 2012). Recently, however researchers have started to question this formalisation, since it extends the metacognitive label to any form of cognitive control as well as a variety of other psychological phenomena, which do not directly require a meta-level representation (Shea et al., 2014). For the purposes of the present thesis, metacognition is more narrowly operationalised as ‘behaviour about behaviour’ and reflects a metacognitive response about past or future behaviour (Fleming, Dolan & Frith, 2012; Fleming & Lau, 2014). This definition is preferred, since it means metacognition directly encompasses the ability to successfully evaluate one’s own decisions and in practice can be measured through overt subjective evaluations in perceptual decision-making (Fleming, Dolan & Frith, 2012). The following section will briefly outline some of the types of confidence reports adopted in this domain, highlighting the strengths and weaknesses of these measures.

1.4.1 Measures of Metacognition in Perceptual Decision-Making

Research into the relationship between perceptual decision-making and metacognition have previously adopted behavioural paradigms from various cognitive domains, such as memory (Chua, Pergolizzi & Weintraub, 2014), response inhibition (Murphy et al., 2015) and value-based decisions (de Martino et al, 2013). In these tasks perceptual judgements are typically followed by some form of metacognitive judgment, such as an error awareness rating (Charles, van Opstal, Marti & Dehaene, 2013) or confidence judgements (Zylberberg, Roelfsema & Sigman, 2014). In this context, the initial perceptual choice is considered to be the first-order or ‘type I’ decision and the metacognitive report the second-order or ‘type II’ judgement. (Zylberberg, Roelfsema & Sigman, 2014; Zylberberg, Barttfeld & Sigman, 2012; Fleming, Huijgen & Dolan, 2012; Boldt & Yeung, 2012; Steinhauser & Yeung, 2011; Charles, van Opstal, Marti & Dehaene, 2013; Gherman & Philiastedes, 2015). Although recent studies have also employed prospective confidence judgements (Fleming, Dolan, 2012; Siedlecka et al., 2016; Boldt, Schiffer, Waszak & Yeung, 2019) as well as integrated first- and second-order decisions (Kiani, Corthell & Shadlen, 2014; Van den Berg et al., 2016; Gugenmos, Wilbertz, Hebart & Sterzer, 2016; Zylberberg et al., 2016).

In a recent overview, Zehetleitner & Rausch (2013) outline three groups of subjective retrospective measures of metacognition. Firstly, visibility ratings are used to investigate the visual experience of sensory information on either categorical or continuous scales (Charles et al., 2013; Del Cul, Baillet, & Dehaene, 2007; Tagliabue et al., 2019). A second group of measures explores metacognitive experiences through post-decisional wagering (PDM), rewarding correct assessments of the first-order response, while either punishing incorrect estimations (Persaud, McLeod, & Cowey,
2007) or providing opt-out choices on certain trials (Gherman & Philiastedes, 2015). An advantage of this approach is that the wagering tools do not require language skills and therefore can be applied in the investigation of non-human metacognition (for a recent overview see, Insabato, Panuzzi & Deco, 2016). Moreover, post-decision wagering can be combined with other measures, in order to incentivise participants to give accurate ratings (see for instance, Moses-Payne et al., 2019). Finally, the most common method to assess metacognitive experiences is confidence ratings, where subjects are asked to judge the accuracy of their responses (Peirce & Jastrow, 1884). These ratings have been found to provide the most detailed insight into metacognitive process, capturing complex behavioural patterns, such as first-order performance and changes of mind (Zehentleitner & Rausch, 2013; Rausch, Müller, Zehentleitner, 2015; Charles & Yeung, 2019; although see, Sandberg, Timmermans, Overgaard & Cleeremans, 2010; Wierzchoń et al., 2014). Furthermore, in a follow-up experiment Rausch & Zehentleitner (2016) showed that visibility ratings capture subtly distinct processes on a contrast orientation task when compared to confidence judgements. The latter was found to provide a closer approximation of the accuracy of orientation whereas visibility ratings more directly reflected the physical strength of the stimulus (see also, Rausch, Hellman & Zehentleitner, 2018).

A further distinction can be made between the subjective indicators of metacognition, which involve subjects reporting on their experiences, and more detailed metrics of metacognition obtained through the application of computational models of metacognition. Specifically, Maniscalco & Lau (2012) proposed an extension of the classic signal detection theory (SDT) framework, which provides estimations of subject’s metacognitive abilities independent of the ‘type I’ sensitivity and response bias. However, while ‘type I’ parameters reflect the decision process with respect to an external stimulus, ‘type II’ properties are made contingent on the accuracy of the subject. In addition, ‘type II’ SDT defines analogous quantities for response bias, which measures the tendency towards over- or underconfidence, and sensitivity or meta-d’, which forms an indicator of the ability to correctly indicate high confidence for a given level of performance (Fleming & Lau, 2014). Another advantage of this approach is that d’ and meta-d’ are quantified on the same scale so they can be directly compared in a single metacognitive efficiency score, usually defined as meta-d’/d’ (Maniscalco & Lau, 2014; Barett, Dienes & Seth, 2013; Fleming & Lau, 2014). Metacognitive efficiency can be easily interpreted, since if meta-d’ > d’, this means subjects are more accurately indicating confidence compared to the ‘type I’ decision, which potentially indicates some form of post-decisional processing (Charles et al., 2013; Rausch & Zehentleitner, 2016). Comparatively, d’ > meta-d’ indicates metacognitive judgements are less accurate then the first-order choice and forms an indicator of further evidence accumulation (Fleming & Lau, 2014; Charles et al., 2013). A major limitation of type II SDT is that it does not provide a window into the temporal dynamics that govern the formation of a
representation of metacognition or deeper insight into the latent structure underlying this process (Fleming & Daw, 2017).

In summary, research into the relationship between perceptual decision-making has adopted a variety of methods to quantify metacognitive experiences. While multiple subjective measures exist, confidence judgements are by far the most popular instrument to measure metacognition, providing the most extensive insight into the metacognitive decision formation process. More recently, objective measures of metacognition have been developed through the SDT model, which allows for direct investigation into people’s ability to estimate their own performance. However, this framework does not provide a window into the latent structure of metacognitive decision formation. One solution to this problem involves the application of computational models based on the sequential-sampling framework. The following section will provide an overview of the models of metacognitive decision formation.

1.4.2 Computational Models of Metacognition

Bolstered by the success of the sequential-sampling framework in parsing the latent structure of perceptual decision formation, extended versions of these models have been developed in an effort to account for the emergence of a graded representation of confidence in addition to type-I decision making. A fundamental assumption of all these ‘decision locus’ models is that the information accrued in the decision variable is read-out for metacognitive judgements. Therefore, this framework presumes some level of direct access to the parameters that informed the initial choice or some property of the decision process (Peirce, 1877; Plescak & Busemeyer, 2010; Yeung, 2014; Davelaar, 2009). In contrast, ‘inferential models’ predict confidence is formed by sources of information separate from the evidence accumulation process (Moreno-Bote, 2010; Allen et al., 2016). The following section will provide an overview of the sequential-sampling models that aim to elucidate the functional role of evidence accumulation in the construction of metacognitive judgements, focusing on two classes of models that differ with respect to the locus of decision termination for the second-order decision (Yeung & Summerfield, 2012).

1.4.2.1 Decisional-Locus Models

Decisional-locus models generally assume that confidence ratings directly reflect the quantity of sensory evidence available at the time of the first-order choice. However, two categories of computational models can be observed within the decisional-locus framework that describe different mechanisms for the emergence of confidence. Firstly, Link (1992, 2003) formulated a version of the drift-diffusion model (DDM) in which confidence was estimated from the quality and quantity of the
accumulated evidence for the perceptual decision, measured through the drift rate \( (d) \) and decision bound \( (b) \) of the accumulation process (also see, Kiani & Shadlen, 2009; Fetsch, Kiani, Newsome & Shadlen, 2014; Kiani, Corthell & Shadlen, 2014; Zylberberg, Fetsch & Shadlen, 2016). Secondly, an extended version of the race or accumulator model has been proposed to account for confidence judgments. In contrast to the DDM, this model assumes independent accumulation traces for each response alternative. Therefore, confidence can be directly read-out from the difference in the level of evidence between choice alternatives at the time of the first-order response, with more equal activation across both accumulators leading to lower confidence (Vickers, 1977, 2001; Merkle & Van Zandt).

Decisional-locus models do suffer from drawbacks when attempting to capture certain common features of metacognitive behaviour. Firstly, research in metacognition has consistently observed higher confidence on correct decisions compared to error trials, even when the subjective difficulty is matched (Fleming, Huijgen & Dolan, 2012). The drift-diffusion variant of the decisional locus model does not provide an intuitive explanation for this, since the decision bounds are constant across different levels of accuracy (Plescas & Busemeyer, 2010). Secondly, the decisional-locus models also do not account for the infrequent occurrence of changes of mind in decision-making. This phenomenon reflects a unique characteristic of metacognition, namely choices where participants changed beliefs about the accuracy of their first-order decision after response commitment. Crucially, the occurrence of ChoM can only be explained when models allow for post-decisional processes, which will be discussed in the following section.

1.4.2.2 Post-Decisional Locus Models

In contrast to the previous class of models, post-decisional locus models all share the assumption that evidence accumulation in the decision variable (DV) continues after the first-order decision in order to inform confidence judgements (for a recent overview see Moran et al., 2015). Resulaj and colleagues (2009) were among the first researchers to extend the sequential-sampling framework to encompass post-decisional evidence accumulation processes. In a seminal study, these researchers examined the occurrence of changes of mind (ChoM) in a random dot motion task in which participants reported coherent motion judgements by moving a handle to a left- or rightward target location (Figure 1.4 A). On a small portion of trials participants were found to change the initial trajectory in favour of the opposite target location, indicating the occurrence of ChoM after motion onset (Figure 1.4 A, Insert). At the behavioural level, two trends characterised ChoM trials. Firstly, ChoM reflect a small proportion of the overall trials in the random dot motion task. Secondly, ChoM occurred more frequently following movements towards the incorrect location compared to correct choices. In order to explain these results Resulaj and colleagues (2009) proposed an extended
version of the drift-diffusion model (DDM), where the evidence accumulation in the DV is allowed to continue beyond the first-order decision bound \((b)\). Specifically, the evidence accumulation process persists until either a second ‘change-of-mind’ bound is crossed or until the response deadline for metacognitive judgements (Figure, 1.4 B). This model successfully predicted the average frequency of ChoM trials while also accounting for the relationship between accuracy and ChoM. Additionally, a follow-up study with a similar paradigm, where simultaneous motion and confidence were made, found this post-decisional accumulation model effectively predicted both changes of mind in the perceptual decision and confidence (van den Berg et al., 2016).

![Figure 1.4 Visual representation of the random dot motion task and the extended drift-diffusion model adapted from Resulaj et al. (2009). A) Schematic of the random dot motion task in which participants made motion judgements by moving a handle (black circle) to one of two target locations. Insert: motion trajectories for a single subject, on some trials trajectories change midway indicating changes of mind (ChoM). B) Extended drift-diffusion model (DDM) where accumulation continues beyond the initial decision bound (blue line), leading to either the crossing of a ‘change-of-mind’ bound after the first-order decision (red line) or further commitment to the initial decision (green line).](image)

In recent years, many variants of post-decisional evidence accumulation models have been developed, which make diverse assumptions about the underlying mechanisms that determine confidence. For instance, Ratcliff & Starns (2009, 2013) proposed an extension of the standard drift diffusion-model with independent evidence accumulators for every level of confidence. In contrast, Plescak & Busemeyer (2010) suggested a model in which evidence accumulation continues in a singular DV beyond the first-order decision bound until a metacognitive judgement is required (for similar models see, Yu, Plescac & Zeigenfuse, 2015; Moran, Theodorescu & Usher, 2015). More recently, Fleming & Daw (2017) proposed an alternative computational framework for metacognitive
evaluations, where post-decisional evidence accumulation occurs with respect to the accuracy of one’s own performance, in contrast to other models where the accumulation in the decision variable reflects specific choice alternatives. Importantly, while the models of metacognitive decision formation make different predictions about the latent structure of the second-order evidence accumulation process, they nevertheless make very similar predictions at the behavioural level (Morgan et al., 2015). Variants of post-decisional locus models can also be distinguished based on the assumptions they make about the nature of the post-decisional accumulation process. For instance, the model Plescak & Busemeyer (2010) assumes evidence accumulation throughout both first- and second-order decision formation is perfect without any loss of information. However, a recent extension of the model introduced a leak or decay parameters to the post-decisional accumulation through which evidence decays over time (Yu, Plescak & Zeigenfuse, 2015). Similarly, Moran and colleagues (2015) proposed a model where confidence is read-out from a DV accumulating towards a collapsing bound after the initial decision. Moreover, in some models the duration of the post-decisional processing only comprises a short time window, relying on information already present in the sensory pipelines (Resulaj et al., 2009; van der Berg et al., 2016). In contrast, other models do allow for longer post-choice integration but provide no clear cut-offs for the second-order accumulation (Plescak & Busemeyer, 2010; Yu, Plescak & Zeigenfuse, 2015). Finally, some models suggest physical evidence is required to drive the post-choice accumulation process (Resulaj et al., 2009; van der Berg et al., 2016), while other post-decisional locus model do not place constraints on the nature of the evidence accumulated after the first-order choice (Yu, Plescak & Zeigenfuse, 2015; Moran, Theodorescu & Usher, 2015; Fleming & Daw, 2017).

Regardless of the different assumptions, post-decisional locus models have provided novel insights into the latent structure of metacognitive processing and have captured many metacognitive behavioural patterns (for an overview see, Moran, Theodorescu & Usher, 2015). For instance, post-decisional locus models provide an intuitive explanation for the finding that confidence is lower on error trials, since the DV is more likely to regress to the mean in the post-decision window after inaccurate decisions (Figure 1.4 B; Plescak & Busemeyer, 2010; Resulaj, 2009). Secondly, post-decisional locus models can account for a variety of heuristic biases in metacognitive decision-making. For example, research has often shown a confirmation bias in post-decisional evidence accumulation, which creates an insensitivity to information that disproves the first-order choice (Zylberberg, Bartfelt & Sigman, 2016; Rollwage, Dolan & Fleming, 2018; Bronfman et al., 2015; Talluri et al., 2018). Different post-decisional locus models have suggested mechanisms for this processing bias, such as a leak of evidence in the post-decision accumulation process (Yu, Plescak & Zeigenfuse, 2015). Finally, the post-decisional locus models can further help elucidate trial-sequence effects, for instance the impact of previous decisions on the current accumulation process (Navajas, Bahrami & Latham, 2016).
1.4.2.3 Limitations of Computational Models of Metacognition

The application of the sequential-sampling framework in the study of metacognition has yielded novel insight into the latent structure of the second-order decision process (Navajas, Bahrami & Latham, 2016). Despite the relatively recent surge of interest in these models, to date only a handful of studies have formally contrasted the behavioural predictions of different versions of the sequential-sampling models in metacognition. This is especially relevant given the occurrence of model mimicry in the computational modelling field, which means that models invoking qualitatively different mechanisms for metacognitive decision formation are empirically indistinguishable because they make nearly identical behavioural prediction (Moran et al., 2015; Zisch et al., 2017). For instance, a recent comparison of the balance of evidence model (Vickers, 1977; Merkle & van Zandt, 2006), the two stage dynamic signal detection model (2DSD; Plescak & Busemeyer, 2010), the model of Resulaj et al. (2009) and the collapsing bound model (Moran et al., 2015) revealed that all four models produced nearly identical predictions about confidence judgements (Moran et al., 2015). Similarly, Zisch and colleagues (2017) obtained comparable behavioural predictions in a model comparison of the 2DSD (Plesckac & Busemeyer, 2010), the balance of evidence model (Vickers, 1977; Merkle & van Zandt, 2006) and the model of Ratcliff & Starns (2009, 2013), which showed all models except the balance of evidence model provided similar behavioural predictions.

A second limitation inherent to the application of the sequential-sampling framework to metacognition refers to the scaling parameters utilised across models. Model fitting procedures require one variable of the evidence accumulation model to remain constant across conditions (see, 1.3.3). By convention, the within-trial noise or variability parameter is usually selected for this purpose (Ratcliff, 2006; Voss, Nagler & Lerche, 2013), a tradition that was transposed when models were applied to the metacognitive domain (Busemeyer & Plesckak, 2010; Yu, Plesckak & Zeigenfuse, 2015). However, while this is assumption generally acceptable in the context of perceptual-decision making, there is substantial evidence that suggests internal and external variability directly impact and metacognitive decision formation (de Gardelle & Summerfield, 2011; Zylberberg, Roelfsema & Sigman, 2014; de Gardelle & Mamassian, 2014; Spence, Dux, & Arnold, 2016; Bang, Sekhar & Rahnev, 2018; Allen et al., 2016). With recent evidence, showing variability has a stronger influence on the second-order sensitivity and bias compared to the first-order decision process (Boldt, de Gardelle & Yeung, 2017). Therefore, it is possible effects attributable to within-trial noise are captured by other parameters in current model.

Finally, while not an overt limitation of sequential-sampling framework, most mathematical models have narrowly focused on the functional role of the type I decision variable in guiding
metacognitive judgments. In contrast, relatively few studies have proposed computational mechanisms that involve other sources of relevant information such as conflict (Davelaar, 2009). In this respect, neurophysiological explorations into the neural basis of metacognitive decision-making are crucial to identify the exact mechanism and information that governs the emergence of confidence. For instance, electrophysiological experiments have shown response conflict, defined as the coactivation of two mutually inhibiting response alternatives, influences the emergence of error awareness and the subjective experience of conflict at the neural level (Murphy et al., 2015; Desender et al., 2016). Importantly, the standard version of the DDM does not capture response conflict, since the biggest conflict occurs when both responses are equally activated (Yeung et al., 2004). In the standard DDM, this corresponds to the decision variable remaining at the starting point in the accumulation process and is therefore, confounded with the absence of evidence accumulation. The concept of response conflict more closely resembles the mechanism of confidence proposed in the balance of evidence models (Merkle & van Zandt, 2006; Vickers, 1977). However, an important difference is that response conflict can be extended to post-decisional processes as opposed to the balance of evidence models (Davelaar, 2009). Although to date, no mathematical modelling studies have directly investigated this possibility at the neural level.

1.4.2.4 Summary

The sequential-sampling framework has provided novel insight into the latent mechanisms that govern metacognitive decision formation, showing a functional role of evidence accumulation in the emergence of a graded representation of confidence. Research has only started applying these models in the domain of metacognition in recent decades. However, limitations present in the sequential-sampling models of perceptual decision-making are observed in this domain as well. Firstly, some evidence has suggested model mimicry occurs across models, although more research is required to fully understand the scope and diverging predictions of different models. Secondly, computational models adopted within-trial noise as a scaling parameter despite the significant evidence that variability in both internal and external evidence has a stronger impact on metacognitive judgements compared to perceptual decisions. Finally, computational models have largely focused on the functional relationship between the decision variable and confidence, leaving open questions about the role of other sources of information in the metacognitive decision process. One possible avenue to these problems is to explore the temporal dynamics in the emergence of confidence along different levels of the sensorimotor hierarchy. The following sections will provide a detailed overview of the neural evidence for these models.
1.5 Neural Correlates of Metacognition

Research into the latent structure of metacognition employing sequential-sampling models suggests that a representation of confidence can arise from the same evidence accumulation process that informed the first-order choice. Specifically, mechanisms have been proposed that suggest metacognitive judgements involve a direct read-out of the decision variable (DV) at the time of response or rely on a continuation of the accumulation after the first-order decision bound is crossed. However many model variants exists, which disagree about the latent structure of how the DV is translated in metacognitive evaluations. The predictions of different models can be tested at the neural level by capitalizing on the recent advancements made in the identification of neurophysiological correlates of decision formation. This research will be reviewed in the following sections, focusing on invasive recording in non-human primates as well as non-invasive recording in humans.

1.5.1 Effect-or-Specific Evidence Accumulation and Metacognition in Primates

The study of metacognitive abilities in non-humans has posed unique challenges to researchers, since it is impossible to obtain explicit confidence reports in animals. Recent experiments have circumvented this issue by developing paradigms that make it possible to infer whether or not an animal can act on internal representations of decision certainty (for reviews see, Insabatoa, Pannunzi & Deco, 2016; Hanks & Summerfield, 2017). For instance, Kiani & Shadlen (2009) utilised a random dot motion paradigm with an ‘opt-out’ procedure, where on some trials the animal could escape the decision in favour of a sure but small reward (Figure 1.5 A). Another example is the temporal wagering task developed for rodent studies (Kepecs & Mainen, 2012; Lak et al., 2014). This paradigm provides a graded measure of confidence by utilising a delayed reward procedure on some correct trials. During this delay, the animals have the option of starting the next trial instead of waiting. The waiting time before this button is pressed has been shown to be directly proportional to choice accuracy, suggesting it provides a valid measure of confidence (Lak et al., 2014).

Some of the earliest support for the relationship between neurophysiological signatures of evidence accumulation and metacognitive judgements comes from Kiani & Shadlen (2009). These researchers trained monkeys to perform a random-delay version of the random dot motion task. Crucially, on a minor portion of trials the animals were presented with an ‘opt-out’ choice, while spiking activity from neurons in the lateral-intraparietal cortex (LIP) was recorded (see, Kiani & Shadlen, 2013). Behaviourally, the probability of selecting the opt-out option was directly associated with probability of correct choices, occurring more frequently on low coherent motion trials. At the
neural level, Kiani & Shadlen (2009) first established that the firing rates of the LIP neurons showed an evidence-dependent build-up rate and a threshold crossing effect at response execution (see, Kiani & Shadlen, 2013). In contrast, on trials where the monkey selected the opt-out choice the same neurons were found to exhibit an intermediate pattern of activity (Figure 1.5 B, dashed lines), falling in between the firing rate of the neuron when the motion direction is in the target and non-target receptive field (Figure 1.5 B, solid lines). This suggests the opt-out choice was chosen when the accumulated evidence was particularly scarce (see also, Komura et al., 2013). Finally, computational models indicated that the monkey’s confidence in this context could be estimated through a combination of the quality of the accumulated evidence and the decision time, a pattern that was later replicated in humans (Kiani, Corthell & Shadlen. 2014; Zylberberg et al., 2016).

Figure 1.5 Schematic trial layout of the random dot motion task with ‘opt-out’ choices and neural recordings from lateral intraparietal (LIP) results (images adjusted from Zylberberg et al., 2016; Kiani & Shadlen, 2009). A) A typical trial of the random dot motion task, orange targets reflect the motion direction alternatives, while the red dot reflects a sure bet option that appears on 50% of trials. This allowed monkeys to gain a smaller but sure reward compared to correct choices. B) Firing rates in the lateral-intraparietal (LIP) cortex obtained through single-cell recordings in monkeys. The upper row shows LIP activity on the trials were no opt-out response option was given, while the lower row reflects the firing rates in the opt-out condition. The dashed lines reflect the activity in the LIP neurons when the sure bet option was selected, while the solid lines is the activity in the trials were this option was present but waived.
In a follow-up study, Fetsch and colleagues (2014) applied microstimulation to the motion sensitive middle temporal (MT) area in monkeys during a fixed-delay random dot motion task. The trained animals were found to be more likely to select the stimulated motion direction, replicating previous studies in this domain (for a review see, Gold & Shadlen, 2007). Furthermore, stimulation of area MT impacted opt-out choices in a manner consistent with how extra sensory evidence would influence certainty, leading to increased proportions of opt-out choices when stimulation was in the non-preferred target and vice versa. More recently, Zylberberg and colleagues (2016) showed the effect of evidence variability on neurons in area MT of monkeys. By adopting a novel version of the dot motion paradigm, which introduced different levels of variability across trials, these researchers showed that a higher level of noise induced faster responses that were less accurate but paradoxically decreased the proportion of opt-out choice. A residual motion energy analysis of the firing rates of neurons in area MT provided deeper insight into these behavioural patterns. Specifically, firing rates were found to ramp up more quickly when evidence was more variable and on trials were the opt-out choice was presented but not selected. These results indicate that sensory evidence is directly represented in firing rates of neurons in area MT and is used by the monkey to inform both confidence and perceptual decisions.

1.5.2 The Relationship between Domain-General Evidence Accumulation and Metacognition

Explorations into the neural underpinnings of metacognition in humans have started utilising a variety of non-invasive methodologies. Studies using functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) has started to investigate which structures of the brain are functionally involved in metacognitive computations (for recent reviews see, Rouault, McWilliams, Allen & Fleming, 2018; Fleming & Dolan, 2012). In particular, research has started to converge on a fronto-parietal network involving areas of the brain, such as the lateral prefrontal cortex (Lau & Passingham, 2006; Rounis et al., 2010; Fleming, et al., 2010; Cortese et al., 2016), the medial prefrontal cortex (Baird et al., 2013; De Martino et al., 2013; Molenberghs et al., 2016; Hilgenstock, Weiss & Witte, 2014) and interoceptive cortices (Ridderinkhof et al, 2004; Baird et al., 2013). Additionally, recent fMRI studies have started to investigate the neural basis of post-decisional evidence accumulation in metacognition, which demonstrates the involvement of distinctive brain areas in representing the post-decision evidence and the translation of this evidence into confidence ratings (Fleming, van der Putten & Daw, 2018).
Taken together, these experiments highlight the important insights that can be garnered from TMS and fMRI in the investigation of the neural underpinnings of metacognition. However, as mentioned earlier the temporal resolution of fMRI is suboptimal to gain a full understanding of the temporal dynamics that influence the emergence of metacognitive judgements, since blood flow generally occurs on a slower timescale than decision formation processes (Logothetis, 2008; Raichle & Mintun, 2006). Hence, electroencephalography (EEG) reflects an important extension to these experiments, allowing to directly investigate the assumption of the different models of metacognitive decision formation. To date, research exploring the emergence of confidence with EEG broadly falls into two categories discussed in the following sections.

1.5.2.1 Evidence for the Relationship between Domain-General Evidence Accumulation and Metacognition

A first line of experiments investigates the relationship between domain-general evidence accumulation in the first-order decision and confidence judgements. Gherman & Philiaistides (2015) adopted a task with an opt-out choice presented randomly across trials. Through multivariate discriminant analysis, these researchers isolated a parietal component that showed significantly lowered amplitudes when the opt-out choice was selected, compared to trials where the opt-out choice was present but waived. This signal was also sensitive to the strength of the evidence, which lends support to the idea that evidence accumulation signatures are read-out in order to inform metacognitive judgements.

More recently, Herding et al. (2019) adopted a vibrotactile discrimination paradigm, where participants had to discriminate a target frequency stimulus ($f_2$) compared to an earlier presented sample ($f_1$). This task allowed these researchers to estimate the subjectively perceived frequency differences, which reflect the tendency of subjects to weigh $f_2$ to the average set of stimuli presented as opposed to directly contrasting the target to $f_1$. Since no explicit metacognitive judgements were made throughout the task, confidence was measured indirectly as the probability of a correct response given the evidence (Lak et al., 2014; Urai et al., 2017). Results indicated the CPP amplitude traced the subjective evidence difference even when no objective difference existed between $f_1$ and $f_2$, resembling the patterns predicted by the statistical confidence. Tagliabue and colleagues (2019) investigated the relationship between CPP amplitude and subjective visibility ratings during a perceptual discrimination task. Results further extend on the findings of Herding et al. (2019), showing that the build-up rate and amplitude of the CPP after stimulus onset directly scales with the strength of the physical stimulus, as well as the subjective visibility of the sensory evidence. Furthermore, subjective visibility mediated the effect of the evidence strength in the CPP build-up rate, which shows
the level of the accumulated evidence during the decision formation process directly mirrors the subjective experience of the stimulus.

In summary, studies have gathered some support for the role of domain-general evidence accumulation in the emergence of metacognitive judgements. The CPP is a strong candidate to function as a read-out for confidence judgements without the need for additional signal transformations, since this signal has previously been shown to form a pure reflection of the cumulative sensory evidence and insensitive to urgency (Steinemann, O’Connell & Kelly, 2018). In this respect, the CPP differs from results LIP neurons in the primate brain, which show a sensitivity to both evidence and urgency. This results in a model where confidence is a function of the LIP amplitudes and the elapsed time for the decision (Kiani & Shadlen. 2009).

Nevertheless, many questions remain about the role of the CPP in the emergence of metacognitive judgements. For instance, the temporal dynamics of this accumulation process are understood relatively poorly. This is caused by the overall focus of studies on stimulus-aligned traces. However, a key prediction of some computational models of metacognitive decision formation is that the decision variable at the time of the response or in the post-choice window might be most informative of confidence ratings (Merkle & van Zandt, 2006; Plescak & Busemeyer, 2010). Hence, a full investigation of these dynamics requires analyses aligned to the initial response. Furthermore, recent evidence has shown temporal characteristics of the evidence accumulation process are strategically adjusted to the constraints of perceptual decision-making tasks (Devine et al., 2019), which might influence the ability to detect the emergence of confidence at the neural level. As such, understanding of these strategic adjustments and temporal features is crucial to gain deeper insights into the neural mechanics of metacognitive decision formation.

1.5.2.2 Post-decisional Evidence Accumulation and Metacognition

A second line of neurophysiological research explores the role of post-decisional evidence accumulation in the formation of metacognitive judgements. Initial support for this account came from the literature on error monitoring, which examines the neural signatures associated with the detection of action errors. Specifically, recent studies have demonstrated the latency and amplitude of the Error Positivity (Pe), a positive-going parietal component that arises after erroneous actions, is directly associated with emergence of error awareness (Wessel et al., 2011; Steinhauser et al., 2008, Steinhauser & Yeung, 2010; Hughes & Yeung, 2011; Endrass, et al., 2007; Nieuwenhuis et al., 2001; Murphy et al., 2012, 2015; Boldt & Yeung, 2015).

In a recent study, Murphy and colleagues (2015) adopted a go/no-go inhibition paradigm to explore the temporal dynamics of evidence accumulation in the emergence of error awareness. In this
task, subjects were required to press a button if the semantic content of a word was incongruent with the colour of the font, while responses were withheld on congruent trials or when the word was repeated on two subsequent trials. Crucially, participants were told to signal errors by pressing a second button as soon as they became aware of them, which allowed these researchers to precisely trace the emergence of error awareness at the neural level. Results revealed that the CPP continues to build beyond the initial perceptual decision at a rate that predicted both the timing and probability of error signalling (see also, Murphy et al., 2012). Furthermore, mistakes were associated with elevated response conflict at the time of the initial decision, measured through fronto-central theta band activity. Larger theta was associated with faster CPP build-up rate and higher error signalling probability suggesting that response conflict may function as an additional source of information that influences metacognitive judgements. In another study, Boldt & Yeung (2015) showed that a pattern classifier trained to detect differences in error awareness based on the Pe amplitudes could also successfully predict the level of confidence on correct decisions. This suggests a common mechanism might underlie both error awareness and confidence judgements. Finally, Desender and colleagues (2019) adopted a novel information-seeking paradigm, where participants could sometimes gather more information after an initial perceptual decision before committing to a final choice and confidence rating. Analysis revealed the CPP after the initial response was significantly modulated by the level of confidence and information-seeking choices, with higher amplitudes found on lower confidence and trials where additional stimulus information was sought. Additionally, a pattern classifier trained to decode low versus high confidence judgements from the EEG data also predicted information seeking choices, which suggests confidence plays a functional role in guiding information seeking behaviour (see also, Desender et al., 2018).

To summarize, studies of the neural underpinnings of perceptual decision formation have provided support for the hypothesis that post-decisional accumulation of evidence informs metacognitive evaluations. Recent studies have shown error awareness and confidence judgements might rely on the same neural mechanisms (Boldt & Yeung, 2015). Furthermore, Murphy et al. (2012) showed that post-choice response conflict provides a separate input to metacognitive representations, irrespective of the domain-general evidence accumulation. While studies have found support for post-decisional evidence accumulation, comparatively little is known about what information drives this continuation of accumulation in the CPP prior to confidence judgements. It is possible that sensory evidence for the first-order decision is re-examined from memory or alternatively, post-decision accumulation may depend entirely on the availability of external stimulus evidence (Resulaj et al., 2009’ Fleming, van der Putten & Daw, 2017; although see, Desender et al., 2018). Previous experiments have not attempted to explore this question, since every study so far interrupted external
evidence when the first-order decision was made. As such, the nature of the evidence accumulated in the CPP after the first-order decision remains unclear.

1.5.3 Motor Level Processes and Metacognition

Motor level processes have been heavily implicated in the construction of confidence in a multitude of experiments. Firstly, a recent behavioural experiment has shown that the subjective visibility of a stimulus increases when preceded by an irrelevant motor response, when the response modality overlaps with the motor commands for the visibility ratings (Siedlecka et al., 2019). Secondly, Gajdos and colleagues (2019) found subthreshold muscle activity in participant’s hands prior to responses on a perceptual discrimination task correlated with higher confidence (see also, Palser et al., 2018). Thirdly, Fleming et al (2015) applied transcranial magnetic stimulation (TMS) over premotor areas of the cortex during a perceptual discrimination task with confidence judgements. TMS pulses were found to disrupt the emergence of confidence regardless of their timing, occurring either prior to or after the first-order decision. Finally, imaging studies have also shown brain structures related to motor preparation contribute to metacognitive judgements (Fleming & Dolan, 2012), such as the pre-supplementary motor area (Heereman, Walter & Heekeren, 2015; Fleming, van der Putten & Daw, 2017) and the bilateral striatum (Molenberghs et al., 2016).

To date few experiments have investigated the role of mu/beta band motor preparation in the emergence of confidence. Specifically, Wokke et al. (2019) developed a diagnosis paradigm where participants formed decision about whether or not patches of dots indicated the presence of an illness while EEG was recorded. After every diagnosis, subjects indicated metacognitive adequacy, a measure of the ability to correctly indicate confidence, and strategy, which indexes if the diagnosis was more intuitive or rational. EEG analyses showed that beta power over the premotor areas was not associated with either metacognitive variables. Similarly, Herding and colleagues (2019) adopted a vibrotactile discrimination paradigm (see 1.5.2.1) that for an investigation into the relationship between left-hemispheric beta and the dynamics of the CPP. This study distinguished an early and late component in the CPP but only the late component exhibited similar activation patterns as a measure of statistical decision confidence. However, left-hemispheric beta was only associated with the early CPP component. These studies suggest pre-decisional beta power over the motor cortices is not associated with metacognitive outcomes. However, neither studies explored the temporal characteristics of effector-specific motor preparation in confidence judgements. Therefore, it remains an open question if response-aligned or post-decisional motor level processes shape metacognitive representations. One possibility is that effector-specific motor preparation signals indirectly influence metacognition through the experience of response conflict, which measures the coactivation of two mutually
inhibiting choice alternatives. Computational models (Davelaar, 2009; Yeung et al., 2004) tentatively support such an account but to date this prediction has yet to be tested at the neural level.

1.5.4 Summary

Recent advancements in the development of computational models of metacognitive decision-making have provided testable predictions that have guided many recent explorations of the neural underpinnings of metacognition. Research in non-human primates has demonstrated that neurons in areas implicated in the first-order sensory evidence accumulation process also reflect the observer’s confidence in these choices. In humans, most experiments investigated the role of domain-general evidence accumulation in metacognition, since this signature has been found to directly index the accumulated sensory evidence. Studies have suggested the amplitude of the CPP prior to the first-order perceptual decision is associated with metacognitive judgements. However, evidence accumulation has also been shown to continue into the post-decisional window to inform a graded representation of confidence or error awareness. In contrast, relatively little is known about how other levels in the sensorimotor hierarchy influence metacognitive representations, although response conflict has received some empirical support. The final section of this chapter will shift the focus from neurophysiological experiments and instead explore the relationship between daily-life experiences of decision-making and metacognition and the experimental paradigms commonly deployed in laboratory experiments in neuroscience. This will highlight a potential role of computational models of perceptual decision-making and metacognition to further enhance our understanding of daily-life experiences of (meta-)cognition as well as a novel avenue for data collection to test these relationships.

1.6 Examining Real-World Cognitive Function through Laboratory Tasks of Decision-Making and Metacognition

Laboratory experiments with computerised paradigms of perceptual decision-making and metacognition form an integral part of psychology, offering researchers detailed and empirically testable predictions about behaviour and neurophysiology. Nevertheless, an implicit assumption of this work is that these simplified tasks engage the same core mechanisms and strategic adaptations that govern daily-life decision-making and metacognition. One common method to test this assumption is to test for relationships between laboratory-derived metrics and self-reported real world cognitive and meta-cognitive abilities (for a review see, Kennis, Rademaker & Geuze, 2013). The following sections of the introduction will highlight some of the general challenges faced by experiments that aim to investigate these relationships. However, a full overview of all cognitive and metacognitive functions
that have been associated with perceptual decision-making and metacognition would fall outside the scope of the current thesis. For more comprehensive reviews on this literature see, Kennis, Rademaker & Geuzze (2013) and Caceda Nemeroff & Harvey (2014). Afterwards, computational models and online studies will be discussed as extensions to laboratory studies, which will reveal the potential contributions of both when exploring these relationships.

1.6.1 Challenges of Investigation of Real-World Decision-Making and Metacognition

Many studies have demonstrated associations between real-world cognitive abilities and laboratory tests of perceptual and cognitive functions (for instance, Green & Myerson, 2013; Martin, Potts, 2004; Stahl et al., 2015; Zermatten et al., 2005; Sonuga-Barke, 2002; Levine, Waite & Bowman, 2013; Sale, Anderson & Yantis, 2013; Sharot, Korn & Dolan, 2011). However, despite this wide application challenges have emerged across experiments that limit the interpretation of results across experiments. Firstly, meta-analyses examining the convergent validity of laboratory tasks, through examination of the correlations between different paradigms that are thought to measure the same construct, have oftentimes observed only weak to moderate correlations (Duckworth & Kern, 2011; Green & Myerson, 2013; Aleman et al., 2006; Nair, Palmer, Aleman & David, 2014). For instance, a recent meta-analysis on trait impulsivity observed only a moderate convergent validity across different tasks, noting the wide variety of correlations within and across types of paradigms that are thought to measure self-control and inhibition (Duckworth & Kern, 2011). Secondly, the nature of the observed relationships between task-related behaviour and questionnaire construct can be inconsistent across experiments. For example, research investigating the relationship between perceptual decision-making and perfectionism has shown higher perfectionism induces a more cautious response strategy (Barke et al., 2017; Stahl et al., 2015; Schrijvers et al., 2010). However, results across studies have varied significantly, with some researchers noting the opposite pattern or no significant association between perfectionism and behavioural outcomes (Tops et al., 2013; Drizinsky, Zülch, Gibbons & Stahl, 2016).

1.6.2 Application of the Sequential-Sampling Framework in the Study of Real-World Cognition Functioning

Investigations into the relationship between behavioural markers of perceptual decision-making and metacognition with real-world cognitive functions have often yielded inconsistent results (Tops et al., 2013, Barke et al., 2017). This might reflect, at least in part, the issue that behavioural
variables in traditional laboratory perceptual decision-making paradigms are subject to a wide range of underlying influences and processes, which might counteract or nullify upon averaging. A solution to this issue is to adopt computational models, such as the sequential-sampling framework, that decompose human behaviour into the latent decision formation mechanisms not readily observable in human behaviour (Forstmann et al., 2016; Ratcliff, Smith, Brown & McKoon, 2016). Indeed, studies have shown that the sequential-sampling models, and in particular the drift-diffusion model (DDM), are a powerful tool to explore individual and group differences in decision formation in a variety of domains, such as ageing (for a recent review see, Dully, McGovern & O’Connell, 2017), clinical populations (Banca et al., 2014; White, Ratcliff, Vasey & McKoon, 2009; Pe, Vandekerckhove & Kuppens, 2013; Metin et al., 2013) and intelligence (Ratcliff et al., 2010, 2011; Schmiedek et al., 2007).

More recently, experiments have started to capitalise on technological advancements in online recruitment and data collection in order to investigate whether differences between the drift-diffusion model parameters in clinical groups are also observable in larger naturalistic samples. For instance, multiple studies have replicated the finding that the severity of obsessive-compulsive symptoms is associated with increased decision thresholds in the general population (Hauser et al., 2017; Marton et al., 2019) and clinical populations (Banca et al., 2014), although the application of computational models has yielded mixed results across experiments (Rouault et al., 2018; Hauser et al., 2018). Nevertheless, this online approach has great potential to explore the validity of computational models of perceptual decision-making. Yet, to date little research systematically has adopted this approach to investigate the relationship between the sequential-sampling framework and other measures of real-world decision-making and metacognition.

1.6.3 Metacognition and the Study of Real-World Cognitive Functioning

Similar to the relatively sparse nature of research on the relationship between perceptual decision-making and daily-life cognitive processes, few studies have investigated if metacognitive behaviour in computerised decision-making tests involve the same processes used in daily-life decision-making and metacognition. This question has received some attention in the domain of cognitive aging. For instance, Harty and colleagues (2013) showed older adults have diminished error awareness on a response inhibition task, which was associated with poorer attention and memory function in daily-life. Similarly, Fitzgerald, Mahnaz & Dockree (2017) showed that metacognitive efficiency, quantifying how efficient subject’s metacognitive judgements discriminate between correct and incorrect choices, in older adults significantly correlates with real-world cognitive memory and attentional failures measured.
Further evidence for this relationship comes from the investigation of metacognitive abilities in online studies. For instance, Rollwage, Dolan & Fleming (2018) provided evidence for a link between metacognitive sensitivity in perceptual decision-making tasks and radical political beliefs. Specifically, these researchers showed that radical beliefs were associated with decreased metacognitive sensitivity and a greater insensitivity to post-decisional evidence that disconfirms the first-order decision. Secondly, Rouault and colleagues (2018) found that psychiatric symptom scores predicted confidence biases but not objective accuracy in a perceptual decision-making task. An additional factor analysis identified two dimensions underlying psychiatric symptom scores. Specifically, a depressive-anxious symptom cluster that was associated with lower confidence and increased metacognitive efficiency, and a second dimension associated with obsessive and intrusive thoughts, which was associated with higher confidence and lower metacognitive efficiency. However, the relationship between confidence bias, metacognitive efficiency and psychiatric symptoms has been inconsistent across studies (Moses-Payne et al., 2019; Hauser et al., 2017). A further complication to in these experiments is that multiple studies in this domain have utilised some form of adaptive staircase procedure (for instance see, Fitzgerald, 2017; Rouault et al., 2018), which has recently been suggested to inflate estimates of metacognitive efficiency (Rahnev & Fleming, 2019). Since the amount of inflation is correlated to the stimulus variability, it is not clear how this would impact the observed results in previous studies because stimulus variability is likely to be systematically associated with psychiatric symptoms as well.

Taken together, these experiments provide insight into the potential link between metacognitive behaviour in perceptual decision-making tasks and real-world cognition. However, many questions remain about the nature of this relationship. For instance, while metacognitive performance has been associated with discrepancy scores of daily-life awareness, which contrast self-reports and informant reports, it remains unclear to what extent subjects’ direct estimations of real-world metacognitive experiences are associated with metacognitive behaviour in perceptual decision-making. Moreover, explorations differ on what metacognitive behavioural variables are associated with real-world cognitive functions. This suggests more systematic research is required to fully understand the scope and nature of these relations.

1.7 Thesis Overview and Objectives

The purpose of this introductory chapter was to provide a detailed overview of the theoretical and empirical literature that investigates the relationship between perceptual decision-making and metacognition. In order to accomplish this, the chapter provides an overview of recent advancements in computational models, particularly the sequential-sampling framework, which has shaped the main
theories on how metacognitive representations might arise in the context of perceptual decisions. Specifically, most mathematical models of metacognitive decision formation have suggested the accumulated sensory evidence decision variable might be read-out for metacognitive judgements but there is substantial disagreement regarding the exact nature of that read-out. The chapter also outlined progress in the discovery of neurophysiological correlates of perceptual decision-making in primates and humans, which has helped to test fundamental assumptions of the computational models about the underpinnings of perceptual decision-making. Finally, the current evidence for the involvement of these neurophysiological signatures in metacognitive judgements was summarised. This highlighted some of the limitations of experiments in this domain, including the understanding of the temporal dynamics of sensory evidence accumulation, the involvement of motor level processes and the impact of temporal uncertainty of evidence duration in the emergence of a representation of confidence. These issues are important, since this furthers our understanding of the functional role of metacognition plays in adapting and learning from perceptual decisions.

The present thesis aims to build on recently developed paradigms from human electrophysiology (EEG) that make it possible to parse distinct information processing stages in the perceptual decision-making process. Here in particular the thesis focuses on establishing the distinct functional contributions and temporal dynamics of domain-general evidence accumulation (CPP) and limb-specific motor preparation (mu/beta desynchronization) in the emergence of choice confidence (Kelly & O’Connell, 2015; Steinemann, O’Connell & Kelly, 2018).

The aim of the research presented in Chapter 2 is twofold. Firstly, two separate EEG experiments will investigate how temporal uncertainty in evidence duration and response modalities influences the accumulation of evidence in perceptual decision-making and the emergence of decision confidence. Previous research has suggested this causes strategic adjustments in the accumulation process. However, to date no study has investigated how foreknowledge, or lack thereof, influences the emergence of choice certainty. Secondly, this study will explore if response conflict, measured through effector-specific mu/beta desynchronization and theta band activity, can function as a source of information for confidence judgements. This experiment aims to extend on previous findings in this field, which has shown theta band activity influences error awareness, while also providing novel insight into the functional role of distinct levels of processing along the sensorimotor hierarchy in the construction of choice confidence.

Following this, Chapter 3 will provide a natural extension of these findings and examine how pre- and post-decisional evidence accumulation influence metacognitive judgements. Some research in the error-monitoring domain has suggested that after errors the CPP continues to accumulate evidence to inform error awareness. However, to date there have been few systematic investigations that have
demonstrated the CPP continues to accumulate after the first-order decision outside of errors and whether this post-decisional activity is predictive of delayed confidence judgements. Additionally, this study further aims to provide novel insight into the neural mechanisms underlying changes of mind by investigating effector-specific mu/beta motor signals as well as the domain-general evidence accumulation in the CPP. Finally, this experiment will aim to address whether or not post-decisional evidence accumulation processes are contingent on the presence of external stimulus presentation or can occur in the absence of such information.

Chapter 4 will focus on the fundamental assumption that perceptual decision-making tasks and models tap into the same cognitive processes that govern daily-life cognitive functioning. This experiment aimed to contribute to the emerging literature that focuses on this relationship, capitalising on recent technological advancements in online data collection. Specifically, this study collected data from a large sample of participants, who performed an online version of the random dot motion task with confidence ratings and completed a test battery of questionnaires that measure daily-life cognitive and metacognitive experiences. Behavioural data for each subject was decomposed into the corresponding parameters of the standard drift-diffusion model, while metacognitive efficiency and bias were also quantified. These variables were correlated against the questionnaire scores of subjects, which allowed for a thorough exploration between the relationships of the mechanical underpinnings, metacognition and real-world cognitive and metacognitive experiences.

Finally, Chapter 5 contains a general discussion, which summarises the main research contributions of this thesis and provides suggestions for potential future research.
Chapter Two
Tracing the Emergence of a Graded Representation of Choice Confidence across Multiple Levels of the Sensorimotor Hierarchy

2.1 Introduction

Recent developments in computational modelling have proposed that the same evidence accumulation process that underlies perceptual decision-making might also govern the emergence of metacognitive judgements, suggesting that a unified account of decision making and metacognition may be within reach (Yeung & Summerfield, 2012; Moran, Theodorescu & Usher, 2015). Compelling support for this contention has also been garnered from recent explorations of neural decision signals across species (Kiani & Shadlen, 2008; Kiani, Corthell & Shadlen, 2014; Zylberberg et al., 2016; Tagliabue et al., 2019; Herding et al., 2019; Desender et al., 2019; Boldt & Yeung, 2015; Murphy et al., 2015; Desender et al., 2016). However, beyond the basic contention that evidence accumulation processes might function as a common neural currency between perceptual decision-making and metacognitive judgements, existing models disagree regarding precisely how and when the evidence accumulation process is read-out to inform metacognition. For example, some models suggest confidence can be read-out from the activation of the unchosen response (Vickers, 1977, 2001; Merkle & van Zandt, 2006) or reflects a combination of the quantity of accumulated evidence with other factors such as evidence quality or elapsed time (Kiani & Shadlen, 2009; Kiani, Corthell & Shadlen, 2014; Zylberberg et al., 2016; Yeung & Summerfield, 2012).

Evidence for the relationship between perceptual decision-making and metacognitive judgements comes from two major sources. Firstly, invasive recordings in primates have shown neural populations involved in perceptual decision formation also are informative for certainty of these decisions (Kiani & Shadlen, 2008; Zylberberg et al., 2016; Fetsch et al., 2014). Secondly, in humans most evidence comes from experiments that have focused on the role of the centro-parietal positivity (CPP), which indexes the accumulated sensory evidence (O’Connell, Dockree & Kelly, 2012; Kelly & O’Connell, 2015; Steinemann, O’Connell & Kelly, 2018). Investigations into this neural signature have suggested the amplitude of the CPP covaries with subjective visibility ratings (Tagliabue et al., 2019);
the experience of conflict (Desender et al., 2016), error detection (Murphy et al., 2015; Bold & Yeung, 2015) and the decision to opt out of choices in favour of smaller but guaranteed rewards (Gherman & Philiastedes, 2015). Additionally, the P3b, an ERP component that bears a striking functional similarity to the CPP (Twomey et al., 2015), has also been shown to index discrimination confidence (Hillyard et al., 1971; Squires et al., 1973) and experimental manipulations of that influence certainty (Mars et al., 2008; Duncan-Johnson & Donchin, 1977). However, many questions about the involvement of the CPP in the emergence of confidence remain. Firstly, some computational models suggest the level of the accumulated evidence at response is most predictive of confidence judgements (Vickers, 1976, Merkle & van Zandt, 2006). Despite this, most studies investigating the CPP and P3b have focused on stimulus-aligned, trial-averaged peak amplitude measurements and did not examine amplitude modulations at the time of choice commitment (Tagliabue et al., 2019; Herding et al., 2019; Gherman & Philiastedes, 2015; Squires et al., 1973; Desender et al., 2016). Secondly, while initial experiments have found a relationship between the CPP and metacognitive experiences, relatively little is known about the temporal characteristics of the emergence of choice confidence in this domain-general evidence accumulation signal. In a recent study, Steinemann and colleagues (2018) found that increasing speed emphasis lowered both the amplitude of the CPP at the time of response execution and participants’ choice accuracy, while mu/beta motor preparation over the contralateral hemisphere of the chosen option reached a stereotyped amplitude irrespective of speed or accuracy emphasis. Additionally, speed instructions increased the starting level mu/beta activation while failing to impact the CPP prior to evidence onset. This suggests the CPP amplitude provides a pure index of cumulative sensory evidence, which could be directly read-out for representations of choice confidence without the need for any signal transformations. This contrasts with effector-selective decision signals such as premotor beta and LIP activity, which combines sensory evidence with other strategic signal components such as urgency (Steinemann et al., 2018). Moreover, recent studies have shown that accumulated evidence in the CPP returns to baseline prior to response execution in fixed-delay tasks (Twomey, Kelly & O’Connell, 2015) and that the onset time of the evidence accumulation can be strategically adjusted when the timing of evidence is uncertain (Devine et al., 2019). Therefore, exploring the influence of these temporal characteristics in the emergence of confidence is crucial in order to fully understand the relationship between the mechanics of evidence accumulation that shape metacognitive judgements.

Another limitation of most existing studies that investigate the relationship between perceptual decision-making and metacognition is that these solely focus on one decision-related signal or processing level (Gherman & Philiastedes, 2015; Desender et al., 2016; Tagliabue et al., 2019; Boldt & Yeung, 2015). As such, little is known about the distinct contributions that each signature may have
towards the emergence of metacognitive judgements. Specifically, effector-specific mu/beta motor preparation and lateralisation indices have been implicated in perceptual decision formation (Donner, et al., 2009; De Lange et al., 2013; Gould et al., 2012; O’Connell et al., 2012; Kelly & O’Connell, 2015). Wokke and colleagues (2017) found a significant relationship between mid-frontal theta and metacognitive adequacy, a measure of the accuracy of confidence ratings, but found no systematic relationship between beta band activity over the premotor areas and metacognitive adequacy. Similarly, Herding et al. (2019) did not observe a systematic relationship between beta and statistical decision certainty in a vibrotactile discrimination task. A limitation of these studies is that these researchers did not measure effector-specific mu/beta motor preparation, instead using a singular response effector. This means that the activation for the unchosen or ipsilateral effector is unclear and as such, to date no study has simultaneously investigated the involvement of effector-specific and domain-general decision-making signatures in the emergence of confidence. Despite this, there is some evidence that alternative sources of information influence metacognitive judgements. Firstly, post-decisional evidence accumulation involves distinctive cortical areas to those involved in perceptual decision formation (Fleming, van der Putten & Daw, 2018; Fleming & Daw, 2017). Secondly, research has shown mid-frontal theta band activity is implicated in the emergence of error awareness as well as metacognitive efficiency (Murphy et al., 2015; Wokke et al., 2017). This neural signature has long been considered as an index of response conflict that function as cue for cognitive control and action (Cohen & Cavanagh, 2011, Cohen & Donner, 2013; Cavanagh et al., 2012). The exact nature of activation in the theta band has remained unclear, with some accounts suggesting it reflects the read-out of two competing evidence accumulators (Vickers, 1979, 2001; Merkle & van Zandt, 2006) and others that it reflects the co-activation of action alternatives at the motor level (Yeung et al., 2004; Botvinick et al., 2001). Finally, motor levels processes have implicated in the emergence of confidence in multiple studies (Siedlecka et al., 2019; Gajdos et al., 2019; Palser et al., 2018; Fleming et al., 2015).

Capitalising on recent studies that have successfully parsed different stages of processing during perceptual decision making (Steinemann, O’Connell & Kelly, 2018; O’Connell & Kelly, 2013, Kelly & O’Connell, 2015), the aim of this chapter is twofold. Firstly, to provide novel insight into the temporal dynamics of the emergence of metacognitive representations in the domain-general evidence accumulation of the CPP and effector-specific mu/beta motor preparation (8-30Hz) across the premotor areas of both hemispheres (Steinemann, O’Connell & Kelly, 2018; Kelly & O’Connell, 2015). To achieve this, two experiments were conducted that employed a random-delay version of the random dot motion task in which participants made simultaneous first- and second-order decisions upon the appearance of a temporally unpredictable response cue. This allowed for an investigation of the effect
of temporal uncertainty in the evidence duration in on perceptual decision formation and how this influenced the emergence of a representation of confidence. The second aim of this study was to provide a deeper understanding of the relationship between mid-frontal theta band power (5-7Hz), motor-level conflict and metacognitive judgements (Murphy et al., 2015; Wokke et al., 2017). This was accomplished by varying foreknowledge about the motor requirements across both studies. If theta band activity represents the difference between competing evidence accumulators, as opposed to motor level processes, a modulation of by confidence would emerge in this neural signature during decision formation even when the appropriate motor command is unclear.
2.2 Methods

2.2.1 Participants

2.2.1.1 Experiment 1: Saccadic Dot Motion Task

Twenty-four subjects aged 19-35 (11 males, 13 females) were recruited to take part in two testing sessions on separate days during which they performed a random dot motion discrimination task. All participants had normal or corrected-to-normal vision, no history of personal or familial neurological or psychiatric illness and no personal or family history of epilepsy or unexplained fainting. One subject was removed from the dataset retrospectively after they reported that they failed to meet one of the inclusion criteria. Two further subjects were removed from all analyses due to excessive blink and/or EEG artefact (>50% trials lost). The final sample size for this study therefore consisted of a total of 21 participants (11 females, 10 males; Age: M = 21.42, SD = 1.56).

Participants received a gratuity (€35) or research credits in compensation for their time. To ensure compliance with all instructions participants were informed that a monetary bonus could be earned over the course of the two testing sessions for correctly estimating confidence and performance on a trial-by-trial basis throughout the experiment (see ‘Design and Procedure’). Monetary bonuses could be earned of up to €6.5 in extra payment and were paid after the experiment concluded, ranging from €1 to €6 (M = 3.60, SD = 0.80). Written informed consent was obtained from all subjects prior to the start of the experiment. Ethical approval for all procedures and methods was acquired from the Trinity College Dublin ethics committee and the experiment was conducted in accordance with the Declaration of Helsinki and European General Data Protection Regulations.

2.2.1.2 Experiment 2: Bimanual Dot Motion Task

Twenty-seven participants aged 18-32 (13 females, 14 males) were recruited to take part in a dot motion perceptual decision-making task with metacognitive judgements. All subjects had normal or corrected-to-normal vision, no history of personal or familial neurological or psychiatric illness and no personal or family history of epilepsy or unexplained fainting. Two people were removed from all electrophysiological analyses due to excessive blink and/or EEG artefact (>50% trials lost), their data were not retained for behavioural analyses. This led to a final sample size of 25 (12 females, 13 males; Age: M = 22, SD = 3). All participants received a gratuity of €35 or research credits in compensation for their time. Monetary bonuses of up to €6.5 were also given for accurate and correct confidence and motion responses across the experiment (see ‘Design and Procedure’). On average participants earned
a monetary bonus of €4.40 (SD = 1.10, range: 1-6). Written informed consent was obtained on the first day of testing prior to the experiment. All procedures and methods were fully approved the Trinity College Dublin ethics committee and the experiment was conducted in accordance with the Declaration of Helsinki and European General Data Protection Regulations.

2.2.2 Design and Procedure

2.2.2.1 Experiment 1: Saccadic Dot Motion Task

The current study uses a challenging version of the random dot motion task with variable evidence durations. In this paradigm, participants are required to judge the overall direction of motion (left or rightward) of a patch of dots after a response cue is presented. The current paradigm asked subjects to indicate motion direction and choice confidence simultaneously, through fixation on a portion of a dual-coloured dial (Figure 1. A). Testing took place across two consecutive days. On the first day, participants were introduced to the dot motion task and received training on the behavioural paradigm. Subsequently, performance was titrated to approximately 75% choice discrimination accuracy; ensuring subjective difficulty was similar across subjects at the start of the experiment (see ‘Staircase Procedure’ below). On the second day of testing participants performed 8 blocks of 72 trials (572 trials in total), during which electrophysiological and behavioural data were recorded. For the purposes of all analyses only data from the second day is considered. Both sessions took place in a dark, sound-attenuated room with participants seated in front of a 51 cm CRT monitor (luminance: 65.2 cd/m²; refresh rate: 75Hz; resolution: 1024 x 768). Participants were seated at a distance of ~57cm from the visual display, resting their head on a comfortable chin rest. Stimuli in this experiment consisted of random dot motion kinematograms (RDK), which were created in Psychtoolbox in Matlab version 2013b (Mathworks, Natick, MA). RDKs consisted of 75 white dots (size: 6x6 pixels) which were presented within a circular aperture (outer radius = 4˚) against a grey background. The random dot motion task used a self-paced rhythm in which participants initiated trial by pressing the spacebar. Next, a central white fixation point appeared on the screen, followed 400ms later by the appearance of the dot motion stimulus. The position of the dots in the circular aperture was updated randomly for 1500ms on every frame, creating the perception of incoherent motion during this initial period. Afterwards, a proportion of dots were randomly selected to move coherently in the same direction, either left or right along the horizontal axis at a fixed distance of 0.2 visual degrees compared to the previous frame. This resulted in an overall motion speed of 15 degrees per second. All other dots were displaced randomly to a new location every frame, while every 3 frames a novel set of coherently
moving dots were selected. This ensured participants could not reliably discern motion by following individual dots.

The percentage of dots moving coherently was determined prior to testing for every subject individually (see ‘Staircase Procedure’ below). The duration of the coherent motion was randomised across trials, lasting for 350, 500 or 750ms. After coherent motion concluded a response cue appeared, which consisted of a bicoloured dial (Figure 2.1 A). Participants simultaneously indicated motion and metacognitive judgements through a saccadic response to the bicoloured dial. The primary colours of this dial indicated the left- or rightward motion direction, while the gradient of the bicoloured dial reflected the overall confidence in this motion judgement. Participants were told perform saccades to darker colours when they felt very confident and use lighter colours to indicate lower confidence levels. Responses were registered once a stable fixation of 350ms was registered on the response dial. A confidence score was computed by rescaling the visual angle of the final fixation coordinates with the centre of the screen to a value on a 100-point scale. The colours and orientation of the dial were randomised across trials to ensure participants could not prepare responses prior to the onset of the response cue. Once the dial appeared participants were required to provide a stable fixation within 1500ms as soon as they identified what point on the dial reflected their motion and confidence. Feedback was given on a trial-by-trial basis as well as at the end of every block (see ‘Bonus and Feedback’ below).

2.2.2.2 Experiment 2: Bimanual Dot Motion Task

The bimanual version of the dot motion task followed procedures identical to the saccadic dot motion paradigm (see ‘Experiment 1: Saccadic Dot Motion Task’ above) except that the response cue consisted of a 6-point scale on which participants simultaneously indicated both the direction of motion and their confidence in this decision (Figure 2.1 B). The scale was presented immediately after the dot stimulus was withdrawn and ranged from ‘Certain Left’, ‘Probably Left’, ‘Maybe Left’, ‘Maybe Right’, ‘Probably Right’ and ‘Certain Right’, which were mapped to the ‘s’, ’d’, ‘f’, ’j’, ’k’ and ‘l’ keys respectively. The keyboard bindings of the 6-point scale remained constant throughout the experiment. Participants were instructed to use three fingers on each hand for every level of the of the 6-point scale. Specifically, the ring, middle and index finger of the left were bound to the ‘s’, ’d’ and ‘f’ key, while the index, middle and ring finger of the right hand were bound to the ‘j’, ’k’, ‘l’ keys. This allowed participants to provide simultaneous motion and confidence judgements. Responses were registered if any of the six keys pressed within 1500ms of the onset of the response cue. Feedback was given after every trial as well as at the end of every block (see ‘Bonus and Feedback’ below).
Figure 2.1 Schematic depiction of a typical trial in the saccadic and bimanual dot motion task. A) Trials began with a spacebar press, which started stimulus presentation after 400ms. For the first 1,500ms positions of all dots were randomly updated on a frame-by-frame basis in order to create the perception of random motion. Afterwards a proportion of dots were selected to coherently move on the y-axis across frames, creating motion favouring left- or rightward directions. The proportion of coherently moving dots was randomly reselected every
3 frames. The overall level of coherent motion was determined in a titration session prior to the experiment, which ensured similar levels of subjective difficulty across subjects. Durations of coherent motion varied randomly across trials (350, 500 or 750ms) and were interrupted by a response cue. Responses were given by performing a saccade to the portion of the confidence dial that reflected the motion and choice certainty within 1,500ms of the onset of the response cue. Colours and gradient of the dial were variable across trials to ensure participants could not prepare the motor response during evidence presentation. B) Timings of stimulus presentation were identical to the saccadic dot motion task. However, responses were given by pressing a keyboard button corresponding to a 6-point scale with three levels of confidence for each motion direction. The key bindings on the scale remained constant throughout the experiment. Participants were required to respond within 1,500 ms of the onset of the response cue.

2.2.2.3 Staircase procedure

In both experiments, participants were introduced to the behavioural paradigm on the first day of testing. Participants received instructions on how to perform the task and were trained with a brief version of the random dot motion task. Training commenced with a short block of 50 trials at a high coherence level, meaning almost the entire patch of dots moved coherently to the left or right on each trial. Once participants performed the task with close to 100% accuracy on the motion judgements and were comfortable concurrently indicating confidence and motion, the percentage of coherent motion was lowered over the course of short titration blocks. These consisted of 30 trials and continued until participants performed at roughly 75% accuracy. The average coherence level obtained through this staircase procedure in the saccadic motion task was 12.73% (SD = 4.89, range: 6-20), while the average coherence was 11.19% in the bimanual task (SD = 4.66, range: 6-25).

2.2.2.4 Feedback and Bonus

In both experiments, participants received feedback at the end of every trial in the form of a string of text presented for 500ms above the fixation point. This informed participants whether or not the motion judgement was correct or incorrect, with ‘Correct’ and ‘Error’ respectively. In the saccadic dot motion task, if no saccades were made prior to the onset of the response cue or if no stable fixation was registered within the response deadline participants were given ‘Clicked too soon!’ or ‘Too Late’ feedback. In the bimanual dot motion experiment ‘Too Fast’ and ‘Too Slow’ feedback was given to subjects when the response keys were prematurely pressed and when no response was registered within the response deadline. At the end of every block participants received feedback on their average accuracy and response time. This feedback remained on the screen until the experimenter pressed a button on the mouse. Finally, participants were awarded a bonus of maximally €6.5 based on their
performance on a random trial in every block throughout experiment. The bonus was computed with the following formula:

$$\text{Bonus score} = 0.5 \times \theta(\text{conf}_n, \text{accuracy}_n)$$

Where the monetary reward in a given block is calculated as 0.5 multiplied by a scaling parameter $\theta$. This parameter has a value between 0 and 1, depending on the confidence and accuracy on trial $n$. Higher scores were obtained on trials where subjects indicated high confidence on correct decisions and when participants correctly indicated errors. If the random trial selected on a given block was a miss or a premature response, no bonus was awarded. No information about the level of score was given to participants until the end of the experiment. This ensured the overall level of the bonus did not adversely influence performance on the dot motion task. Monetary bonuses were paid out after the experiment.

### 2.2.3 EEG acquisition and Preprocessing

Continuous EEG data were acquired using an ActiveTwo Biosemi system (BioSemi, The Netherlands) from 128 scalp electrodes digitized at 512 Hz. Vertical eye movements were measured with two Vertical electrooculogram (VEOG) electrodes placed above and below the left eye. Data were analysed using custom scripts in MATLAB (The MathWorks), drawing on EEGLAB (Delorme and Makeig, 2004) routines for reading in data files and spherical spline interpolation of noisy channels. Prior to preprocessing, continuous EEG data were detrended to remove the influence of slow drift from recorded channels. Afterwards data was low-pass filtered at 35 Hz and high-pass filtered above 0.1 with a Hamming-windowed sinc finite impulse response (FIR) filter. Data was then re-referenced offline to the average reference of all 128 electrodes, excluding external VEOGs.

EEG data was subsequently segmented into epochs. In both experiments, stimulus-locked epochs were extracted from -500 ms to 1,500ms relative to coherent motion onset and -1,500 to 1,500ms relative to the presentation of response cue. The length of the response cue locked epoch was selected to allow enough sample points for time-frequency decomposition. In the bimanual dot motion task, response-aligned traces were also extracted in the period spanning from –1500 to 500 ms relative to response execution. No response-locked traces were examined in the saccadic dot motion task. The reason for this is two-fold. Firstly, the uncertain nature of the response dial may have required additional saccadic decision processes that could have mixed with the sensory evidence accumulated in the CPP. Secondly, ocular artifacts occurred immediately after the response cue that would have lead to
disproportionate rejection of epochs. All epochs were baseline-corrected relative to the 200 ms interval preceding coherent motion onset.

Epochs were rejected in both studies if any scalp channel exceeded 100 µV or if the bipolar VEOG signal (upper minus lower) exceeded 200 µV at any point from 200ms prior to evidence onset until the onset of the response cue. However, in the bimanual traces the time window for rejection was extended from -200ms coherent motion onset to the final response. To avoid excessive loss of data during artefact rejection, channels with extreme variance and excessive artefact count were interpolated. An upper limit on the interpolated number of channels per subject was determined to avoid over-interpolation of the EEG data (defined as 10% of all recorded channels). Participants were removed from electrophysiological analyses if the blink and/or EEG artefacts still exceeded more than 50% after the interpolation stage. Accordingly, two people were excluded from the electrophysiological analyses in the bimanual dot motion task, while two people were removed from the final sample in the saccadic dot motion task. These participants were also removed from any behavioural analyses conducted. The single-trial EEG data were converted to current source density (Kayser and Tenke, 2006) to increase spatial selectivity and to reduce the spatial blurring effects of volume conduction. This was done to minimise the influence of the fronto-central negativity to the centro-parietal electrodes (O’Connell et al., 2012).

The time-frequency power decomposition for 8-30Hz of both stimulus and response-aligned windows in the bimanual dot motion task were obtained through the Fast Fourier Transformation (FFT). The FFT was computed using time segments of 256 sample points or 500 ms, sliding across both epochs in steps of roughly 20 ms or 8 sample points. The duration of the time segments was determined to allow for 4 cycles in the lowest frequency measured, allowing for accurate power estimation of the 8Hz frequency band. The power estimates obtained through the FFT were not baseline-corrected. A second set of power estimates from the 5-7Hz frequency range in the bimanual dot motion task were extracted through complex Morlet wavelet convolution (Cavanagh et al., 2009; Murphy et al., 2012). Defined as a set of Gaussian-windowed complex sine waves, the complex Morlet wavelets increased in 80 logarithmic spaced steps from 1 to 30 Hz, with the number of cycles per wavelet increasing from 4 to 12. The resulting power was normalised using decibel (dB) transformation (dB = 10*log10[- power/baseline]) to allow for direct comparison of different frequency bands. Power estimates were subsequently baseline-corrected by subtracting the subject-average power from -300 ms to coherent motion onset and was applied separately in each condition. The complex Morlet wavelet deconvolution was preferred for this analysis as it afforded greater control over frequency characteristics and temporal precision compared to the FFT. However, the FFT was also computed for the frequency range of 5-7Hz with both approaches yielding similar results.
2.2.4 Behavioural Analysis

In order to examine the effect of different coherent motion durations at the behavioural level in both experiments, data were averaged within every subject for every level of dot motion duration (350/500/750ms). Response accuracy was defined as the percentage of correct motion judgements across the experiment. Reaction times (RT) were measured as the elapsed time in millisecond from response cue onset until a decision was registered. Confidence was computed by averaging the single-trial confidence levels in both studies. This resulted in an average confidence score between 1 and 3 in the bimanual dot motion task, reflecting low, medium in high confidence in each choice, and between 0 and 100 in the saccadic dot motion task. The effect of coherent motion duration on each behavioural variable was explored using one-way repeated-measure ANOVAs. The relationship between accuracy, confidence and RT was further examined through one-way repeated-measure ANOVAs. In these analyses, accuracy was entered as a categorical predictor with two levels (error and correct) while confidence and RT were dependent variables. Post-hoc t-test were used to characterise the observed effects across every analysis and p-values were corrected for multiple comparisons with the Bonferroni-Holm procedure (Bonferroni, 1979).

2.2.5 Signal Analysis: Measurement Approach

Details in the following sections describe the procedure for isolating the neural correlates for analyses. Only the centroparietal positivity (CPP) and theta band activity were examined in both experiments. The procedure for the identification of these signals was identical across both studies. Effector-specific mu/beta band activity was only obtained in the bimanual dot motion experiment, since saccadic motion does not elicit traceable motor preparation at the neural level.

2.2.5.1 Centroparietal Positivity (CPP): Decision Formation

Sensory evidence accumulation was assessed through an examination of the temporal dynamics of the CPP. Channel selection for the CPP was conducted on a subject-by-subject basis from a cluster of predetermined electrodes. Electrode sites were identified based on the grand average topography immediately preceding the onset of the response cue, averaging the time window from -150 to -50ms across all trials and subjects (Figure 2.3 A, D & G; Figure 2.5 B, F & J). A visual inspection of this topography revealed a positive going ERP component across centroparietal areas, from which four and five electrodes sites were selected in the saccadic and bimanual dot motion paradigms respectively. For each participant the channel in this cluster with the maximal amplitude
surrounding the response cue onset was chosen for all further CPP analyses. Single-trial CPP amplitudes were identified as outliers if the response-aligned amplitude deviated more than 3 standard deviations from the within subject mean amplitude in either direction.

2.2.5.2 Mu/Beta band Activity: Effector-Specific Motor Preparation

Effector-specific motor preparation was examined through mu/beta desynchronization from 8-30Hz, tracing the decision-related motor activity across contralateral and ipsilateral hemispheres. The mu/beta lateralisation index was obtained by subtracting the hemispheric mu/beta power, allowing for the examination of the temporal dynamics in the motor preparation for the chosen response. Previous studies have shown effector-specific mu/beta desynchronization exhibits key build-to-threshold characteristics (Steineman, O’Connell & Kelly, 2018).

In order to detect channels where effector-specific decision-related activity was strongest, a grand average topography was generated for the time window from -150 to -50ms prior to response execution (Figure 2.5 A, D & G). This figure was obtained by subtracting all right-hand responses from left-hand responses and averaging across all trials and subjects. Inspection of the topography identified two clusters of two electrode sites over the premotor regions of each hemisphere on the scalp. The electrode in each hemisphere that produced the strongest lateralisation index, measured as largest difference between left and right choices, at response execution were selected on a within-subject basis. After the channel selection procedure, single trial lateralisatiion indexes around response execution were computed and inspected for outliers. All trials with amplitudes that exceeded 3 standard deviations from the within-subject mean in either direction were removed from subsequent analyses.

2.2.5.3 Theta band Activity: Conflict

Midfrontal theta band activity was measured as decibel converted power from 5-7Hz. Previous studies have suggested theta power functions as a direct index of response conflict or the coactivation of two mutually inhibiting choice alternatives (Botvinick et al., 2001; Yeung et al., 2004; Cohen & Cavanagh, 2011; Cohen & Donner, 2013; Cavanagh & Frank, 2014).

In order to identify channels where mid-frontal theta was maximal, a grand average topography of theta band activity immediately preceding response execution was generated for both experiments. This figure averaged the time window from -150 to -50ms across all trials and subjects (Figure 2.7 A & B). A visual inspection of both topographies revealed a positive component across mid-frontal areas, from which four and three electrodes sites were identified for the selection procedure in the bimanual and saccadic dot motion task respectively. The channel in this cluster with the maximal amplitude immediately preceding the response was selected on a within-subject basis. Response cue and
response-aligned theta band activity were examined separately. Single-trial theta amplitudes were identified as outliers if the response-aligned power deviated more than 3 standard deviations from the within subject mean amplitude in either direction.

2.2.6 Signal Analysis: Statistical Approach

Details in this section outline the rationale and time windows taken for the measurement of the neural signatures in the previous section. The subtitles below specify the behavioural paradigms of both studies, aligning with the headings of the results in both experiments later in this chapter. Experiment 1 corresponds to the saccadic version of the dot motion task, while experiment 2 denotes the bimanual dot motion paradigm.

2.2.6.1 Motion Durations Reveal Temporal Dynamics of Evidence Accumulation in the Emergence of Choice Certainty (Experiment 1 & 2)

To examine the role of decision formation dynamics in the emergence of a representation of confidence, CPP build-up rate and amplitude were computed during coherent motion presentation. Recent evidence suggests these measures provide a direct window in the domain-general sensory evidence accumulation, whereas contralateral mu/beta was found to reflect strategic decision-related adjustments (Steinemann, O’Connell & Kelly, 2018).

A first analysis in both experiment 1 & 2 focused on the decision formation immediately preceding the response cue, calculating the average amplitude from -100 to 0ms relative to the onset of the response cue. The build-up rate of the CPP was measured as the slope of a line fit to the traces from the time window -200 to 0ms relative to the response cue. In experiment 1, a second analysis was conducted after visual inspection of temporal dynamics of the CPP across coherent motion durations that focused on the build-up rate and amplitude of the CPP immediately prior to the peak amplitude across subjects measured in each duration. The amplitude was obtained by averaging the time window -100 to 0ms prior to the peak of the CPP for every coherent motion duration. The build-up rate of the CPP was quantified as the slope of a line fit to the traces from the time window -200 to 0ms relative to the peak amplitude. In experiment 2, analysis was conducted on the response-aligned, focusing on the evidence accumulation in time window prior to response execution. The amplitude of the CPP for this analysis was computed from -150 to -50ms, while the build-up rate was measured as the slope by fitting a line to the CPP traces from -500 to -200 ms. No response-aligned analysis was conducted on the data from experiment 1, due to the ocular activity immediately after the response cue.

The impact of coherent motion duration and confidence on the amplitude and slope of the CPP were examined with two-way repeated measures ANOVA in both experiments. Prior to all analyses
and averaging procedures in experiment 1, a within-subject median-split of confidence ratings was conducted that allowed confidence judgements to be entered in the ANOVAs as a categorical variable with two levels (lower/higher). Furthermore, the dichotomisation of choice certainty was conducted within coherent motion durations in order to ensure equal trial counts of each level of duration in each confidence bin. Coherent motion duration was entered as a second categorical independent variable with three levels (short, medium & long). However, the median-split procedure has substantial drawbacks that impact both the estimation and interpretation of statistical effects (Mac Callum et al., 2002). One alternative to this method is to utilise single-trial mixed-effect regression, which combine single-trial confidence data and single-trial derived EEG measures. Therefore, the final analysis utilised single-trial mixed-effect regression to investigate the ability of the CPP to predict small fluctuations in confidence independent of other task-related variables. Single-trial choice certainty ratings were added to this analysis as a dependent variable. A random slope was added to the model for each subject, allowing to capture between-subject differences in the overall level of confidence. Single-trial CPP amplitudes, reaction times, accuracy and the coherent motion durations were entered as predictors in the regression in a stepwise fashion. Random slopes were added for each predictor only when a model fit comparison indicated a significant increase of the fit compared to the previous best fitting regression model. This resulted in a model with fixed effects and random slopes for single-trial CPP amplitudes, reaction time, accuracy and the coherent motion durations.

In experiment 2, the amplitudes and slope of the CPP were examined through two-way repeated-measure ANOVAs with the factors coherent motion duration (short, medium & long) and confidence level. In order to minimise data attrition due to low trial counts, caused by the relatively small number of low confidence ratings in the longest coherent motion duration, all low and medium confidence judgements were concatenated prior to analyses. This created a new categorical variable for choice certainty with two levels (lower/higher). An analysis of all electrophysiological signals conducted with three levels of confidence nevertheless yielded similar results, despite the removal of 10 or more subjects (~40%) from the total sample in each analysis.

2.2.6.2 Response-locked Conflict Predicts Choice Certainty across Evidence Durations (Experiment 1 & 2)

In order to investigate the functional role of response conflict in the emergence of choice certainty, amplitudes and build-up rates of theta band activity were examined in experiment 1 & 2. In both studies, amplitudes prior to the response cue were obtained by averaging theta band activity from -300 to 0ms relative to the response cue. Build-up rates were measured as the integral of a line fit to theta traces in the time window of -300 to 0ms. In the bimanual dot motion task, an additional analysis
examined response-aligned amplitudes and build-up rates. Amplitudes were measured by averaging theta band activity from -600 to -300ms relative to response execution, while the build-up rate was computed as the slope of a line fit to the theta band activity from -600 to -300ms prior to response. Response-aligned time windows were determined in consideration of the temporal precision of decibel converted power values of the time-frequency decomposition as well as the temporal dynamics of the beta lateralisation indices.

The effect of coherent motion duration and confidence on theta band amplitudes and build-up rates were examined through two-way repeated-measures ANOVAs, with categorical predictors confidence (higher/lower) and evidence duration (short, medium & long). Separate analyses were conducted on the response cue-locked and response-aligned variables in the bimanual dot motion task. In the saccadic dot motion task, analyses were only conducted on the response cue-aligned theta amplitude and build-up rate.

2.2.6.3 Effector-Specific Motor Preparation Influences Choice Certainty (Experiment 2)

The impact of coherent motion durations on decision-related motor preparation was examined through temporal characteristics of effector-specific mu/beta band activity and beta lateralisation index prior to the response cue. The amplitude of effector-specific mu/beta band activity was measured from -200 to 0ms relative to the onset of the response cue, while build-up rates in mu/beta band activity was measured as the slope of a line fit from from -300 to 0ms compared to the onset of the response cue. Beta lateralisation index amplitudes were measured from -200 until 0ms compared to the onset of the response cue, while build-up rates were measured as the slope of a line fit to the lateralisation indices spanning -300 to 0ms compared to the onset of the response cue.

Recent evidence has suggested mu/beta band activity contralateral to the chosen option reaches a fixed threshold prior to response execution (Steinemann, O'Connell & Kelly, 2018; Donner et al., 2015). Therefore, variability in the motor preparation over the ipsilateral hemisphere is more likely to be informative of confidence judgements. This hypothesis was investigated through an examination of the temporal dynamics of effector-specific mu/beta band activity and beta lateralisation indices prior to response execution. Response-aligned amplitudes of the beta lateralisation indices and effector-specific mu/beta band activity were computed by averaging the traces of both measures from -250 to -100ms prior to response execution, while build-up rates were obtained by computing the slope of a line fitted to the traces in the time window from -600 to -300ms prior to response.

The effect of coherent motion duration and confidence on the build-up rate and amplitude of effector-specific mu/beta band activity was explored with three-way repeated-measures ANOVAs with the categorical independent variables: coherent motion duration (350/500/750ms), confidence
(lower/higher) and the hemisphere (ipsilateral/contralateral). The effect of coherent motion duration and confidence on the amplitude and build-up rate of beta lateralisation indices was investigated with two-way repeated-measures ANOVAs with coherent motion duration and confidence as categorical predictors. Separate analyses were conducted for response cue- and response-aligned variables.

2.2.7 Statistical Analysis

In every repeated-measure ANOVA conducted, data were tested for suitability for parametric analysis in two steps. Firstly, the normality assumption was tested through an examination of the outliers in the standardised residuals. Subjects that had standardised residual with absolute values exceeding three were removed from that analysis. Secondly, Mauchly’s test of sphericity was used to assess the assumption of equal variances across all factors with two or more levels. Where these assumptions were violated the Greenhouse-Geisser or the Huynh-Feldt corrected degrees of freedom and p-values are reported (the correction applied was contingent on the degree of violation). All post-hoc paired-sample t-tests reported were corrected for multiple comparisons by using Bonferroni-Holm procedure and only corrected p-values are reported (Holm, 1979).
2.3 Results: Experiment 1

2.3.1 Behavioural Findings

Figure 2.2 shows the effects of the different levels of coherent motion duration on choice behaviour in the saccadic dot motion task. Coherent motion durations significantly impacted all behavioural indicators, with longer durations being associated with significantly higher response accuracy (F(2,40) = 11.98, p < 0.001; long vs short: t(20) = 4.05, p < 0.001; long vs medium: t(20) = 1.57, p = 0.133; medium vs short: t(20) = 4.67, p <0.001), higher levels of confidence (Figure 2.2 A; F(2,40) = 15.62, p < 0.001; long vs short: t(20) = 4.39, p < 0.001; long vs medium: t(20) = 2.59, p = 0.017; medium vs short: t(20) = 4.21, p <0.001) and faster reaction times (Figure 2.2 B; F(2,40) = 68.85, p < 0.001; short vs long: t(20) = 9.39, p < 0.001; short vs medium: t(20) = 5.89, p < 0.001; medium vs long: t(20) = 9.26, p <0.001). In particular, longer coherent motion durations not only impacted the average reaction time (RT) but also resulted in a less pronounced rightward skew in the reaction time distribution as a function of evidence duration across subjects (Figure 2.2 D). Taken together, these results indicate beneficial effects of longer coherent motion duration, showing faster and more accurate response with elevated choice certainty.

A second analysis focused on reaction time and confidence as a function of accuracy, which revealed that erroneous choices were associated with slower reaction times (Figure 2.2 D; F(1,20) = 28.60, p <0.001) and lower choice accuracy (Figure 2.2 E; F(1,20) = 72.97, p < 0.001). However, subjective confidence in errors was not significantly lower compared to a ‘guess’ score of 50 on the continuous confidence scale (t(20) = 0.95, p = 0.35). This is perhaps unsurprising given the relatively great number of high confidence errors across subjects, which is shown on the right-hand side of the confidence scale in Figure 2.2 G.
Figure 2.2: The effect of coherent motion duration and accuracy on behavioural indicators of decision formation in the saccadic dot motion task. Error bars across panels indicate the standard error of the mean. Asterisks indicate the level of significance after Bonferroni-Holm's correction for multiple comparisons, with p < 0.05: *, p < 0.01: **, p < 0.001: ***. A) Confidence plotted across coherent motion duration; choice certainty was higher when coherent motion duration was longer. B) Reaction time (RT) for the integrated motion and confidence judgements plotted as a function coherent motion duration. RT increased with shorter evidence presentation duration. C) Percentage of correct motion judgements plotted across the different levels of coherent motion duration. Accuracy increased with length of the evidence duration. D) Reaction time distribution across subjects plotted as a function of coherent motion duration. Vertical lines denote the average RT in each level of duration. E) Confidence plotted as a function of accuracy; higher confidence was found on correct motion decisions. F) RT plotted for errors and correct decisions, showing erroneous choices were committed significantly slower. G) Distribution of responses on the confidence scales across subjects plotted as a function of accuracy.

2.3.2 Motion Durations Reveal Temporal Dynamics of Evidence Accumulation in the Emergence of Choice Certainty

A first analysis examined the relationship between confidence and the average amplitude and build-up rate of the CPP immediately prior to the response cue. Repeated-measures ANOVAs showed no significant effect of coherent motion duration or choice certainty on CPP amplitude ($F(2,40) = 1.07$, $p = 0.352$; $F(1,19) = 2.66$, $p = 0.120$). CPP slope did show a significant effect of coherent motion...
duration (F(2,40) = 11.95, p < 0.001) with the highest build-up in the short evidence duration followed by the medium and longest durations (long-short: t(20) = 4.52, p < 0.006; long-medium: t(20) = 2.98, p = 0.0147; medium-short: t(20) = 2.22, p = 0.038). However, no effect of confidence was found in the build-up immediately preceding the response cue (F(1,20) = 0.84, p = 0.369). An inspection of Figure 2.3 provides further insight into these results, displaying the steepest CPP build-up in the shortest coherent motion duration relative to the response cue (Figure 2.3 B & C). In contrast, the CPP in the longest coherent motion condition on average shows a negative slope immediately prior to the response cue (Figure 2.3 H & I).

In order to elucidate the relationship between the CPP and emergence of choice certainty a second analysis was conducted on the build-up rate and amplitude that took into account differences in signal dynamics across coherent motion durations. Specifically, we observed that the CPP peaked and returned toward baseline well before the response cue in the longest curation. This accords with observations from a similar paradigm by Twomey et al (2016) and suggests that participants did not accumulate throughout the entire stimulus presentation window of the longest duration. Consequently, this analysis measured amplitude and slope immediately prior to the average peak latency in each duration. As such, if confidence reports reflect cumulative evidence accrued at the time of decision termination then they should be most strongly correlated with CPP peak amplitude. Indeed, the CPP amplitude and build-up rate showed a significant effect of confidence (F(1,20) = 8.15, p = 0.009; F(1,20) = 5.34, p = 0.032), with significantly higher slopes and amplitudes observed on high confidence trials.

Finally, the continuous scale on which the confidence ratings were recorded allowed this study to directly examine if single-trial differences in CPP amplitude, predicted trial-by-trial variability in metacognitive judgements. This hypothesis was tested through a mixed-effect regression, which indicated that single-trial amplitudes of the CPP were a significant predictor of trial-to-trial variation in choice confidence (t(21) = 2.31, p = 0.021) even after controlling for the effects of coherent motion duration, response accuracy and RT. Two additional separate mixed-effect regressions were conducted on the single-trial RT and response accuracy, which showed CPP amplitudes did not significantly predict variability in either when controlling for the unique variability captured by confidence ratings and other task-related variables (t(21) = -0.80, p = 0.424; t(21) = 1.12, p = 0.262).
Figure 2.3 Domain-general evidence accumulation (CPP) plotted as a function of coherent motion duration (350/500/750ms) and confidence level (lower/higher) in the saccadic dot motion task. A) Topography of the ERP signal immediately preceding response cue in the 350ms coherent motion duration, which shows a positive going component over centroparietal areas. B) CPP plotted as a function of confidence level in the 350ms coherent motion duration. The vertical line marker indicates onset of the response cue. C) Topography of ERP signals
immediately prior to response cue in the 500ms coherent motion representation, displaying a positive going centroparietal component. D) CPP plotted as a function of confidence level in the 500ms coherent motion duration. E) Topography of the ERP signal immediately preceding response cue in the 750ms coherent motion duration, which shows a positive going component over centroparietal areas. F) CPP plotted as a function of confidence level in the 750ms coherent motion duration.

2.3.3 Response Conflict Fails to Predict Confidence during Evidence Presentation (Experiment 1)

The temporal dynamics of response conflict were examined by measuring the amplitude and build-up rate of theta band activity prior to the response cue. As shown in figure 2.4 (B, C & D), theta exhibits a gradual increase during coherent motion presentation. Analysis of theta power in the interval immediately preceding the response-cue revealed a significant increase as a function of coherent motion duration (F(2,40) = 4.17, p = 0.023; short vs medium: t(20) = 2.32, p = 0.062; short vs long: t(20) = 4.38, p = 0.016; medium vs long: t(20) = 2.19, p = 0.062). No significant effect of coherent motion duration on confidence (F(1,20) = 0.01, p = 0.946) or interaction was observed (F(2,40) = 0.27, p = 0.763). Similarly, build-up rates of theta power prior to the response cue were significantly different across coherent motion duration (see figure 2.4; F(2,40) = 6.01, p = 0.005; short vs medium: t(20) = 1.96, p = 0.064; short vs long: t(20) = 3.02, p = 0.020; medium vs long: t(20) = 1.85, p = 0.079), with lower build-up in the longest coherent motion duration (see Figure 2.4 D). Finally, analysis of build-up rate also showed no effect of confidence (F(1,20) = 0.41, p = 0.527) or interaction effect between both categorical predictors (F(2,40) = 0.64, p = 0.54). Taken together, these results show that neural signals of response conflict dynamically evolve across coherent motion durations. However, theta band activity did not differ as a function of confidence, which suggests this signal did not directly represent response conflict during the coherent motion presentation.
Figure 2.4 Response cue-aligned theta band activity plotted as a function of coherent motion duration (350/500/750ms) and confidence (lower/higher) in the saccadic dot motion task. Time point 0ms, marked by the vertical black line indicates the onset of the response cue. A) Topography of decibel converted power (Db) from 5-7 Hz, revealing a large positive mid-frontal component prior to the onset of the response cue in the saccadic dot motion task. B) Response cue-aligned power separated by confidence in the shortest evidence duration trials. C) Response cue-aligned power plotted as a function of different levels of confidence in the medium evidence duration trials. D) Response cue-aligned power separated by confidence in the longest evidence duration trials.
2.4 Discussion: Experiment 1

The aim of experiment 1 was to establish a clear link between the domain-general evidence accumulation process reflected in the CPP and choice confidence reports. The key finding of this study is that the build-up rate and amplitude of the CPP during the period of decision formation are predictive of forthcoming confidence ratings, with higher choice certainty being associated with steeper build-up rates and higher amplitudes during coherent motion presentation. This relationship remains even at the single-trial level, where the accumulated evidence in CPP amplitude significantly predicts the trial-by-trial confidence ratings regardless of other behavioural factors that influence choice certainty.

Interestingly, the relationship between sensory evidence accumulation and confidence was only present when accounting for the temporal dynamics of the CPP across coherent motion durations. Specifically, we found that the CPP did not continue to build across the entire coherent motion period but peaked at roughly 500ms after evidence onset in the medium and longest coherent motion duration (Figure 2.3 E & H). These observations are similar to the temporal dynamics of domain-general evidence accumulation observed in previous delayed response paradigms (Twomey, Kelly & O’Connell, 2016). However, the current study extended on these findings, by adopting a paradigm that allowed for an investigation into the influence of variable coherent motion durations on the evidence accumulation process. The impact of this variable coherent motion presentation shows that participants strategically adjust the duration of their evidence accumulation process to coincide with the average motion duration. This interpretation is further supported by two observations. Firstly, the temporal characteristics of the CPP in the longer coherent motion durations show a similar peak latency across different levels of confidence despite differences in average amplitude. This suggests that evidence accumulation was strategically terminated at an internally set deadline and not due to the decision bound having been reached. Secondly, the temporal dynamics of theta band activity show a similar slow-down in the build-up rate of the longest coherent motion duration, which is indicative of a strategic disengagement from the decision formation process. This serial processing strategy would afford subjects to focus on the saccadic response, which requires a non-trivial and careful analysis of the response dial to identify the appropriate fixation point. These results highlight the occurrence of strategic modulations in domain-general evidence accumulation in response to temporal uncertainty in the duration of external evidence (see also, Devine et al., 2019).

A limitation of experiment 1 is that the use of saccadic responses did not allow for direct investigation of action-selective motor preparation processes. Studies that have used hand movement (button push) reports have demonstrated that contralateral premotor mu/beta band activity contralateral traces a bounded evidence accumulation process (Twomey et al., 2016; De Lange et al., 2013; Kelly &
O’Connell, 2012). A recent study from Steinemann and colleagues (2018) suggested evidence accumulation dynamics measured in the CPP and effector-specific mu/beta band activity are functionally distinct. This suggests that motor preparation signals could function as an alternative information source that influences metacognitive judgements, independent from the pure sensory-driven evidence accumulation measured in the CPP. Further support for this comes from computational models of response conflict, which suggests that the level of coactivation of two competing response alternatives functions as a direct proxy for confidence (Davelaar, 2009; Yeung et al., 2004). At the neural level, response conflict can be measured through theta band activity. Although the exact functional role of theta remains unclear, studies have demonstrated theta is sensitive to manipulations of response conflict (Cohen & Cavanagh, 2011, Murphy et al., 2012; Murphy et al., 2015; Wang et al., 2018). Furthermore, in a recent study Wokke and colleagues (2017) found a significant relationship between theta and metacognitive adequacy, a measure of the accuracy of confidence ratings. However, this study did not address whether or not theta reflects a read-out of the conflicting activations between independent evidence accumulators at the decision level (Vickers, 1979; Merkle & van Zandt, 2006) or a motor level signal that indexes the relative preparation for decision reporting actions (Cohen & Cavanagh, 2011). The current study provided some insight into the nature of theta band activity, showing some support for the prediction that response conflict in theta does not directly arise in parallel to the evidence accumulation process when the response requirements are unknown, since no modulation of theta by conflict was observed during coherent motion presentation. However, a clear limitation of this experiment is that no analyses could be conducted on this signal after the onset response cue, due to the ocular artifacts in this time window.

Therefore, we conducted a follow-up study where integrated motion and confidence ratings were given on a 6-point scale, using a bimanual response modality that remained constant across trials. This allowed experiment 2 to trace the separate contributions of pure sensory-driven evidence accumulation, measured in the temporal dynamics of the CPP, and decision-related motor preparation, examined through effector-specific mu/beta band activity in the emergence of a graded representation of confidence. Furthermore, this allowed for an examination of both stimulus- and response-aligned theta power, allowing for a more thorough examination of the nature of response conflict in theta band activity.
2.5 Results: Experiment 2

2.5.1 Behavioural Findings

The relationship between task-related behavioural variables and coherent motion duration is presented in figure 2.5 (A-D), revealing behavioural trends in line with in experiment 1. Coherent motion duration was significantly impacted all behavioural outcomes, monotonically increasing response accuracy (Figure 2.5 C; F(2,48) = 16.06, p < 0.001; long vs short: t(24) = 5.43, p < 0.001; long vs medium: t(24) = 1.59, p = 0.13; medium vs short: t(24) = 4.62, p < 0.001), increasing confidence (Figure 2.5 A; F(2,48) = 20.71, p < 0.001; long vs short: t(24) = 5.21, p < 0.001; long vs medium: t(24) = 2.41, p = 0.024; medium vs short: t(24) = 5.30, p < 0.001) and faster reaction times (RT; Figure 2.5 B; F(2,48) = 123.22, p < 0.001; long vs short: t(24) = 12.23, p < 0.001; long vs medium: t(24) = 7.68, p < 0.001; medium vs short: t(24) = 12.53, p < 0.001). An examination of the Figure 2.5 D reveals this effect is caused by a more pronounced rightward skew in the tail of the RT distribution in the shorter motion duration, which suggests evidence accumulation was slower and more variable on these trials.

An analysis contrasting correct and erroneous choices furthermore showed errors were associated with significantly lower confidence and slower RT (Figure 2.5 E & F; F(1,24) = 45.92, p < 0.001; F(1,24) = 47.60, p < 0.001). A comparison of RT distributions split by accuracy and coherent motion duration further shows the interplay between these behavioural variables, with the characteristic of the error RT distribution showing a resemblance with the rightward skew with the shortest evidence duration. These results are in line with the behavioural patterns found in the previous experiment and further suggest that behavioural strategies were not influenced by the categorical nature of the confidence rating scale in experiment 2 contrary to previous studies that highlight differences across metacognitive measures (Tunney, 2005; Overgaard & Sandberg, 2012; Dienes, 2007).
Figure 2.5 The effect of coherent motion duration and accuracy on behavioural indicators of decision formation in the saccadic dot motion task. Error bars across panels indicate the standard error of the mean. Asterisks indicate the level of significance after Bonferroni-Holms correction for multiple comparisons, with p < 0.05: *, p < 0.01: **, p < 0.001: ***. 

A) Confidence plotted across coherent motion duration, choice certainty was higher when coherent motion duration was longer. B) Reaction time (RT) for the integrated motion and confidence judgements plotted as a function of coherent motion duration. RT increased with shorter evidence presentation duration. C) Percentage of correct motion judgements plotted across the different levels of coherent motion duration. Accuracy increased with length of the evidence duration. D) Reaction time distribution across subjects plotted as a function of coherent motion duration. Vertical lines denote the average RT in each level of duration. E) Confidence plotted as a function of accuracy, higher confidence was found on correct motion decisions. F) RT plotted for errors and correct decisions, showing erroneous choices were committed significantly slower. G) Distribution of responses on the confidence scales across subjects plotted as a function of accuracy.

2.5.2 Motion Durations Reveal Temporal Dynamics of Evidence Accumulation in the Emergence of Choice Certainty

Examination of the domain-general evidence accumulation prior to response cue reveals temporal dynamics of the CPP are remarkably similar to the results obtained in experiment 1 (Figure 2.6 A, E & I). An analysis of the accumulation dynamics prior to the response cue revealed a significant main effect of duration CPP amplitude (F(2, 48) = 7.08, p = 0.002). The highest amplitude
was found in the longest evidence duration, while the lowest amplitude CPP was observed in the short coherent motion duration (long vs short: \( t(24) = 2.90, p = 0.0157 \); long vs medium: \( t(24) = 0.76, p = 0.45 \); medium vs short: \( t(24) = 3.36, p = 0.008 \)). Similarly, the slope of the CPP was significantly modulated by coherent motion duration (\( F(2,48) = 5.69, p = 0.006 \)), with the fastest build-up observed in the medium coherent motion duration (long vs short: \( t(24) = 2.31, p = 0.059 \); long vs medium: \( t(24) = 3.43, p = 0.007 \); medium vs short: \( t(24) = 1.07, p = 0.300 \)). Again, we observed a marked slow down in the build-up of the CPP prior to the response cue in the longer coherent motion durations. Experiment 2 did not find a significant increase in amplitude between the medium and long coherent motion duration, which may be caused by a slow-down of the average evidence accumulation in the longest evidence duration at +500ms (Figure 2.5 I). In contrast to the first study, experiment 2 did observe a significant modulation of the CPP amplitude and slope by confidence immediately preceding the response cue (\( F(1,24) = 10.21, p = 0.004 \); \( F(1,24) = 5.78, p = 0.024 \)), with higher amplitudes and build-up rates observed on higher confidence trials. These results suggest that the difference in accumulation by confidence was maintained across the entire evidence duration window. One potential explanation is that this reflects the non-random nature of the response cue in experiment 2, which would have afforded participants the ability to start response preparation in the longer stimulus durations (see section 2.5.3 below).

An examination of the response-aligned CPP traces revealed the modulation of CPP by confidence remained traceable in the evidence accumulation up until response execution (Figure 2.6 C, G & K). Specifically, CPP amplitude and build-up prior to choice commitment were significantly higher on high confidence compared to low confidence decisions (\( F(1,24) = 9.49, p = 0.005 \); \( F(1,23) = 27.79, p < 0.001 \)). No significant main effect of coherent motion duration or its interaction was found in either CPP amplitude or build-up rate prior to response execution (Main effects: \( F(2,48) = 0.53, p = 0.59 \); \( F(2,48) = 0.59, p = 0.557 \); Interaction effect: \( F(2,48) = 0.449, p = 0.641 \); \( F(2,48) = 2.05, p = 0.140 \)). Finally, CPP amplitudes immediately prior to response were significantly elevated compared to the moments prior to the response cue (\( t(24) = 4.30, p < 0.001 \)), indicating accumulation continued up to the response despite the absence of external stimulus evidence. This pattern of findings shows the CPP reaches a similar amplitude for dot motion judgements irrespective of coherent motion duration. However, the accumulated evidence does significantly vary as a function of confidence, a difference that emerges gradually in the amplitude and slope of the CPP during stimulus presentation and persists until response execution.
Figure 2.6 Domain-general evidence accumulation separated by durations (350/500/750ms) and confidence level (lower/higher) in the bimanual dot motion task. Note that the scale of response-aligned signal in the right column is roughly twice as large as the response cue-aligned signals in the left column. **Duration 350ms**

A) Response cue-locked CPP traces separated for higher and lower confidence in the shortest coherent motion presentation. B) Topography of the ERP traces from -100 to 0ms relative to response cue onset, revealing a positive going component across centroparietal areas. C) Response-aligned CPP traces plotted as a function of confidence for the shortest coherent motion duration. D) Topography of the ERP traces from -150 to -50ms relative to response execution, revealing a positive going component across centroparietal areas. **Duration 500ms**

E) Response cue-locked CPP traces plotted for higher and lower confidence in the medium coherent motion presentation. F) Topography of the ERP traces from -100 to 0ms relative to response cue onset, showing a positive going centroparietal component across the scalp. G) Response-aligned CPP traces plotted as a function of confidence for the medium coherent motion duration. H) Topography of the ERP traces from -150 to -50ms relative to response execution, revealing a positive going component across centroparietal areas. **Duration 750ms**

I) Response cue-locked CPP traces plotted across confidence in the longest coherent motion presentation. J) Topography of the ERP traces from -100 to 0ms relative to response cue onset, showing a positive going centroparietal component across the scalp. K) Response-aligned CPP traces plotted as a function of confidence.
for the longest coherent motion duration. L) Topography of the ERP traces from -150 to -50ms relative to response execution, showing a positive going component across centroparietal areas.

2.5.3 Effector-Specific Motor Preparation Influences Choice Certainty

The relationship between decision-related motor preparation signals and metacognitive judgments was examined through the analysis two motor preparatory signatures. A first signal of interest is the lateralisation index, which is a widely adopted measure in the study of effector-specific motor preparation. The computation of this index involves subtracting the motor preparation in the hemisphere of unchosen and chosen option so that more negative values indicate a stronger preparation in favour of the chosen response (Pfurtscheller & Lopes da Silva, 1999; Donner et al., 2009). Prior to the response cue, the amplitude of beta lateralisation indices showed a significant effect of coherent motion duration (F(2,46) = 7.60, p = 0.001), with stronger beta lateralisation in favour of the contralateral hemisphere in the longest coherent motion duration compared to the shortest evidence duration (see inserts Figure 2.7 B, E & H; low vs high: t(23) = 3.05, p = 0.011; low vs medium: t(23) = 1.12, p = 0.273; medium vs long: t(23) = 3.63, p = 0.004). However, no significant effects on the build-up rate of the lateralisation indices in the time window preceding the response cue were found (F(1,22) = 1.12, p = 0.356). Prior to the response cue no significant effect of confidence was observed on the amplitude (F(1,23) = 1.91; p = 0.184) or the build-up rate (F(1,22) = 0.04, p = 0.837). In contrast, analyses of the response-aligned traces only showed a significant effect of confidence on the amplitude the lateralisation indices (see inserts Figure 2.7 C, F & I; F(1,23) = 9.24, p = 0.006), while no effect of coherent motion duration was observed (F(1,46) = 1.89, p = 0.163). No significant effects of confidence and coherent motion duration on the build-up rate of lateralisation indices immediately preceding response execution were found(F(1,23) = 1.92, p = 0.180; F(2,46) = 0.68, p = 0.51).

In order to gain a deeper understanding of the contribution of each effector, a second analysis examined the limb-specific mu/beta band motor preparation. Visual inspection of the mu/beta waveforms prior to the onset of the response cue in Figure 2.7 (B, E & H) shows a substantial increase in motor preparation across coherent motion durations and the typically observed enhancement contralateral or to the decision-reporting hand. Analyses confirmed this pattern, revealing a significant interaction between coherent motion duration and hemisphere (contralateral/ipsilateral) on mu/beta band amplitude measured immediately prior to response cue onset (F(2,46) = 7.56, p = 0.001). This was driven by increased lateralisation for longer durations (Figure 2.7 B & H; long ipsi-contra: t(23) = 5.12, p <0.001; medium ipsi-contra: t(23) = 3.15, p = 0.009; short ipsi-contra: t(23) = 1.50, p = 0.147). The build-up rate of mu/beta traces prior to response cue showed only a significant effect of hemisphere, with stronger desynchronization occurring over the contralateral premotor areas (F(1,22) = 14.49, p <
Taken together, these results suggest contralateral motor preparation was influenced only by the duration of the coherent motion evidence, with stronger preparation in the contralateral hemisphere for the longer coherent motions durations prior to the response cue. Analysis of effector-specific mu/beta band amplitudes prior to response execution showed a significant interaction between confidence and hemisphere (F(1,22) = 8.10, p = 0.009). This reflects differences in the motor preparation as a function of confidence, with stronger ipsilateral motor preparation for low confidence judgements (t(22) = 2.97, p = 0.021). Additionally, as demonstrated in previous studies, contralateral motor preparation reached a similar pre-response amplitude across the different levels of confidence and coherent motion durations (lower vs higher: t(22) = 1.12, p = 0.273; short vs medium: t(22) = 0.62, p = 0.546; short vs long: t(22) = 1.74, p = 0.382; medium vs long: t(22) = 1.20, p = 0.486). Build-up rates of effector-specific mu/beta showed a significant main effect of coherent motion duration (F(2,46) = 7.48, p = 0.002), with the fastest build-up found in the shortest coherent motion duration compared to longer evidence durations (medium vs long: t(23) = 1.47, p = 0.154; short vs medium: t(23) = 3.19, p = 0.012; short vs long: t(23) = 2.69, p = 0.026). However, the absence of a three way interaction between confidence, coherent motion duration and hemisphere (F(2,44) = 0.09, p = 0.918) suggests the mu/beta build-up impacted ipsilateral and contralateral motor preparation equally. One possible explanation is that the appearance of the response cue could have introduced a larger urgency component in the shorter coherent motion durations due to their being less cumulative evidence available to inform the choice on average. This would cause an increase in the desynchronization at the motor level across both hemispheres, as has been observed in previous experiments (Murphy, Boonstra & Nieuwenhuis, 2016; Steinemann, O'Connell & Kelly, 2018).
Figure 2.7 Mu/beta motor preparation and lateralized beta index across coherent motion durations and confidence (lower/higher) in the bimanual dot motion task. Time point 0, indicated by the black vertical line, in the first column denotes response cue onset, while in the second column 0ms indicates response execution. **Duration 350 ms** A) Topography of mu/beta motor preparation prior to the response cue, obtained by subtracting left and right choices. B) Mu/beta motor preparation aligned to the response plotted as a function of confidence level in the shortest coherent motion duration. Vertical lines denote reaction time (RT) on lower and higher confidence trials. Insert: response cue-aligned lateralized beta index, obtained by subtracting ipsilateral and contralateral traces, across different levels of confidence. C) Response-aligned mu/beta plotted as a function of confidence in the shortest evidence duration. Insert: response-aligned lateralized beta index separated according to confidence. 


2.5.4 Response-locked Conflict Predicts Choice Certainty across Evidence Durations (Experiment 2)

Temporal dynamics of response conflict were examined by measuring the amplitude and build-up rate of theta band activity. As shown in Figure 2.8 (B, D & F), theta band activity exhibits a gradual increase during coherent motion presentation and peaking after response execution when feedback is presented on the screen (Figure 2.8 C, E & G). Results from response cue-aligned analyses are broadly similar to the results of the saccadic experiment, with amplitudes showing a significant effect of coherent motion duration (F(2,44) = 12.13, p < 0.001). As visible in figure 2.8 (B, D & F) the highest theta amplitude was found in the longest coherent motion duration, while the lowest amplitude observed in the shortest duration (short vs medium: t(22) = 3.49, p = 0.006; short vs long: t(22) = 2.22, p = 0.0074; medium vs long: t(22) = 0.26, p = 0.792). No effects of confidence were found in this time window (F(1,22) = 0.01, p = 0.928; F(1,22) = 0.01, p = 0.968) nor were there any differences in theta build-up rates for any categorical predictor (F(1,22) = 0.01, p = 0.928; F(1,22) = 0.01, p = 0.968).

Interestingly, visual inspection of theta traces in Figure 2.8 (B, D & F) suggests that, as was the case for mu/beta activity, modulations with choice confidence emerged after the onset of the response cue and prior to response execution in the bimanual experiments. A response-aligned analysis shows a significant modulation of theta band amplitude by confidence (F(1,22) = 4.82, p = 0.039), with significantly elevated theta in lower confidence judgements visible across all coherent motion durations (Figure 2.8 C, E & G). Furthermore, the differences by confidence emerge on a similar timescale, from -600 to -300ms relative to the response, as differences in the beta lateralisation indices prior to response execution. Another similarity between beta and theta band activity is the build-up rate of theta was significantly impacted by evidence duration (F(2,44) = 5.14, p = 0.010). Theta slopes were comparatively higher in shorter coherent motion durations (Figure 2.8 C, E & G; short vs medium: t(22) = 3.49, p = 0.006; short vs long: t(22) = 2.22, p = 0.0074; medium vs long: t(22) = 0.26, p = 0.792). Taken together, these results suggest that neural signals of response conflict closely track the emergence of confidence representations, with higher theta band activity observed prior to low confidence judgements.
Figure 2.8 Theta band activity plotted as a function of coherent motion duration and confidence in the bimanual dot motion experiment. Time point 0ms in column one, marked by the vertical black line, denotes the onset of the
response cue, while the black vertical in the second column indicates response execution. A) Topography of decibel converted power (Db) from 5-7 Hz, revealing a large positive mid-frontal component prior to the onset of the response cue. B) Response cue-aligned power separated by confidence in the shortest evidence duration trials. C) Response-aligned power plotted as a function of confidence in the shortest motion duration. D) Response cue-aligned power separated by confidence in the medium evidence duration trials. E) Response-aligned power plotted as a function of confidence in the medium coherent motion duration. F) Response cue-aligned power separated by choice certainty in the longest evidence duration trials. G) Response-aligned power plotted as a function of confidence in the longest motion duration.
2.6 Discussion: Experiment 2

Results from experiment 2 broadly converged with behavioural and neural results from study 1. Behavioural effects were remarkably similar across experiment 1 & 2, showing that longer coherent motion led to faster reaction times (RT) and increases in both confidence and accuracy. Errors likewise were associated with slower RT and lower confidence. Equally consistent patterns were observed at the neural level, where the evidence accumulation dynamics measured through the CPP amplitude and slope showed substantial overlap between experiment 1 & 2. Specifically, in the longest coherent motion duration in both experiments the CPP peaks roughly around 500 ms. This resulted in slower build-up rates immediately prior to the response cue and a similar peak latency across different levels of confidence regardless of the difference in the accumulated evidence. A crucial difference between both studies is that experiment 2 employed a constant response mapping across the task. This affected decision-formation in two distinct ways. Firstly, motor preparation commenced prior to the response cue, leading to more pronounced mu/beta activity in longer evidence durations. Secondly, experiment 2 found a modulation of the CPP amplitude by confidence in the moments prior to the response cue, reflecting the effect motor preparation occurring in parallel to domain-general accumulation.

Experiment 2 provided a more detailed exploration of the functional role of response aligned processes. Firstly, domain-general evidence accumulation assessed through the CPP was shown to continue to accumulate after the response cue, despite the absence of external stimulus evidence, and have a sustained modulation of amplitude by confidence prior to response. Secondly, motor preparation in the emergence choice certainty through examination of effector-specific mu/beta desynchronization. Specifically, showing motor preparation for the ipsilateral or unchosen hand is stronger on lower confidence trials, while contralateral motor preparation reaches a stereotyped level of activity prior to response execution similar to previous studies (Donner et al., 2009; O’Connell et al., 2012). These findings mirror results from theta band activity, a measure theorised to index response conflict (Cohen & Cavanagh, 2011, Cohen & Donner, 2011; Cavanagh et al., 2012), which was similarly elevated prior to low confidence choices.

Taken together, both experiments provide converging indications that temporal uncertainty in coherent motion duration leads to strategic adjustments in evidence accumulation processes in order to maximise behavioural performance. However, these adjustments occur regardless of foreknowledge of the response modality and modulate the emergence of choice certainty at the neural level. Finally, experiment 2 shows the construction of confidence does not solely rely on evidence accumulated during stimulus presentation, demonstrating a systematic relationship between effector-specific motor preparation and response conflict. This suggests choice certainty depends on the interplay between different levels of processing along the sensorimotor hierarchy.
2.7 General Discussion

In order to successfully adapt to changes and learn in the sensory environment, humans and animals alike must be able to discriminate whether or not decisions were based on reliable sources of information. However, choices are frequently made in the absence of external feedback about the decision outcome, requiring the computation of subjective confidence or choice certainty in order to estimate objective performance and guide future decision strategies. An important question in this respect is to what extent the accumulated evidence shapes the emergence of confidence, especially when evidence duration and response requirements are variable. The current study investigated this question by manipulating the duration of changes in sensory stimuli across two experiments whilst also manipulating foreknowledge of the stimulus-to-response mapping modality across studies. Electrophysiological and behavioural results in both experiments indicate subjects strategically adjusted to the temporal uncertainty as domain-general evidence accumulation in both studies peaked at the average stimulus duration. Sensory evidence accumulation in both experiments was also seen to be predictive of the final level of confidence, with higher amplitudes and faster CPP build-up observed on higher confidence trials. Experiment 1 further showed the effect remained at the single-trial level with CPP amplitudes significantly predicting variability in confidence judgements, independent of other variables known to influence decision-making, such as reaction time and accuracy (Fleming et al., 2010; Kiani, Corthell & Shadlen, 2014).

The observed results accord neatly with the reported relationship between CPP and metacognitive judgements observed in previous research (Tagliaabue et al., 2019; Gherman & Philiastedes, 2015; Murphy et al., 2015; Herding et al., 2019; Boldt & Yeung, 2015’ Desender et al., 2016; Desender et al., 2019). However, this study expands on previous research in several ways. Firstly, to date no study has directly adopted a choice confidence scale to investigate the relationship between perceptual decision-making signatures and metacognitive judgements. While previous studies have adopted visibility ratings and opt-out decision (Tagliaabue et al., 2019; Squires et al., 1973). However, research has shown that these ratings might invoke significantly different processes (Rausch & Zehentleitner, 2013, 2016).

Secondly, previous studies mainly focused on stimulus-aligned measurements of the evidence accumulation process despite strong predictions about the relationship between the dynamics of CPP prior to response and confidence. In contrast, experiment 2 allowed for the exploration of response-aligned decision formation. This showed that despite the absence of external evidence, CPP build-up persisted after the response cue, potentially reflecting accumulation of evidence from memory. Moreover, a significant modulation of amplitude and build-up rate by confidence was found across all evidence durations prior to response execution, which suggests two distinctive stages in the decision
formation of the longest coherent motion durations. This possibility could be investigated by utilizing a more canonical second order decision-making task tailored to investigate pre- and post-decisional processing (Carpenter et al., 2019; Desender et al. 2019; Insabato, Pannuzi & Deco, 2017) and this was the inspiration for the experiment reported in Chapter 3 of this thesis.

Furthermore, the current experiment aimed to explore the temporal characteristics of domain-general evidence accumulation in the emergence of confidence through a manipulation of the evidence duration and response modality. Results across both experiments highlight the influence of both on the dynamics of evidence accumulation, with a significant scaling in CPP amplitudes by confidence prior to response cue in experiment 2. This effect was absent in experiment 1, unless the analysis centred on the time window preceding the peak amplitude of the CPP. This pattern of results suggests the absence of a predictable stimulus- and confidence-response mapping in experiment 1 appeared to promote a serial processing strategy, which caused the evidence accumulation to terminate early in the longer evidence durations in order to facilitate preparation of the non-trivial saccadic response. This account is further supported by the similar peak latency of the CPP across different levels of confidence and the apparent slower build-up in theta band power in the longer coherent motion duration. In comparison, experiment 2 had a fixed stimulus- and confidence-response mapping throughout the task that allowed motor preparation to commence during coherent motion presentation. A formal test of this serial processing strategy would be to use reverse correlation approaches to investigate whether or not noise in the random dot motion kinematograms (RDK) immediately preceding response cues predict the amplitude of the CPP only in the short and medium evidence durations. Nonetheless, these results highlight that it is critically important to carefully consider the temporal dynamics of the neural decision process when selecting time windows for its measurement. Additionally, these results extend on previous research, which has shown neural regulations occur to temporal uncertainty in the onset of evidence (Devine et al., 2019). In contrast, the current study focused on temporal uncertainty in evidence duration that resulted in strategic adjustments in the average peak amplitude of the CPP regardless of the decision bound and the presence of external sensory information. Nevertheless, results in both experiments provide convergent evidence into the internal control participants have over the evidence accumulation dynamics in order to pursue optimal performance outcomes and rewards.

Finally, experiment 2 aimed to elucidate the relationship between confidence and decision-related motor preparation, examined through dynamics of effector-specific mu/beta activity and beta lateralisation indices. Congruent with previous research, the current study observed a threshold crossing effect across in the contralateral motor preparation (Donner et al., 2009; De Lange et al., 2013; Kelly & O’Connell, 2015), while additionally showing an effect of urgency on ipsilateral and contralateral motor preparation in the shortest evidence duration (Steinemann et al., 2018). Crucially,
response-aligned beta laterisation indices prior to response exhibited a significant modulation by confidence, indicating greater motor preparation for the final decision when choice certainty was higher. Investigation of effector-specific mu/beta traces revealed that this effect originated in the ipsilateral hemisphere, where stronger motor preparation for the unchosen option was observed with lower levels of confidence. These findings were complemented by investigation of response conflict, which found theta power was elevated prior to low confidence responses similar to previous research (Wokke et al., 2017). Importantly, the current study extends on the results from Wokke and colleagues (2017) by providing novel insight into the nature of theta band activity in perceptual decision-making. Specifically, the absence of an effect of confidence on theta amplitude prior to the response cue indicates theta band activity might not be related to the evidence accumulation per se but is more likely to reflect motor level processes (Cavanagh et al., 2011). Additional support for this interpretation comes from the response-locked signals for both theta and mu/beta band activity. Firstly, there is substantial overlap in the timing of the emergence of the response-aligned effect of confidence on the theta amplitude and beta laterisation indices. Secondly, both theta power and effector-specific mu/beta show the same sensitivity to urgency, noted through increased build-up rates in both signals prior to response in the shortest evidence durations. Taken together, these results provide new evidence for the close relationship between neural signatures of response conflict and decision-related mu/beta motor preparation, in line with predictions of computational models of conflict monitoring (Botvinick et al, 2001; Botvinick, Cohen & Carter, 2004; Yeung et al., 2004). Nevertheless, interpretation of the response cue-aligned theta patterns must be made with caution as the duration of coherent motion presentations was suboptimal for time-frequency decomposition, which would be more problematic in the shorter evidence durations. This issue is further compounded by the natural loss of temporal precision in the lower frequency bands (Cohen, 2014), which makes analysis of the temporal dynamics in these signals inherently difficult. Therefore, future research could further explore the observed relationship between beta and theta band activity, adopting paradigms more specifically tailored to address this question. One possible solution would be to utilise longer evidence durations in conjunction with lower proportions of coherent motion. This would require participants to accumulate over prolonged time windows, further enabling greater temporal resolution in the lower frequency ranges (see for instance Twomey et al., 2016).

In summary, the current chapter aimed to further our understanding of how metacognitive representations might be informed by perceptual decision formation signals. To this end, two experiments were conducted which establish a direct relationship between the dynamics of sensory evidence accumulation and metacognitive judgements, showing higher levels of evidence accumulation directly translated into higher confidence judgements both on continuous and categorical scales.
Furthermore, in response to temporal uncertainty in the duration of external evidence, the timing of the peak amplitude of evidence accumulation was strategically adjusted to correspond with average evidence duration in both experiments. This directly influenced the visibility of the modulation of sensory evidence accumulation by confidence, highlighting the importance of careful experimental design when examining the relationship between perceptual decision-making and metacognition. A final set of analyses revealed a functional role of effector-specific mu/beta activity and response conflict in the emergence of a representation of confidence, with stronger motor preparation for the unchosen hand and response conflict present on low confidence trials. The next chapter of this thesis will aim to further explore the observation that sensory evidence accumulation continued up to the response in the absence external evidence, indicating participants might have accumulated evidence from memory. Furthermore, the next chapter will aim to elucidate the temporal dynamics of first- and second-order evidence accumulation processes in the emergence of confidence, focusing exclusively on domain-general evidence accumulation and effector-specific motor preparation.
Chapter Three
Temporal Dynamics of Pre- and Post-Decisional Evidence Accumulation in the Construction of a Graded Representation of Confidence

3.1 Introduction

Extensive theoretical, computational and neurophysiological evidence suggests perceptual decisions are made through accumulation of noisy sensory evidence up to an action-triggering threshold (Gold & Shadlen, 2007; Shadlen & Kiani, 2013; Kelly & O’Connell, 2015; Forstmann, Ratcliff & Wagenmakers, 2016). Recent models have proposed these basic evidence accumulation processes may provide the necessary information for metacognitive experiences, (Moran et al., 2015; Fleming & Daw, 2017; Yu, Pleskac & Zeigenfuse, 2015) a proposal that is receiving growing support from neurophysiological studies in primates (Kiani & Shadlen, 2009; Fetsch et al., 2014; Zylberberg et al., 2016), rats (Kepecs et al., 2008; Lak et al, 2015) and in the human brain (Desender et al., 2016; Tagliaabue et al., 2019, Fleming, van der Putten & Daw, 2018; Boldt & Yeung, 2015; Murphy et al., 2015; Desender et al., 2019; Herding et al., 2019, see also Chapter 2 of this thesis). However, many questions regarding the role of evidence accumulation processes in metacognition remain.

In response to this, two distinct classes of model have emerged in the literature that can be distinguished based on the types of behavioural data they are devised to address. Firstly, behavioural data from tasks with simultaneous perceptual and metacognitive reports can be explained through ‘decisional-locus’ models, in which metacognitive judgments are directly informed by the quantity of sensory evidence accumulated at the time of the initial decision (Zylberberg et al., 2012; Zylberberg et al., 2016; Kiani, Corthell & Shadlen, 2014; German & Philiastides, 2015; Fletsch et al., 2014). Secondly, studies of tasks involving retrospective metacognitive judgements have invoked ‘post-decisional locus’ models in which the accumulation process can continue beyond the ‘first-order’ decision bound in order to inform the ‘second-order’ metacognitive judgement (Moran, Teodorescu & Usher, 2015; Van den Berg et al. 2016; Pleskac & Busemeyer, 2010; Yu, Pleskac & Zeigenfuse, 2015; Fleming & Daw, 2017). Both accounts have been successful in capturing many metacognitive behavioural effects but a particular strength of post-decisional locus models has been the ability to
capture ‘changes of mind’, in which the final second-order judgment is in disagreement with the first-order decision (Resulaj et al., 2009; van der Berg et al., 2016). This behavioural phenomenon can only occur through some form of additional processing taking place after the initial choice report. However, experiments substantially vary on the nature and timescale of this processing. For instance, some studies have suggested changes of mind are caused by brief additional samples of sensory evidence that were still proceeding up the processing pipeline at the time of the first-order decision (Resulaj et al., 2009; van der Berg et al., 2016; Charles & Yeung, 2019), whereas other post-decisional models allow for a more prolonged continuation of the accumulation process up until the delayed confidence judgements (Pleskac & Busemeyer, 2010; Yu, Pleskac & Zeigenfuse, 2015; Moran et al., 2015). Additionally, recent models have challenged the assumption that confidence is read-out from the level of the accumulated evidence. For instance, Fleming & Daw (2017) proposed metacognitive judgements involve an assessment of the accuracy of the original decision, which is distinct from the accumulation of post-choice stimulus information mapped to the original choice alternatives.

At the neural level, support for post-decisional evidence accumulation processes comes from two sources. Firstly, Fleming and colleagues (2018) had participants perform a random dot motion task with retrospective confidence judgements, while collecting functional imaging data. Crucially, after every motion judgment additional stimulus information was shown, which substantially impacted metacognitive evaluations. Specifically, continued presentation of stimulus information lead to lower confidence on errors, while confidence increased on correct choices. Imaging data revealed a distinctive set of brain areas encoded the initial perceptual decision compared to the metacognitive judgements. Moreover, results further indicated that post-choice accumulation reflects an assessment of the accuracy of the original decision. A second line of research on post-decisional accumulation comes from electrophysiological studies that investigate the emergence of error awareness. For instance, Murphy and colleagues (2012, 2015) demonstrated that the build-up rate and amplitude of the error positivity (Pe) forms a continuation of the CPP for the first-order choice. Additionally, the Pe was found to predict the timing of error signalling responses, with similar build-to-threshold dynamics to those that govern the first-order decision (see also, Steinhauser & Yeung, 2010, 2012). Secondly, Boldt & Yeung (2015) showed that a pattern classifier trained to distinguish the Pe can also differentiate between confidence judgements on correct trials.

However, electrophysiological studies have some drawbacks that limit the interpretation of findings. Firstly, errors represent a relatively infrequent subset of all trials in experiments and as such, it remains unclear if and how post-decisional processes occur in the more general context of perceptual decision-making (Ullsperger et al., 2010; Wessel, 2012). Secondly, most research on post-decisional processing commonly deploys a baseline aligned to the first-order response (see for instance, Boldt &
Yeung, 2015; Desender et al., 2019; although for an exception see, Murphy et al., 2015). However, as analyses in Chapter 2 of this thesis have shown, differences in the by CPP remain present until response execution. Hence, it is possible that utilising a baseline prior to response not only obscures these first-order characteristics but also further confounds the interpretation of post-choice accumulation in these studies, since this activity will reflect a mixture of both pre- and post-choice amplitude differences. Finally, research in this domain has observed post-decisional activity well after the disappearance of external sensory evidence (Murphy, et al., 2015; Boldt & Yeung, 2015). This means that the exact nature of the accumulated evidence after the initial decision bound is crossed has not been examined. One explanation is that sensory representations are held in memory after the first-order decision to inform metacognitive judgements, which could emerge as meaningful variations in the post-decisional CPP amplitude. Alternatively, in the absence of new evidence, confidence levels are maximally predicted by neural activity in the CPP at the time of the initial choice.

The aim of the present study was to fully examine the contribution of post-decisional evidence accumulation to choice confidence representations. To this end, the present experiment asked participants to make speeded contrast discrimination reports and then, after a delay of 1000ms, to report their confidence in that choice. Crucially, trials were divided into two conditions. In the first, the stimulus remained on screen throughout the delay period between the perceptual choice and confidence report. In the second, no stimulus was presented during this delay. Analyses centred on the same evidence accumulation signal discussed in the previous chapter. Specifically, dynamics of decision formation were examined through domain-general evidence accumulation, measured in the CPP, and effector-selective motor preparation, by measuring mu/beta band activity over the motor cortex (Kelly & O’Connell, 2013; 2015). This allowed the current study to examine both the pre- and post-decisional evidence accumulation dynamics that influence the emergence of confidence. Firstly, this experiment aimed to assess if the continuation of evidence accumulation requires external sensory information or can instead rely on the internal representation of the evidence for the first-order decision. Second, the current study aimed to extend on the relationship between motor preparatory signals and confidence observed in the previous chapter. Specifically, since threshold-crossing effects are commonly observed at the motor level, decisions that result in changes of mind might produce traceable changes in the ipsi- and contralateral mu/beta motor preparation after the first-order decision that represent the change in the decision bound for the final choice.
3.2 Methods

3.2.1 Participants

Thirty participants aged 18-32 (18 females, 12 males) were recruited. All participants had normal or corrected-to-normal vision, no history of personal or familial neurological or psychiatric illness and no personal or family history of epilepsy or unexplained fainting. Electrophysiological data collected on the final block of one participant was excluded due to a corrupted storage file on the recording computer (this participant was not removed from the analysis). One person was removed from the analysis after their objective accuracy was found to be at chance level across both testing days. Two further participants were removed due to excessive blink and/or EEG artefacts, (>50% trial loss). In total, three subjects were removed from analysis, leading to a final sample of 27 (16 females, 11 males; Age: M=24.12, SD=3.21).

Participants took part in this study over the course of two days and received a gratuity (€45) or research credits in compensation for their time. Subjects were also told that they could gain an additional monetary bonus of up to €16 by obtaining a high score for correctly estimating performance when making metacognitive judgements on a trial-by-trial basis throughout the experiment (see ‘Design and Procedure’). Monetary bonuses were paid after the experiment concluded and ranged from 6 to 11€ (M = 8.5, SD = 1.5). Written informed consent was obtained from all subjects prior to the start of the experiment. Ethical approval for all procedures and methods was obtained from the Trinity College Dublin ethics committee and the experiment was conducted in accordance with the Declaration of Helsinki and European General Data Protection Regulations.

3.2.2 Design and Procedure

Participants performed a two-alternative forced-choice contrast change detection task, in which they were asked to discriminate the direction of tilt in a grating (left or rightward) of a circular compound overlay-pattern after a change in the relative contrast compared to a baseline level. After every decision participants were asked how certain they were in their direction discrimination on a six-point confidence scale (see Figure 3.1 A). To allow a substantial number of trials to be collected on each participant and hence facilitate robust neural measurements, the experiment was conducted across two consecutive days. On the first day participants were familiarised with the experimental paradigm in a short practice session, consisting of 50 trials of the experimental paradigm at maximal contrast change. Afterwards trial difficulty was titrated until participants were at approximately 70% accuracy, which ensured a similar level of subjective difficulty across subjects at the start of the experiment (see
Participants performed 8 blocks of 80 trials on each testing day (640 trials per session; 1280 trials in total). For the purposes of all analyses, data were averaged across both testing sessions. Testing took place in a dark, sound attenuated room with participants seated at a distance of approximately 57 cm from the screen on a comfortable chin rest. Stimuli were presented on a 40.5 cm wide Cathode Ray Tube (CRT) monitor on a dark grey background (luminance: 65.2 cd/m²; refresh rate: 60 Hz; resolution: 1024 x 768). The stimuli were created using Psychtoolbox in Matlab 2013b (Mathworks, Natick, MA) and consist of two overlaid gratings (spatial frequency = 2 cycle) presented in an annulus shape around a fixation point on the center of the screen (inner radius = 1°, outer radius = 6°). The grating stimuli were tilted 45° relative to the vertical midline (left tilt = -45°, right tilt = + 45°) and were ‘phase-tagged’, with left and right gratings presented in anti-phase at a flicker frequency of 30 Hz. This method allows for tracing of the sensory evidence in favour of either choices at the frequency of 15 Hz. The presentation cycles of left and right gratings were counterbalanced across trials.

The experimental paradigm utilised a self-paced rhythm, where participants started every trial by pressing the spacebar. A fixation point was presented on the centre of the screen with the overlaid grating appearing after short delay of 250 ms. The stimuli were presented at 50% contrast for 1000 ms after which the gratings changed contrast to a predetermined titrated level (see Adaptive Staircase Procedure below) with the grating representing the target direction increasing contrast while the grating representing the non-target decreased by an equivalent amount. The magnitude of this contrast difference was drawn on a frame by frame basis from a normal distribution with mean equal to the titrated contrast change level and a standard deviation of 0.2 (see figure 3.1 B). Participants were required to indicate whether the stimulus appeared left or right tilted within a 1500 ms deadline by using the ‘f’ and ‘j’ key on the keyboard to indicate the left and rightward direction, respectively. ‘Too Fast’ and ‘Too Slow’ feedback was given to subjects when the response keys were prematurely pressed and when no response was registered within the response deadline. These trials were removed from all behavioural and electrophysiological analyses. Participants were asked to indicate the contrast change direction using the index finger of their left and right hand for left and rightward contrast directions. On half of all trials, participants were afforded the possibility to accumulate more sensory evidence for 1000 ms after the initial decision, while a blank screen was presented on the other trials. This post-decision evidence manipulation was varied randomly across trials. Afterwards, a 6-point confidence scale appeared on the screen ranging from ‘Certain Left’, ‘Probably Left’, ‘Maybe Left’, ‘Maybe Right’, ‘Probably Right’ and ‘Certain Right’ mapped to ‘s’, ‘d’, ‘f’, ‘j’, ‘k’ and ‘l’ keys. Subjects used three fingers on each hand to make the metacognitive judgements. Specifically, the ring, middle and index finger of the left were placed on the ‘s’, ‘d’ and ‘f’ keys, while the index, middle and ring finger
of the right hand were placed on the ‘j’, ‘k’, ‘l’ keys. All participants received training with utilising the keyboard presses for both judgements prior to the experiment. Feedback was presented at the end of each block, informing participants.

3.2.2.1 Adaptive Staircase procedure.

Prior to the experiment, the level of contrast change in the grating stimuli was determined for each participant. Participants were first trained at the discrimination task under relatively easy conditions. Specifically, all subjects performed 50 trials of the task at the maximal contrast change, which creates an obvious tilt to the left or right on each trial. Once participants performed at approximately 100% accuracy for this level of contrast change, performance was titrated to a threshold level of approximately 70% accuracy by adopting a two-down one-up staircase procedure. The staircase procedure was repeated for five short blocks of 30 trials or until a stable threshold was reached on two subsequent blocks. The average threshold for the change in contrast across subjects in this study was 13.19% (SD = 4.61; range: 7-26%).

3.2.2.2 Scoring and bonus

At the start of the experiment participants were informed that the metacognitive judgements would be scored according to a quadratic scoring rule adopted from von Holstein (1970), which has been utilised in previous research on metacognitive abilities (Moses-Payne et al., 2019; Carpenter et al., 2019):

\[
\text{points} = 100 \times [1 - (\text{accuracy}_n - \text{conf}_n)^2]
\]

\textit{accuracy}, equals 1 on correct contrast judgements and 0 on erroneous contrast detection judgements, while \textit{conf}.reflects the confidence rating on trial \textit{n} scaling from 0 to 1 in increments of 0.2. In order to maximise points participants were instructed to accurately report their confidence based on their best estimate of the accuracy of their initial decision, since high confidence in correct choices and low confidence on errors would lead to higher points and vice versa. In order to ensure participants understood the scoring rule, all subjects were asked how many points they would be given in the theoretical situation where they responded incorrectly but indicated a high confidence in the initial decision. If participants failed to pass this question, the quadratic rule was re-explained until they felt comfortable with the scoring procedure. Afterwards participants were told that they could earn 100 points per trial (8 000 per block; 128 000 across both sessions) and for every 8 000 points accrued across both testing sessions they would earn €1 in bonus (with a maximal bonus of €16).
3.2.3 Reverse Correlation Analysis

Since the magnitude of the contrast change of the gratings was drawn from a normal distribution on a frame-by-frame basis, sensory evidence was allowed to vary around the titrated contrast change level on every trial. Hence, both the momentary and cumulative evidence could be quantified for each decision. The momentary evidence was obtained by subtracting the titrated contrast change level from the values of the contrast change on every frame and were negative when evidence was weaker than the average contrast change level. Conversely, positive values indicated evidence strongly favoured the target contrast change direction. On the trials where sensory evidence was present in both the pre–and post-decision windows, the cumulative noise was computed by summing the momentary random noise across all frames. The slope of the cumulative noise was computed separately for pre- and post-decision windows, allowing the current study to separately estimate the contributions of variability in the sensory evidence (see Figure 1. C). Subsequently, all trials were classified on a within-subject basis according to the sign of the slopes, with positive rates reflecting stronger evidence in favour of the target direction and negative slopes reflecting weaker stimulus evidence (Figure 1. B). This reverse correlation method has previously been successful applied to elucidate the temporal dynamics of evidence integration in the metacognitive domain (Resulaj et al., 2009; Charles & Yeung, 2019).
Figure 3.1 A) Schematic depiction of a trial in the contrast discrimination task with no post-decisional evidence. Trials started when participants press the space bar, a fixation point appeared for 250ms. Stimulus presentation began by presenting overlaid left and rightward gratings at 50% contrast for 1000ms. Afterwards, the contrast of the stimulus was adjusted by increasing the contrast of one grating while lowering the contrast of the other grating by a corresponding amount. The level of contrast change varied on a frame-by-frame basis during a trial and was drawn from a normal distribution with predetermined mean and standard deviation of two units of luminance. Participants were asked to discriminate the direction of the grating that increased in contrast. On half of trials, a post-decisional stimulus was presented for 1000ms, otherwise participants were shown a blank screen with a fixation point. Subsequently, a 6-point confidence scale appeared on the screen and participants were required to make a metacognitive judgement about the initial direction decision. There was no response deadline for metacognitive judgements. However, participants were instructed to respond as fast and accurately as possible for both decisions. B) Time course of single trial cumulative noise for one subject in the contrast change paradigm. Cumulative noise is aligned to the response, denoted by the vertical line at 0ms. Trials are plotted as a function of the overall slope of the pre-decisional evidence. C) The correlation between the average pre-decision and post-decisional evidence across subjects. This shows stimulus presentation was successful in providing independent measures for both time windows since no significant relationship was found between either variables.
3.2.4 EEG acquisition and Preprocessing

Continuous EEG data were recorded through a Biosemi ActiveTwo system (BioSemi, The Netherlands) from 128 scalp electrodes at a sampling rate of 512 Hz. Vertical eye movements were measured with two vertical electrooculogram (VEOG) electrodes placed above and below the left eye. Electrophysiological data were preprocessed and analysed using custom scripts and routines in MATLAB (Mathworks, Natick, MA) and the EEGLAB toolbox (Delorme & Makeig, 2004). Continuous EEG data were firstly detrended to remove all slow drift from recorded channels. Afterwards data was low-pass filtered at 35 Hz and high-pass filtered above 0.1 Hz. Data was then re-referenced offline to the average reference of all 128 electrodes, excluding external VEOGs.

Subsequently, data were divided into epochs. Stimulus-aligned epochs were extracted from 1000 ms prior to evidence onset until 3 seconds after evidence offset, this was done in order to ensure the epoch would encompass both the evidence presentation period as well as the post-decision window (1500ms and 1000ms). The length of these epoch windows were additionally selected to allow enough sample points for time-frequency decomposition. Response-aligned epochs were measured from –1,000 ms pre-response to 1000 ms post response. All epochs were baseline-corrected using the time window immediately preceding evidence onset from -200 to 0ms. Epochs were rejected if recorded activity in any scalp channel exceeded 100 µV or if the bipolar VEOG signal (upper minus lower) exceeded 200 µV at any point from -200 until the confidence scale appeared in the stimulus-aligned window. To avoid disproportionate data loss during artefact rejection, channels with extreme variance and excessive artefact count were interpolated. An upper limit on the interpolated number of channels per subject was determined to avoid over-interpolation of the EEG data (defined as 10% of all recorded channels). Participants were removed from electrophysiological analyses if the blink and/or EEG artefacts were still present on more than 50% of trials after the interpolation stage. Accordingly, two people were excluded from the electrophysiological analyses. These participants were also removed from any behavioural analyses conducted.

The time-frequency power decomposition of both stimulus and response-aligned windows were obtained through the Fast Fourier Transformation (FFT). The FFT was computed using time segments of 256 sample points or 500ms sliding across both epochs in steps of 8 sample points or approximately 20 ms. The duration of time segments was determined to allow for 4 cycles in the lowest frequency measured, allowing for accurate measurement of the 8Hz frequency band (Cohen, 2018).
3.2.5 Behavioural Analysis

3.2.5.1 Examining the Relationship Behavioural Markers of Decision-Making, Metacognition and Post-Decision Evidence Presentation

In order to investigate the relationship between post-evidence accumulation at the behavioural level, data were collapsed within-subject according to whether an additional stimulus was presented or if the post-decision window consisted of a blank screen. Analyses centred on the response accuracy, confidence, reaction time (RT) and response time for confidence judgements (RTconf). Response accuracy was measured as the overall percentage of trials where participants correctly judged the direction of the grating. Confidence was computed by averaging the level of certainty selected on the 6-point confidence scale relative to the target direction. RT was calculated as the elapsed time in milliseconds since the contrast change occurred on the screen. RTconf was measured as the time in milliseconds until a metacognitive judgement was registered from the onset of the confidence scale. Scores were defined as the average number of points earned per trial, excluding trials where participants responded prematurely or missed the response deadline. An additional analysis was conducted on the proportion of trials where participants experienced ‘Changes of Mind’ (ChoM), defined as changing the belief about the initial grating direction judgement by switching to the opposite tilt on the confidence scale. All behavioural dependent variables (DV) were examined using one-way repeated measures ANOVAs, including post-decision evidence presentation (continued/interrupted) as a categorical predictor with two levels. Finally, the relationship between first- and second-order behavioural outcomes was explored with two-way repeated-measures ANOVAs. Separate analyses were conducted with the average RT, scores and the proportion of ChoM, as DV and included the categorical variables confidence (low/medium/high) and the first-order accuracy (error/correct) as predictors.

3.2.5.2 Investigating the Effect of Cumulative Noise at the Behaviour Level

On trials where stimulus presentation continued beyond the initial decision, the relationship between the slope of the cumulative noise and behavioural markers was investigated. Prior to the calculation of the single-trial slopes, premature responses (< 100ms) and outlier RTs (> 3 SDs in either direction of mean RT) were removed from the analysis. This was done to minimise the confounding effects of attentional fluctuation and allow for a substantial accumulation of noise. The slope of the noise build-up was computed independently in pre- and post-decisional time windows on a trial-by-trial basis. The effect of the build-up rate of the cumulative noise was assessed through separate three-way repeated measures ANOVAs with the DVs defined as average response accuracy, confidence,
proportion of ChoM, RT, and RTconf. Categorical predictors in these analyses included the time window for the computation of the cumulative noise (pre –or post decisional) and the direction of cumulative noise slope (strongly and weakly favouring the target grating).

3.2.5 Signal Analysis: Measurement Approach

3.2.5.1 Centroparietal Positivity (CPP): Decision Formation

Domain-general decision formation was investigated through examination of the dynamics of the CPP, which traces the accumulation of perceptual evidence independently of sensory modality or motor requirements (Kelly & O’Connell, 2015). Channel selection for the CPP was conducted on a subject-by-subject basis from a cluster of predetermined electrodes. In order to determine which electrode sites to include for the selection procedure, all electrophysiological data of each participant was averaged together and a grand average topography was generated from activity -150 to -50 ms prior to response execution (see figure 3.3 A). A visual inspection revealed a positive going signal across centroparietal areas, from which five electrodes sites were identified. For each participant the channel in this cluster with the maximal amplitude surrounding response execution was selected. Single trial CPP amplitudes were identified as outliers if the response-aligned amplitude deviated more than 3 SD’s from the within-subject mean amplitude.

3.2.5.2 Mu/Beta band Activity: Effector-Specific Motor Preparation

Motor preparation was examined through mu/beta band desynchronization from 8-30Hz, tracing the effector-specific decision formation in the ipsilateral and contralateral hemispheres. A mu/beta lateralisation index was obtained by subtracting ipsilateral from contralateral power, so that negative values indicate a stronger motor preparation in favour of the chosen option. Furthermore, previous studies have shown mu/beta desynchronization exhibits the build-to-threshold characteristics predicted by sequential sampling models (Twomey et al., 2013; Donner et al. 2009). Channel selection of effector-specific motor preparation was determined from predetermined clusters over the left and right premotor cortex on a subject-by-subject basis. In order to identify hemispheric clusters where decision-related motor preparation was strongest, a grand average topography of left minus right hemisphere beta band activity was generated, averaging across all trials and participants from -150 to -50 ms in the response-aligned trace (see Figure 3.3 E). This identified two clusters of three electrodes over both premotor regions of the scalp, from which the electrode with the strongest lateralisation index at response execution for each subject was selected. Following channel selection, single-trial lateralisation indexes at response time were inspected for outliers. Finally, all trials with amplitudes
more than 3 standard deviations away from the within-subject mean were excluded from subsequent analyses.

3.2.6 Signal Analysis: Statistical Approach

Details in this section outline the rationale and time windows taken for the measurement of the neural signatures in the previous section. Unless mentioned specifically, measurement windows for each electrophysiological signal are identical across all analyses.

3.2.6.1 Temporal Dynamics of Decision Formation in the Emergence of Choice Certainty

To assess the dynamics of evidence accumulation in the emergence of metacognitive judgements the build-up rate and amplitude of the CPP were computed. Recent findings indicate these measures function as indicators of the abstract accumulation of sensory evidence as opposed to contralateral mu/beta, which more closely resemble an action-triggering threshold (Steinemann, O'Connell & Kelly, 2018). CPP amplitude was measured from -150 to -50ms prior to the first-order response, while the build-up rate was measured by fitting a line in the time window -500 to -200ms relative to the initial response execution. The amplitude in the post-decisional window, which spanned 1000ms after the initial decision up to the onset of the confidence scale, was measured in a 200ms wide window centred on -300ms relative to the onset of the confidence scale. The build-up rate of post-decisional CPP was computed as the slope by fitting a line from the indices from -600ms to -300ms prior to the appearance of the confidence scales. These intervals were chosen after inspection of the grand average CPP waveforms.

In order to maximise the power to detect temporal differences in the CPP across pre- and post-decision time windows, all amplitude and slope measures obtained across either interval were included in each regression. This resulted in three-way ANOVAs with the categorical predictors: post-decision evidence presentation (continued/interrupted), measurement interval (pre-/post-decisional) and metacognitive variables. In all subsequent analyses, confidence on the 6-point scale was recoded into 3 bins (low/medium/high) that correspond to the level of certainty of the confidence ratings. Separate regressions were conducted for each of the following metacognitive variables: confidence (low/medium/high), accuracy (error/correct) and change of mind (ChoM/no ChoM). To ensure trial difficulty did not function as a cue for the final metacognitive judgement a separate regression was done on each CPP measure with the predictors confidence (low/medium/high) and accuracy (error/correct). An additional analysis sought to examine the potential influence of dynamic urgency in the evidence accumulation process for metacognitive judgments. Previous research has indicated the CPP shows a sensitivity to urgency, exhibiting a decrease in amplitude with longer response times and
decreased accuracy (Steinmann et al., 2018). As such, a decreased amplitude in the CPP with diminished choice certainty could also reflect the influence of a collapsing bound, rather than a true sensory evidence accumulation difference. This possibility was examined through a single-trial mixed-effect regression with single-trial pre-decision CPP amplitudes as a dependent variable with random slope. The predictors response time, confidence and accuracy were added in a step-wise fashion with random slopes. For every random slope added to the regression, a model fit comparison was made comparing the model to the previous best fitting regression model. This resulted in a model with fixed and random effects for reaction time and confidence. Accuracy did not significantly improve the model fit and was omitted from the analysis.

3.2.6.2 Post-Decisional Motor Preparation Predicts Metacognitive Judgements

The dynamics of effector-specific motor preparation on the representation of confidence was assessed through the mu/beta band and beta lateralisation index. Previous studies have found a reliable threshold crossing effect for motor preparation over the contralateral hemisphere (Kelly & O’Connell, 2013; Steinmann et al., 2018). Theoretical models of response conflict suggest that conflict monitoring might rely on the race between competing response accumulators and can only reflect differences in ipsilateral motor preparation (Botvinick et al., 2001; Yeung et al., 2004; Steinhauser & Yeung, 2011). A visual inspection of the grand average mu/beta and beta lateralisation index traces indicated substantial differences between the pre- and post-response activity. Analysis of amplitude prior to the first-order response for both measures centered on the FFT values within the -150 to -50ms window, with the slope being defined as the desynchronization rate between indices from -500 to -200ms. In the post-decision time window, amplitude was defined as the FFT values between -400 and -200ms relative to the onset of the confidence scale. The build-up rate was measured as the slope of a line fit from -600 to -300ms relative to the appearance of the confidence scale.

To limit the complexity of the ANOVAs for mu/beta and lateralisation index, all amplitudes and rates were separately analysed for the pre- and post-choice interval. This led to all analyses on mu/beta being conducted with three-way repeated measures ANOVAs with the factors: hemisphere (ipsilateral/contralateral), post-decision evidence presentation (continued/interrupted) and metacognitive variables. Separate regressions were conducted for each of the following metacognitive variables: confidence (low/medium/high), accuracy (error/correct) and change of mind (ChoM/no ChoM). Analyses for beta lateralisation indexes were conducted with an identical procedure using two-way repeated-measure ANOVAs.
3.2.6.3 Reverse Correlation Analysis of Decision Formation

To provide novel insight into the relationship between perceptual decision formation and metacognition, a reverse correlation analysis was used to identify trials where cumulative noise in the sensory evidence strongly or weakly favoured the target stimulus (Charles & Yeung, 2019; Resulaj et al., 2009; Zylberberg et al., 2012). This allowed for an investigation of the effect of this cumulative noise on the temporal dynamics of the CPP, building on similar approaches from previous research (see Devine et al., 2019). The amplitude was measured from -400 to -50ms prior to the onset of the confidence scale, while the build-up rate was defined as the slope of a line fit to the CPP in the interval -600 to -300ms preceding the appearance of the confidence scale. The effect of cumulative noise on the CPP amplitudes and build-up rates was investigated through two-way repeated-measure ANOVAs with two categorical predictors: measurement window (pre-/post-choice) and the level of cumulative noise (weakly/strongly favours the correct choice alternative).

3.2.7 Statistical Analysis

In every repeated-measure ANOVA conducted, data were tested for suitability for parametric analysis in two steps, identical to the procedure from the previous chapter. Firstly, the normality assumption was tested through an examination of the outliers in the standardised residuals. Secondly, Mauchly’s test of sphericity was used to assess the assumption of equal variances across all factors with two or more levels. Whenever the assumptions were violated the Greenhouse-Geisser or the Huynh-Feldt corrected degrees of freedom and p-values are reported (the correction applied was contingent on the degree of violation). All post-hoc paired-sample t-tests reported were corrected for multiple comparisons with the Bonferroni-Holm procedure and only corrected p-values are reported (Holm, 1979).
3.3 Results

3.3.1 Behavioural Findings

3.3.1.1 Examining the Effect of Post-Decision Evidence Presentation on Behaviour

All behavioural effects are summarised in Figure 3.2 panels A-E. As expected given that conditions were randomly interleaved, first-order task accuracy did not vary as a function of post-choice stimulus presentation (F(1,26) = 0.9, p = 0.351). Crucially, second-order performance was significantly impacted by the post-decisional evidence manipulation. Firstly, choice certainty was higher on the continued stimulus trials (Figure 3.2 B; F(1,26) = 22.70, p < 0.001) and was reported with slower reaction times (RT) compared to trials on which no additional evidence was presented (Figure 3.2 E; F(1,26) = 155.51, p < 0.001). Similarly, the proportion of changes of mind, where participants changed beliefs about the direction of the first-order contrast discrimination, increased when stimulus evidence persisted beyond the initial decision (Figure 3.2 D; F(1,26) = 26.29, p < 0.001). Finally, participants achieved higher overall scores on continued stimulus presentation trials (Figure 3.2 C; F(1,26) = 33.45, p < 0.001), which suggests these behavioural effects reflect a more accurate assessment of the primary task performance.

A second set of regression analyses were conducted to explore the relationship between first-order task accuracy and confidence across other behavioural variables (Figure 3.2. F-H). This yielded three additional insights. Firstly, first-order reaction time (RT) showed a significant effect of confidence (F(2,52) = 12.92, p < 0.001), with RTs linearly decreasing as a function of increasing choice certainty (Figure 3.2 F; low vs medium: t(26) = 4.20, p < 0.001; low versus high: t(26) = 5.65, p < 0.001; medium vs high: t(26) = 3.73, p < 0.001). First-order RTs did not differ significantly as a function of first-order accuracy (F(1,26) = 0.57, p = 0.458), with no confidence by accuracy interaction (F(2,52) = 2.12, p = 0.132). Secondly, the proportion of changes of mind showed a significant interaction effect between first-order accuracy and confidence (F(2,52) = 7.24, p = 0.002; Figure 3.2 G; error vs correct: t(26) = 5.29, p < 0.001; low vs medium: t(26) = 5.29, p < 0.001; low vs high: t(26) = 8.71, p < 0.001). However, due to the simultaneous rating of changes of mind and confidence the direction of this interaction could not be fully interpreted. Specifically, it is equally possible that low confidence at the time of the first-order decision is associated with a higher frequency of changes of mind or that post-decision evidence prompts a change of mind but is not sufficient to generate a high confidence. Finally, the average level of confidence, measured on a 6-point scale relative to the target response, showed a significant interaction between post-choice stimulus presentation and accuracy.
(F(1,26) = 54.79, p < 0.001), with lower confidence observed after errors when stimulus presentation continued after the first-order decision (Figure 3.2 H, \textit{continued error vs interrupted error}: t(26) = 10.23, p < 0.001; \textit{continued error vs continued correct}: t(26) = 19.30, p < 0.001).

Figure 3.2 Behavioural performance and metacognitive variables plotted as a function of post-decisional evidence presentation, accuracy and confidence in the contrast discrimination experiment. Error bars across panels denote standard error of the mean. A) First-order task performance did not differ across continued and interrupted stimulus presentation. B) Average confidence plotted as a function of post-choice evidence manipulation. Confidence increased when sensory evidence was presented after the initial decision. C) Scores separated by stimulus presentation. Scores were significantly higher when evidence continued beyond the initial choice. D) Changes of mind (ChoM) plotted across different levels of post-decisional evidence presentation. ChoM occurred more frequently on continued sensory evidence trials. E) Metacognitive response times plotted as a function of continued evidence. Confidence judgements were made slower when contrast grating presentation continued. F) First-order reaction time (RT) plotted as a function of different levels of choice certainty. Average response time increased with higher levels of confidence. G) The proportion of ChoM plotted as a function of task performance and choice certainty. The proportion of ChoM varied significantly with accuracy and confidence level, people changed beliefs about the initial decision rarely on correct choices and more frequently on low confidence trials. H) Confidence plotted as a function of post-decisional evidence presentation and accuracy. Confidence was higher on errors on post-decisional evidence presentation trials, reflecting the greater likelihood of changes of mind in this condition.
3.3.1.2 The Impact of Cumulative Noise on Behavioural Markers

To examine whether or not the cumulative noise affected the first-order decision and subsequent metacognitive judgements, the slope of the cumulative noise in the physical stimulus was computed on the continued stimulus presentation trials in two distinct time windows. The first window extended from evidence onset until the first-order response, while the second time window was taken from the first-order decision to the onset of the confidence scale. Trials could then be grouped according to whether the random fluctuations in the physical evidence were strongly or weakly in favour of the correct choice alternative. Analysis of behavioural outcomes revealed that the strength of cumulative noise did not influence first-order RT (Figure 3.3 A; F(1,26) = 1.75, p = 0.197) nor first-order accuracy (Figure 3.3 B; F(1,26) = 0.47, p = 0.498). In contrast, significant increases were found in the average confidence (Figure 3.3 C; F(1,26) = 7.30, p = 0.012), faster metacognitive RTs (Figure 3.3 D; F(1,26) = 6.70, p = 0.016) and a higher proportion of changes of mind when the cumulative noise strongly favoured the correct choice alternative (Figure 3.3 E; F(1,26) = 12.05, p = 0.002). Interestingly, cumulative noise impacted metacognitive behaviour irrespective of when the slope was measured (ChoM: F(1,26) = 0.73, p = 0.40; Confidence RT: F(1,26) = 2.89, p = 0.101; Confidence: F(1,26) = 2.61, p = 0.12), which indicates that random fluctuations in the physical stimulus both prior and after the first-order response had a significant influence on metacognitive decision-making. Taken together, this pattern of results demonstrates that differences in the pre-decisional cumulative noise failed to affect the behaviour on the contrast change decision but did influence confidence.
Figure 3.3 Behavioural outcomes plotted as a function of the cumulative noise slope for the post-decisional evidence trials of the contrast discrimination task. Error bars across panels denote standard error of the mean. **Contrast Detection Behaviour**: A) First-order reaction Time (RT) plotted as a function of cumulative noise slope. RT in contrast change judgements did not vary with cumulative noise strength. B) First-order task performance plotted as a function of cumulative noise strength. First-order accuracy did not show a systematic relationship with the slope of the cumulative noise. **Metacognitive Behaviour**: C) Confidence plotted across the different levels of cumulative noise strength. Confidence was significantly higher when noise strongly favoured the direction of the target grating. D) The average proportion of changes of mind (ChoM) separated by cumulative noise slope. The proportion of ChoM was lower when cumulative noise weakly favoured the target direction. E) Confidence RT plotted across cumulative noise slope conditions. Confidence RTs were significantly slower when cumulative noise strongly favoured the contrast choice.

### 3.3.2 Pre- and Post-decisional Dynamics of Evidence Accumulation and the Emergence of Choice Confidence

*Post-Decisional Evidence Presentation.* A visual inspection of the stimulus- and response-aligned time courses reveals the CPP initially builds and peaks at the time of the first response (Figure 3.4 B & C). Subsequently, rather than simply continuing its build-up, the signal exhibits a return
toward baseline before resuming its build-up to a second peak prior to the onset of the metacognitive response cue (Figure 3.4 C). Consistent with the CPP undergoing two distinct build-ups, the amplitude prior to the onset of the confidence scale was observed to be significantly lower than its amplitude immediately preceding the first-order decision \((F(1,26) = 5.64, p = 0.025)\). Additionally, the continuation or removal of the stimulus presentation did not have any significant influence on the CPP amplitude (Figure 3.4 C; \(F(1,26) = 0.12, p = 0.735\)) or build-up rate (\(F(1,26) = 0.73, p = 0.4\)) in the moments before the confidence scale was presented. Similarly, no significant interactions were found between post-decisional stimulus presentation and metacognitive predictors on the slope (Confidence: \(F(2,52) = 2.30, p = 0.142\); Accuracy: \(F(1,26) = 0.46, p = 0.505\); ChoM: \(F(1,26) = 1.56, p = 0.223\)) or the amplitude of the CPP (Confidence: \(F(2,52) = 2.04, p = 0.165\); Accuracy: \(F(1,26) = 0.04, p = 0.983\); ChoM: \(F(1,26) = 0.02, p = 0.881\)). Taken together, these findings suggest that the evidence accumulation in the CPP after the first-order response occurs independent of the presence of external sensory evidence.

Figure 3.4 Domain-general evidence accumulation (CPP) plotted as a function of the post-decisional stimulus presentation manipulation (continued/interrupted) in the contrast change detection task. **Decision Formation:** A) Topography of the ERP measured at response execution showing a positive centroparietal signal. **B)** Stimulus-aligned CPP plotted as a function of stimulus presentation relative to the onset of the contrast change. Time window -200 to 0ms is used as the baseline for all analyses, while the vertical line at time point 0ms indicates the onset of stimulus evidence. **C)** CPP aligned to the first-order response separated according to the different levels of post-decisional stimulus presentation. Time point 0ms, denoted by the vertical black line, indicates response execution. **D)** Topography of the grand-average wavelet obtained by averaging 500ms to 800ms after the first-order response, which reveals a positive-going centroparietal ERP component.

**Confidence Judgements.** Both the amplitude and build-up rate of the CPP displayed significant interactions with the predictors’ time interval (pre/post-choice) and the level of confidence (Figure 3.5. B; \(F(2,50) = 15.13, p <0.001\); \(F(2,52) = 16.67, p <0.001\)). Post-hoc t-tests indicate that, as in Chapter
2, the amplitude of the CPP relative to the first-order response is significantly lower on low confidence trials. However, the opposite effect was found in the CPP slope prior to the onset of the confidence scale (high vs low pre-choice: t(26) = 4.33, p < 0.001; high vs low post-choice: t(26) = 1.91, p = 0.03). Similarly, the CPP build-up rate prior to the first-order response was significantly lower when confidence was low, with the reverse pattern visible in the moments preceding the onset of the confidence scale (see Figure 3.5 B; high vs low pre-choice: t(26) = 3.60, p = 0.001; high vs low post-choice: t(26) = 3.28, p = 0.002). Finally, a separate single-trial mixed-effect regression analysis showed that the relationship between confidence and the single-trial CPP amplitudes prior to the first-order response remained significant when accounting for the effects of first-order accuracy and RT (F(2,52) = 5.80, p = 0.005; F(2,52) = 10.87, p < 0.001). This suggests that the relationship between the CPP and confidence reflects differences in the evidence accrued at the time of the first-order response independent of reaction time or the perceived trial difficulty (e.g. urgency).

First-Order Accuracy. Both CPP amplitude and slope showed a significant interaction with time interval and first-order accuracy (Figure 3.5 D; F(1,26) = 28.05, p < 0.001; F(1,26) = 7.57, p = 0.01). Specifically, both the amplitude and build-up rate of the CPP were higher on correct choices compared to errors in the moments prior to the first-order response (t(26) = 4.08, p < 0.001; t(26) = 3.55, p = 0.002). In contrast, the CPP amplitude preceding the confidence scale was found to be significantly higher after errors (t(26) = 2.12; p =0.022), as shown visually in Figure 3.5 D by the cross-over of the CPP traces immediately after the first-order response. No significant differences in the build-up rate were found between evidence accumulation signals prior to the confidence scale (t(26) = 0.88; p = 0.19). Finally, the observed effects in the amplitude and build-up rate of the CPP prior to the first-order decision are unlikely to directly reflect the duration of the evidence accumulation process, since first-order RTs did not significantly vary between erroneous and correct choices (F(1,26) = 0.96, p = 0.33).

Changes of Mind. Domain-general decision formation measured through the CPP amplitude and build-up rate showed a significant interaction between the time interval and changes of mind (F(1,26) = 29.84, p < 0.001; F(1,26) = 8.91, p = 0.006). Specifically, as shown in the cross-over between the pre- and post-decision traces in the CPP of Figure 3.5 F, pre-choice CPP amplitude and build-up rate were significantly higher for no change of mind trials (t(26) = 2.28, p = 0.033; t(26) = 3.25, p = 0.006). In the post-decision window the opposite effect is observed, with the significantly higher CPP amplitudes and build-up rates on change of mind trials ( t(26) = 5.01, p < 0.001; t(26) = 2.35, p = 0.027).
Figure 3.5 Abstract decision formation (as measured by the CPP) separated by confidence, accuracy and Changes of Mind (ChoM). A) Stimulus-aligned CPP plotted as a function of confidence level relative to the onset of the contrast change. Grey line: difference in the CPP traces between low and high confidence over time. B) Response-aligned CPP separated according to the level of confidence. Time point 0ms, denoted by the vertical
line indicates the time of the first-order decision. The topography reflects the difference between low and high confidence ratings in the ERP from 600-800ms after the first-order decision. Grey line: difference in the CPP traces between low and high confidence over time. C) Stimulus-locked CPP plotted as a function of accuracy relative to evidence onset at 0ms. Grey line: difference in the CPP between erroneous and correct choices. D) Response-locked CPP separated by accuracy relative to the response. Time point 0ms denotes the first-order response. The topography reflects the difference between errors and correct ERPs from 600-800ms after the first-order response, which reveals a centroparietal positive going component. Grey line: CPP on error trials subtracted from correct choices. E) Stimulus-aligned CPP plotted as a function of ChoM. Grey line: difference in the CPP traces between ChoM and no ChoM trials. F) Response-aligned CPP plotted as a function of ChoM. Time point 0ms in the panel indicates the time of the first-order response. The topography indicates the difference between ChoM and no ChoM ERPs in the ERP from 600-800ms after the first-order decision, showing a positive component across centroparietal electrodes. Grey line: difference in the CPP traces between ChoM and no ChoM trials.

3.3.3 Pre- and Post-Decisional Motor Preparation Predicts Metacognitive Judgements

Post-Decisional Evidence Presentation. A visual inspection of stimulus- and response-locked motor preparation traces in Figure 3.6 B & C, reveals that mu/beta band activity after the first-order response exhibits a characteristic rebound effect, followed by a second desynchronization prior to the confidence judgement. As was the case for the CPP, the average effector-specific build-up rates immediately prior to the onset of the confidence scale were not significantly affected by the presence or absence of post-decisional stimulus presentation (F(1,24) = 0.09, p = 0.77). However, as suggested by the traces shown in Figure 3.6 C, the mu/beta band amplitudes prior to the onset of the confidence scale are slightly lower when stimulus presentation continues, although this effect was only marginally significant (F(1,25) = 3.15, p = 0.088). Interestingly, lateralisation indices showed no significant main effects of post-decisional stimulus presentation on both the build-up rate (F(1,26) = 1.14, p = 0.296) and amplitude (F(1,26) = 0.03, p = 0.861) after the first-order response.

Taken together, this pattern of results indicates that, while the relative motor preparation remained similar after the first-order response, subtle differences were observable in the effector-specific traces prior to the onset of the confidence scale. One potential explanation for these results is that changes of mind are slightly more common in continued stimulus presentation trials, which would lead to a change of the decision bound that would be more apparent in this condition (see ‘Changes of Mind’ below).
Figure 3.6 Effector-specific mu/beta motor preparation separated by different levels of the post-decisional evidence presentation in the contrast discrimination task. **Motor Preparation:** A) Topography of the lateralized mu/beta power for left- minus right-hand responses at time of the first-order response. B) Stimulus-aligned mu/beta for ipsilateral and contralateral hemispheres, separated according to stimulus presentation conditions, relative to onset of stimulus evidence. C) Response-aligned mu/beta traces for contralateral and ipsilateral hemispheres plotted as a function of post-decisional stimulus presentation. Time point 0 denotes the time of the response. *Insert:* response-aligned lateralised beta index, obtained by subtracting ipsilateral and contralateral traces, plotted according post-decisional evidence presentation.

Confidence Judgements. Investigations of effector-specific mu/beta motor preparation and confidence yielded three key insights. Firstly, two analyses were conducted on limb-specific mu/beta amplitudes prior to the first-order decision and the onset of the confidence scale. These analyses focused on the subset of trials where no changes of mind were registered, which removed any possible confound of the hemispheric crossover effect associated with the switch between effectors (see, ‘Changes of Mind’ below). Results on pre-choice amplitudes indicate a significant interaction effect of confidence and hemisphere (F(2,52) = 3.53, p = 0.037). Specifically, comparatively stronger ipsilateral motor preparation was observed on low confidence judgements (ipsilateral low vs high: t(26) = 2.22, p = 0.035; contralateral low vs high: t(26) = 1.55, p = 0.134). Additionally, a similar interaction pattern is observed on the no change of mind trials immediately prior to the confidence scale (F(2,52) = 9.84, p < 0.001; ipsilateral low vs high: t(26) = 2.56, p = 0.033; contralateral low vs high: t(26) = 0.97, p = 0.342). These results replicate the pattern of motor preparation observed in Chapter 2 and extend it by demonstrating that mu/beta activity prior to the first-order decision and confidence response cue both predict retrospective choice confidence reports.

Secondly, mu/beta band amplitudes immediately prior to the onset of the confidence scale showed a significant interaction between the level of confidence and post-decisional stimulus presentation (F(2,50) = 5.69, p = 0.006), while build-up rates displayed a significant three-way interaction between the predictors hemisphere, confidence and post-decisional stimulus presentation
As shown in Figure 3.7 panels A and B, these interactions arise from the differences between the ipsilateral and contralateral traces across the different levels of post-decisional stimulus presentation on low confidence trials. Specifically, in the presence of continued stimulus presentation, contralateral motor preparation was greater on low confidence trials compared to high confidence judgements ($t(25) = 3.21, p = 0.004$). In contrast, when stimulus presentation was interrupted no significant difference in contralateral motor preparation was observed between low and high confidence ($t(25) = 0.22, p = 0.831$). One potential explanation for this pattern of results is the greater likelihood of changes of mind on the trials with post-decisional evidence, which might reflect the crossover of ipsilateral and contralateral motor preparation signals on these trials (see ‘Changes of Mind’ below).

Finally, effector-specific mu/beta amplitudes prior to the confidence scale showed a significant interaction between the level of confidence and hemisphere ($F(2,50) = 27.86, p < 0.001$). As shown in Figure 3.7 B, in the absence of additional stimulus presented ipsilateral mu/beta band amplitudes are significantly elevated prior to high confidence judgements compared to low certainty ratings (low vs high: $t(25) = 2.99, p = 0.012$), an effect not observed in the contralateral hemisphere (low vs high: $t(25) = 1.94, p = 0.12$). This is likely to be a consequence of the contralateral motor activation building to threshold on the first-order decisions, which limits the variability of this neural signature.

First-Order Accuracy. Effector-specific mu/beta amplitudes and build-up rates prior to the confidence scale exhibited a significant three-way interaction between first-order accuracy, post-decision stimulus presentation and hemisphere ($F(1,24) = 9.77, p = 0.005$; $F(1,24) = 6.97, p = 0.014$). Similarly, the amplitude and build-up rate of the lateralisation indices in the same time window showed a significant interaction between accuracy and stimulus presentation ($F(1,25) = 6.86, p = 0.015$; $F(1,24) = 5.43, p = 0.029$), which was driven by a greater lateralisation on error trials when post-decision stimulus information was presented compared to when it was absent (continued error vs correct: $t(25) = 3.31, p < 0.001$; interrupted error vs correct: $t(24) = 0.58, p = 0.567$). This pattern converges with previous analyses and might reflect the higher frequency of changes of mind after erroneous action. Moreover, the contralateral motor preparation signals exhibit a similar threshold-crossing effect in the moments prior to the onset of the confidence scale on correct trials (solid lines in Figure 3.7 D; $t(25) = 1.54, p = 0.136$). This provides further support for the limited variability in contralateral signatures to inform metacognitive judgements, in contrast to motor preparation in the ipsilateral hemisphere (dashed lines in Figure 3.7 D; $t(25) = 3.85, p < 0.001$).

Changes of Mind. Congruent with previous analyses of confidence and first-order accuracy, ipsilateral and contralateral mu/beta traces revealed a crossover effect particular to change of mind trials (Figure 3.7 E & F). This pattern was confirmed in statistical analyses, which showed both
effector-specific mu/beta amplitude and build-up rates displayed a significant interaction between hemisphere and changes of mind (F(1,26) = 35.30, p < 0.001; F(1,24) = 20.44, p < 0.001). Finally, beta lateralisation indices exhibited higher build-up rates and amplitudes prior to the onset of the confidence scale (F(1,25) = 33.48, p < 0.001; F(1,24) = 24.42, p < 0.001). Furthermore, as indicated in the lateralisation plots in Figure 3.7 F (insert), this change of mind effect emerges progressively over time in the motor preparation signals, commencing immediately after the first-order decision and continuing to build until the onset of the confidence scale.
Figure 3.7 Motor preparation (mu/beta) and lateralized beta index separated by stimulus presentation and metacognitive variables. Time point 0ms across panels, indicated by the black vertical line, denotes response time. A) Response-aligned mu/beta plotted as a function of confidence level for trials with post-choice evidence. B) Response-aligned mu/beta plotted as a function of confidence level for trials with no post-choice evidence. Insert: response-aligned lateralized beta index, obtained by subtracting ipsilateral and contralateral traces,
separated according to confidence and stimulus presentation. C) Response-aligned mu/beta plotted according to accuracy for trials with post-decisional stimulus evidence. D) Response-aligned mu/beta plotted as a function of accuracy level for trials with no post-choice evidence. Insert: response-aligned lateralized beta index, obtained by subtracting ipsilateral and contralateral traces, separated according to accuracy and stimulus presentation. E) Response-aligned mu/beta plotted as a function of changes of mind (ChoM) for trials when stimulus presentation continued after the initial decision. F) Response-aligned mu/beta plotted by Changes of Mind when stimulus presentation was interrupted. Insert: response-aligned lateralized beta index, obtained by subtracting ipsilateral and contralateral traces, separated by ChoM and stimulus presentation.

3.3.4 Cumulative Noise Slope Predicts Post-Decisional CPP Amplitude

In order to test the hypothesis that the build-up of the CPP after the first-order choice reflects a post-decisional evidence accumulation process, an additional analysis was conducted on the continued stimulus presentation trials. As outlined in the Methods, random stimulus noise was introduced on a frame-by-frame basis by drawing the differential contrast of the two gratings from a normal distribution. We then divided trials into two bins according to whether the cumulative sum of these random contrast fluctuations either strongly or weakly favoured the target direction (see Figure 3.1 B for an example of a typical single subject). This cumulative noise was quantified separately for the pre- and post-decision time windows.

Results showed that cumulative noise impacted significantly on CPP amplitude measured immediately prior to the onset of the confidence scale (F(1,25) = 5.07, p = 0.033) with no effect of the measurement window (F(1,25) = 0.08, p = 0.786). A visual inspection of figure 3.8 B shows this reflects the higher post-decisional amplitude when the cumulative noise strongly favoured the target direction. Finally, no effects of either categorical variables were observed in the slope of the post-decisional CPP (F(1,25) = 2.47, p = 0.129; F(1,25) = 0.01, p = 0.950). This suggests that the CPP amplitude was significantly modulated by the cumulative noise, with higher CPP amplitudes found on trials where noise strongly favoured the target direction, irrespective of the measurement window. Interestingly, this pattern of findings is not fully in line with the previous results that showed lower confidence, which should function as a proxy of trial difficulty, is associated with higher CPP amplitude. A potential explanation for this dissociation comes from the behavioural impact of the cumulative noise. Specifically, both the proportion of changes of mind and confidence are significantly elevated on trials where the cumulative noise strongly favours the correct choice alternative. This suggests any further interpretation of the CPP amplitude effects in the context of metacognitive evaluations is complicated by the opposing effects of confidence and changes of mind (see Figure 3.5 B & F).
Figure 3.8 Abstract decision formation (CPP) separated according to cumulative noise and measurement window (pre-/ post-choice). A) Stimulus-aligned CPP plotted as a function pre-and post-decisional cumulative noise strength. Time point 0ms indicates the onset of evidence as denoted by the black vertical line. B) CPP aligned to the first-order response separated according to the slope of the cumulative noise in the pre-choice and post-choice time window. Time point 0ms, indicated by the vertical line denotes the response execution. Topography reflects the overall average ERP from 600-800ms after the first-order decision and demonstrates a positive-going component across centroparietal electrodes.
3.4 Discussion

The aim of this study was to extend on the observations of Chapter 2 by exploring the post-decisional temporal dynamics of neural decision signals and their contribution to retrospective choice confidence representations. To this end, an experiment was conducted that utilised a contrast change discrimination task with delayed confidence reports. By varying whether the stimulus disappeared or remained present after the initial choice we were able to verify the degree to which post-decisional accumulation was contingent on the continued availability of physical evidence (Moses-Payne et al., 2019; Carpenter et al., 2019; Murphy et al., 2015; Desender et al. 2019; Insabato, Pannuzi & Deco, 2017; although see, Siedlecka et al., 2016; Boldt et al., 2019). The results replicated the key effects reported in Chapter 2. The amplitudes of the CPP and ipsilateral beta immediately prior to the first-order choice scaled with subsequently reported confidence levels. In addition, both signals were found to exhibit post-choice build-ups that predicted first-order choice accuracy and second-order confidence. These post-decisional dynamics were surprisingly unaffected by the presence or absence of a physical stimulus.

The results of this study provide novel insight into the role that evidence accumulation processes reflected in the CPP play in both first- and second-order decision making. Firstly, an examination of the pre- and post-choice CPP time-courses suggests this signal exhibits two distinctive, yet partially overlapping, accumulation processes in this task. Specifically, the CPP exhibited an initial peak that coincided with the first-order decision but then rapidly declined before resuming a second build-up prior to the appearance of the confidence scale. These dynamics are analogous to some observations from the domain of error awareness. For instance, Murphy and colleagues (2015) reported that the CPP continued to build after erroneous actions and peaked prior to subsequent error signalling reports but they too observed a similar though far more subtle CPP dip after erroneous actions. The paradigm used by Murphy et al (2015) involved easy stimulus discriminations and rapid RTs therefore decision formation and choice evaluation occurred in close proximity, likely preventing the authors from observing what our data indicate to be two distinct accumulation stages. The observation that the CPP undergoes a separate post-decisional build-up is hard to reconcile with some post-decisional locus models, which assume evidence accumulation after the first-order decision continues in the same decision variable until a metacognitive report is required (Pleskac & Busemeyer, 2010; Yu & Pleskac & Zeigenfuse, 2015; Moran et al., 2015). In addition, we found that in a reversal of the relationships observed prior to first-order choices, CPP amplitudes were larger prior to low confidence reports, changes of mind and after errors. These results accord with the observations of Murphy et al (2015) who found that post-decisional CPP accumulation only occurred prior to detected error and was silent when participants failed to signal them. Taken together, our results broadly accord with recent
models of metacognition which propose that pre- and post-decisional accumulation processes are qualitatively distinct, such that evidence is initially mapped to the first-order choice alternatives but then remapped post-choice to a correct/incorrect scale (Fleming & Daw, 2017; Fleming, van der Putten & Daw, 2018). This demonstration that both pre- and post-decisional measurements of the CPP predicts delayed confidence reports but in opposite directions highlights a critical methodological consideration for research in this field. Many previous EEG studies have utilized pre-response intervals when baseline correcting CPP and P3b traces but this is problematic since it would conflated the variability in CPP amplitude prior to the first-order decision with variability in the interval prior to the delayed confidence judgements (Boldt & Yeung, 2015; Desender et al., 2019). For instance, in the current study this procedure would have caused an overestimation of the differences between all levels of confidence levels, due to the positive association between baseline amplitudes and confidence.

Finally, the post-decisional accumulation in the CPP was equally prominent whether the stimulus disappeared or remained following the initial decision. One potential explanation for these results is that participants relied on alternative sources of evidence in the absence of external stimulus information, with a likely candidate being sensory representation held in memory. This interpretation is supported by the lower level of confidence and proportion of changes of mind was lower in the absence of stimulus presentation after the first-order decision, which suggests the metacognitive judgements relied on the same flawed sensory evidence that informed the first-order decision. Secondly, an analysis of the effect of the cumulative noise on the post-decision stimulus presentation trials revealed the post-decision CPP amplitudes were higher when cumulative noise strongly favoured the target direction. This modulation occurred irrespective of the measurement window of the cumulative noise slope, which suggest that the cumulative noise that contributed to the first-order decision similarly impacted the post-decisional CPP amplitude and metacognitive behavioural variables consistent with a relatively lossless integration process.

Analyses of effector-specific mu/beta band activity and beta lateralisation indices also extended on the results from the previous chapter by offering two key insights. Firstly, mu/beta band activity measured over the contralateral hemisphere prior to the first-order decision and onset of the confidence response cue showed limited sensitivity to confidence when subjects did not change their mind, which is likely a consequence of the threshold crossing effect commonly observed in this signal for the first-order response (DeLange et al., 2013; O’Connell et al., 2012). Secondly, on change of mind trials post-decisional mu/beta band activity exhibited a crossover between the motor preparation traces of ipsilateral and contralateral hemispheres, pointing to a novel means of inferring the time-course of changes of mind. In this paradigm changes of mind entailed clicking with the opposite hand to the one used to report the first-order choice. Therefore, accounting for this changeover effect in the
investigation of motor level processes is important, since this might to some degree account for signal modulations relating to confidence and first-order accuracy. For instance, the relative difference in ipsilateral and contralateral motor preparation was found to be smaller on low confidence trials, where changes of mind occur proportionally more frequently. However, in the absence of changes of mind amplitudes only significantly differed in the ipsilateral hemisphere. Furthermore, this strong influence of changes of mind might further explain the counterintuitive finding that stronger post-decisional CPP amplitudes are observed on the low confidence trials, since these trials are most commonly associated with them.

The results from this experiment highlights some avenues for future studies. Firstly, the temporal dynamics of the CPP provided some evidence for the existence of two qualitatively distinct stages in the evidence accumulation process. This raises interesting questions about the neural generators underlying CPP. One possibility is that these characteristics might reflect the involvement of distinct neural populations that encode the first- and second-order decisions. This is congruent with findings that the sub-populations of neurons in the parietal cortex, which source localisation has suggested might be the origin of the CPP (Desender et al., 2016), encodes different stimulus categories (Raposo, Kaufman & Churchland, 2014). Alternatively, the overlap between both decisions could be a direct consequence of the trial averaging procedure. Specifically, it could be that the first-order CPP returns to baseline prior to second accumulation stage but that this occurs at a variable time. Hence, this could explain the partial overlap between the stages observed here. Future studies could aim to fully disentangle these processes, for instance by adopting longer delays after the first-order decision that would allow the CPP to fully return to baseline. Secondly, the results of the reverse correlation analysis were not fully consistent with the dynamics of the CPP across different confidence levels. Specifically, prior to the metacognitive response cue lower CPP amplitudes were associated with higher confidence, while stronger cumulative noise was correlated with a higher CPP amplitude and higher confidence. One possible explanation for this is that the increased amplitude in the cumulative noise analysis reflects a complex mixture of metacognitive behavioural effects, since these trials were also associated with a higher proportion of changes of mind. However, the current study did not collect enough data to reliably separate the different trial types. Therefore, the question of to what extent post-decisional accumulation processes rely on external stimulus information remains to be fully elucidated. Finally, while this experiment focuses on the relationship between neural correlates of perceptual decision-making in metacognitive judgements it does not provide a causal link in how this relationship might form over time. One possible investigation could draw inference from perceptual learning studies. Recent evidence has suggested confidence judgements can influence perceptual learning and minimise uncertainty in order to maximise future rewards (Guggenmos et al., 2016; Herding et al.,
Future studies could explore the causal role metacognitive representations play in guiding perceptual learning by adopting similar paradigms that allow for a thorough exploration of multiple neural signatures of decision formation.

In summary, this study explored the temporal dynamics of well-established neural correlates of perceptual decision-making in the construction of confidence through a contrast discrimination task with retrospective confidence judgements commonly observed in the metacognitive literature. Confidence, accuracy and changes of mind displayed a consistent pattern of activity across pre- and post-decisional signatures of domain-general sensory evidence accumulation. Additionally, the characteristics of this neural signature were more in line with a distinctive second-order evidence accumulation process, which challenges the key assumption of many post-decisional locus models. Finally, motor preparation displays a crossover between effector-specific traces on change of mind trials during the post-decision interval, highlighting the importance of the change in threshold when interpreting motor preparation on low confidence and error trials. Taken together, these findings further our understanding of how confidence arises from neural signatures of decision-making, underscoring the interplay between different levels of the sensorimotor hierarchy in the emerging of choice certainty.
Chapter Four
Exploring the Relationship between Computational Models of Decision-Making, Metacognition, and Real World Cognitive Functions

4.1 Introduction

A fundamental assumption in cognitive neuroscience is that the simplified behavioural paradigms used in laboratory experiments successfully tap into the fundamental cognitive processes that govern our daily life activities. Studies aiming to test this assumption usually test for correlations between lab-based behavioural outcomes in these paradigms, such as reaction time and accuracy, with self-report questionnaire measures that investigate real-world cognitive functions. While research has established associations between both (see, Kennis, Rademaker & Geuzze, 2013; Caceda Nemeroff & Harvey, 2014), this work has also highlighted several important concerns regarding their ecological validity. Firstly, meta-analyses have indicated that the convergent validity of laboratory tasks that purport to measure the same cognitive construct is only low-to-moderate (e.g. trait impulsivity, Duckworth & Kern, 2011; Saunders et al., 2018). Secondly, the nature of the relationship between behavioural variables and self-report measures can be inconsistent across studies. For instance, in the domain of performance monitoring, some experiments have observed a positive association between post-error slowing and perfectionism (Barke et al., 2017; Stahl et al., 2015; Schrijvers et al., 2010), while other studies have reported no association (Tops et al., 2013) or relationships with different behavioural metrics, such as post-error increases in accuracy (Drizinsky, Zülch, Gibbons & Stahl, 2016). Thirdly, experiments are often conducted on university students for convenience, but student samples are not representative of the general population, which calls into question the generalizability of the results of lab-based experiments (Hanel & Vione, 2016; Peterson, 2001). Finally, many laboratory experiments adopt relatively small samples, which limits the interpretation of null results since these might simply reflect a lack of statistical power (Westfall, Kenny & Judd, 2014).

Both methodological and technological advancements have been proposed to help address some of these limitations. Firstly, recent advances have made it possible to conduct experiments online and create online participant databases that allow for fast data collection from large samples (for a recent review see, Gosling & Mason, 2015). For instance, the ‘Great Brain Experiment’ developed a
smartphone application with gamified version of traditional behavioural paradigms, which allowed researchers to test hypothesis in a variety of cognitive domains such as, heuristic decision-making (Hunt et al., 2016), working memory (McNab et al. 215) and subjective well-being (Rutledge et al, 2014). Alternatively, studies can collect data through online crowd-sourcing platforms such as Amazon Mechanical Turk (AMT), which have been found to reliably replicate classical behavioural patterns from tasks that are frequently employed in experimental psychology and provide easy access to more diverse participant samples (Crump, McDonnell & Gureckis, 2013; Enochson & Culbertson, 2015; Gillan et al., 2016; Chetverikov & Upravitelev, 2016; Hauser & Schwarz, 2016; Paolacci, Chandler & Ipeirotis, 2010). However, there are some technical considerations for online studies. For instance, participants on AMT have developed forums where information can be exchanged about manipulation checks, which means participants might be non-naïve to the research question (Chandler, Mueller & Paolacci, 2012, 2014). Additionally, data quality in online experiments is likely to vary with the speed of the internet connection and technical specifications of computers, such as the refresh rate, screen resolution and operating systems (Simcox & Fiez, 2014). These issues highlight the importance of careful experimental design in online studies. Nevertheless, crowd-sourcing platforms are a promising avenue to test the validity of behavioural paradigms adopted in lab-based experiments.

A second solution is to develop more sensitive behavioural metrics to address the fact that, irrespective of the specific task demands, summary behavioural metrics like RT and accuracy are usually subject to influence by a complex variety of perceptual, cognitive and motoric processes. This may, at least in part, account for the poor convergent validity of many cognitive tests and the inconsistency of results across the studies mentioned above. Here, computational decision models hold great promise because they provide a means of parsing and measuring the distinct influences on choice behaviour that are otherwise not readily observable in summary data. The models can thus potentially detect inter-individual differences in the decision-making process that are linked to well defined cognitive constructs (for examples see, Ratcliff, Smith, Brown & McKoon, 2016). While sequential-sampling models, particularly the drift-diffusion model (DDM), are being increasingly applied in studies examining group differences (for a recent review see, Forstmann et al., 2016), thus far comparatively little research has adopted these models to examine inter-individual differences or to examine their sensitivity to real-world decision-making behaviour. Similarly, novel metacognitive measures have been developed through type-II signal detection theory (Maniscalco & Lau, 2012, 2014; Fleming, 2017), which allow for a more precise quantification of metacognitive abilities that are disentangled from first-order choice behaviour. For example metacognitive efficiency, which indicates a person’s ability to correctly estimate their own performance, and metacognitive bias, measuring subject’s tendency for over- or underconfidence for a given level of performance (Fleming & Lau,
2014; Maniscalco & Lau, 2012). These metrics have recently started seeing some application in the study of the impact of healthy ageing and in neuropsychiatric disorders, although research is relatively sparse (Hauser et al., 2017; Fitzgerald et al., 2017).

A small number of recent studies have exploited these twin developments in model-based behavioural metrics and online crowdsourcing platforms to more thoroughly examine associations between lab-based behaviour and real-world cognitive function. For instance, online studies using the DDM found higher obsessive-compulsive symptomatology in the general population was associated with slower drift rates, which indicates lowered quality of the sensory evidence in these subjects (Hauser et al., 2017). In the metacognitive domain, online studies have observed associations between lowered metacognitive efficiency in simple perceptual decisions and holding more radical political beliefs (Rollwage, Dolan & Fleming, 2018). Other experiments have observed higher depressive symptoms scores in online populations are associated with a lower metacognitive bias (Moses-Payne et al., 2019), while lower metacognitive efficiency has been correlated with higher obsessive-compulsive symptomatology in the general population (Hauser et al., 2017). Finally, Rouault and colleagues (2018) collected behavioural data and self-reports of psychiatric symptoms from a large online sample using the crow-sourcing platform Amazon Mechanical Turk (AMT). Crucially, these researchers combined metacognitive measures (type-II SDT) and the decision formation parameters (DDM) in order to provide novel insight into the systematic relationships between these variables and psychiatric symptoms. Results revealed metacognitive bias and efficiency exhibited different relationships with clusters of psychological symptoms. However, no significant relationships were observed between the DDM parameters and self-report measures of psychiatric symptoms after correction for multiple comparisons. Regardless, this study reflects an important leap in online experiments and demonstrates that, with careful study design, crowdsourcing experiments can offer a powerful window onto the mechanistic underpinnings of inter-individual differences in perceptual decision-making and metacognition that generalise beyond the laboratory environment.

The current study aims to further explore the relationship between the latent parameters of the decision making process, metacognitive abilities and real-world decision making styles. To this end, behavioural data on the canonical random dot motion task were collected from a large sample of participants on AMT alongside a battery of self-report questionnaires that broadly fall into two categories. The first set of questionnaires measured aspects of daily-life cognition and personality traits that were hypothesised to be related to the parameters of the DDM. This battery included questionnaires assessing levels of impulsivity (BIS; Barratt, 1995), optimism (LOT-R; Scheier, Carver & Bridges, 1994), cognitive reflection (CRT-2; Thomson & Oppenheimer, 2016) and perfectionism (APS-R; Slaney, Mobley, Trippi, Ashby, & Johnson, 1996). An association between impulsivity and
decision bounds has previously been suggested, which predicts that individuals that score higher on this trait would require less evidence to commit to a decision (Kim & Lee, 2011). Yet, evidence for this has been mixed across studies (Rouault et al., 2018; Ziegler et al. 2016). Higher perfectionism has been associated higher response caution (Barke et al., 2017; Stahl et al., 2015; Schrijvers et al., 2010), which is traditionally captured by increases in the decision bound in the computational modelling field (Ratcliff et al., 2001; Thapar et al., 2003). Similarly, higher CRT-2 scores, which indicate less effortful thinking strategies, should be associated with lower decision bounds. Finally, a recent study of Gesiarz et al. (2019) suggested positive emotional states influence the evidence accumulation process by biasing starting point towards the favoured outcome and increasing the drift rates, which suggests optimism scores might have similar relationships with these DDM parameters. Furthermore, trait optimism has previously been associated with higher confidence in perceptual choices in a small sample of subjects (Ais et al., 2016), although the pattern across studies has been inconsistent (see for instance, Hilton et al., 2011).

A second set of questionnaires was selected to investigate different aspects of real-world metacognition, measuring insight into psychotic-like experiences (CAPE; Konings et al., 2006), distrust in metacognitive operations (MCQ; Wells & Hatton, 2004) and willingness for introspection (BCIS; Beck et al., 2004). Previous research has suggested neuropsychiatric disorders, such as schizophrenia, are associated with diminished error awareness and a loss of symptom insight (Klein, Ullsperger & Danielmeister, 2013; David et al., 2006). These findings indicate higher CAPE and MCQ scores should be positively associated with metacognitive bias, reflecting the maladaptive nature of overconfidence. In contrast, scores on the BCIS, which indexes cognitive insight, should be associated with a lowered metacognitive bias (although see, Fleming, Huijgen & Dolan, 2012).

Finally, we also tested for correlations between the DDM parameters and the metacognitive variables. Compelling neural and computational modelling evidence has shown first- and second-order decisions are tightly coupled and reliant on shared or closely related evidence accumulation processes (Moran, Theodorescu & Usher, 2015; Resulaj et al., 2009). In particular, the role of the accumulated evidence in the decision variable at the of response has been suggested to function as a read-out or confidence (see Chapter 2 & 3), which suggests the decision boundary across subjects could be highly informative of metacognitive variables.
4.2 Methods

4.2.1 Participants

Experimental data and questionnaire measures were collected using the online crowd-sourcing platform Amazon Mechanical Turks. All subjects in this sample were residing in the United States of America at the time of testing and had a previous approval rating of 95%. This rating indicates the percentage of previously approved assignments, functioning as an indicator of the reliability of data a person provides. The total sample size for this experiment was determined by three factors. Firstly, an a priori power analysis was conducted that showed a sample of 432 participants would be sufficient to provide 80% power and detect an effect size of 0.15 in all desired data analyses. Secondly, a recent meta-analysis of online studies found attrition rates that varied between 3-37% (Chandler, Mueller & Paolacci, 2014). With these considerations in mind, we collected data from a total of 615 people (316 women, 298 men; Age: M = 36.04, SD = 11.10, range: 18-71). After application of the rejection criteria (see below), 468 people remained in the sample for analyses (256 women, 212 men; Age: M = 36.31, SD = 11.12, range: 18-71). Additionally, prior to this experiment a pilot study was conducted on a smaller sample of subjects from Amazon Mechanical Turks (N = 83, 46 women, 37 males, Age: M = 38, SD = 10, range: 23-60). This allowed us to test the experimental code and provided useful feedback on the staircase procedure adopted in the final version of this experiment (see ‘Training & Staircase procedure’ below). Subjects that took part in this pilot were prohibited from participating in the final study. Finally, all participants reported corrected-to-normal vision, no sensitivity to flickering lights, and no personal or family history of epilepsy, unexplained fainting, neurological, psychiatric illness, and/or brain injury.

Experimental sessions were designed to last approximately one hour and participants were paid $6 for their time. Subjects were informed they could earn an additional bonus of up to $3.5 on top of the regular payment for correctly estimating their performance (see ‘Design and Procedure’). Monetary bonuses were paid after the experiment concluded and ranged from 0.5 to 3.5 dollars (M: 1.75, SD = .36). Prior to testing all subjects were presented with a printable screen informing them about the general purpose of the study as well as their rights as a participant. If they chose to proceed with the experiment subjects were given a printable version of the consent form. On this page participants indicated consent by clicking a button with ‘I agree’, indicating they consented to the procedures described in the form. Ethical approval for all procedures and methods was obtained from the Trinity College Dublin ethics committee and the experiment was conducted in accordance with the Declaration of Helsinki.
4.2.2 Participant Rejection Procedure

Since participants performed the experimental tasks at home and without researcher supervision, additional steps were taken to ensure and verify compliance with task instructions and to identify non-performers. Firstly, one participant was omitted from the analysis due to a corrupted data file. Secondly, participants were removed as outliers if their primary task performance was more than three standard deviations away from the sample mean on either of the following variables: coherence level (N = 4, 0.65%), proportion of misses (first-order: N = 12, 1.96%; second-order: N = 14, 2.28%), or accuracy (N = 47, 7.65%) and the proportion of guesses on confidence reports (N = 17, 2.77%). Thirdly, participants were removed from all analyses if their confidence reports exhibited no variance (N = 11, 1.79%). Finally, participants were omitted from all analyses if there metacognitive efficiency scores were negative (N = 60, 9.77%), since this was taken as a signal that these subjects did not properly understand the metacognitive response modality. This was further confirmed by an examination of the number of times these subjects failed the introductory quiz, which probed their understanding of the confidence scale (see ‘Training and adaptive staircase procedure below’). Specifically, these participants were found to have failed this quiz at least 15 times, which suggests they were forcing their way into the task. Application of these rejection criteria led to the exclusion of a total of 146 (23.78%) participants, which left 468 subjects for all analyses.

4.2.3 Design and Procedure

Participants performed a difficult, random dot motion discrimination task (Figure 4.1 A) in which they were required to detect the overall motion (left or right) of a circular patch of moving dots. Confidence ratings were given on a trial-by-trial basis after every motion judgement on a 7-point rating scale. The experiment consisted of 350 trials in total, separated into seven blocks of 50 trials. Random dot motion kinematograms (RDK) were presented against a black background and consisted of 100 white dots (radius = 2 pixels) presented in a circular aperture (width = 275 pixels). The position of the dots was updated every frame which creates the overall appearance of motion. Coherently moving dots were displaced along the horizontal axis at the speed of 2 pixels per frame. Moreover, the position of the dots moving coherently was resampled every 15 frames in order to ensure subjects had to integrate the overall motion. Prior to testing participants were instructed to set their monitors to a 60Hz refresh rate and a screen resolution of 1024x764. This ensured stimulus presentation was standardised across subjects. After the dot motion task, data from seven questionnaires were collected from each subject. These measured various aspects of cognition, daily-life metacognitive experiences and personality (see ‘Questionnaire Measures’ below).
The random dot motion paradigm utilised a self-paced style, where participants started every trial by pressing the space bar. After a spacebar press was registered, a fixation point was presented for 500ms. Subsequently, dot motion stimuli commenced with coherent motion present from the start of the RDK stimulus. Coherent motion was achieved by displacing a percentage of dots in either left or right direction relative to the previous position, while all other dots moved in a random direction in the aperture. The percentage of coherently moving dots was adjusted throughout the task based on performance on previous trials (see ‘Continuous Staircase Procedure’ below). Participants were required to estimate the overall motion of the circular patch of dots within 2000ms, by using the ‘f’ and ‘j’ key to indicate left and rightward motion. 250ms after a motion judgement was registered a 7-point confidence scale appeared on the screen with the labels ‘Certain Wrong’, ‘Probably Wrong’, ‘Maybe Wrong’, ‘Neutral’, ‘Maybe Correct’, ‘Probably Correct’, ‘Certain Correct’ mapped on the number keys from 2 to 8 respectively. Participants were given 5000ms to indicate their confidence and were instructed to use the full confidence scale whenever possible to try and accurately estimate their performance. If no responses were registered for 15 minutes during the behavioural task, the experiment timed out. Participants were informed of this prior to the task. This was done to ensure subjects had to perform the task in one sitting and had to remain engaged. At the end of every block subjects were notified of their accuracy and how this compared to the previous block’s accuracy. Performance across both motion and metacognitive judgements was tied to a monetary bonus (see ‘Monetary Bonus’ below). After participation, subjects were thanked for their time and given a printable debriefing screen with contact details of the researchers, in case they had any questions or comments about the experiment.

4.2.3.1 Training & Adaptive Staircase Procedure.

Performance was calibrated in a training session prior to the experiment. In this training session participants were first introduced to the random dot motion paradigm, after an initial introduction of five trials at 100% coherent motion. This was repeated until participants reached a ceiling level of performance. Subsequently, subjects completed a short practice session of 30 trials with the initial staircase procedure. The current study implemented a two-down one-up with equal step sizes for steps up and down (Garcia-Perez, 1998). Steps were computed in log-space with a starting point of 4.6 (100% coherence). Step sizes in log-space decreased over trials with 0.4 for trials 1-5, 0.2 for trials 6–11 and 0.1 for the rest of the experiment. These parameters were selected based on previous research (Rouault et al., 2018), as well as an exhaustive pilot that was conducted with this behavioural paradigm. The staircase was started in the training session to minimise burn-in and remained active throughout the experiment. This ensured a relatively constant level of subjective difficulty was
maintained across the experiment and the entire sample (M = 71.9, SD = 1.25, range: 63-76). Following training on the initial motion judgement, a short introduction and 15 practice trials on the metacognitive judgements were given to all participants. Finally, in order to ensure participants fully understood the instructions presented to them, they were quizzed on the various aspects of the behavioural paradigm with the following three questions: ‘what key should you press if you think you are 'Probably Correct'?’, ‘What button should you press if you think the dots were moving left?’ and ‘What happens to your bonus on a turn where you made a mistake but thought you were certainly correct?’. Each question had three choice alternatives, which were selected from a drop-down menu. If participants failed to answer all the questions correctly, an abbreviated version of the training session restarted with repetition of the written instructions and 10 practice trials for either judgements.

4.2.3.2 Monetary Bonus

In order to incentivise participants to provide accurate metacognitive judgements the current study adopted a bonus scheme. Subjects were told in advance that random trials in each experimental block would be selected and they would receive a bonus of maximal $0.5 depending on the overall performance on the motion judgement and confidence judgement. Bonuses were computed with the following formula:

\[ \text{Bonus score} = 0.5 \times \theta(\text{conf}_n, \text{accuracy}_n) \]

The monetary rewards on a given block are computed as 0.5 multiplied by scaling parameter θ. The scaling parameter has a value between 0 and 1, depending on the confidence and accuracy on trial n. Higher scores were obtained on trials where subjects indicated high confidence on correct decisions and when participants correctly indicated errors. If the random trial selected in a block was a miss, no bonus was awarded for that block. Participants were informed and quizzed about this scoring rule prior to the experiment. Throughout the random dot motion task subjects remained ignorant of their bonus in order to ensure the overall level of the bonus did not influence performance adversely. The bonus accrued on the experiment was paid out after completion of the study.

4.2.3.3 Questionnaire Measures

In order to assess aspects of cognition, daily-metacognitive experiences and personality, the current study identified a battery of seven standard self-report questionnaire. All participants filled in the full questionnaire battery and submitted within an hour after completing the behavioural task. The following section details all questionnaires adopted in the current experiment, providing an insight into
the scoring methods and interpretations. Subsequently a brief overview is provided of the relevant studies that have linked the measured constructs with perceptual decision-making and metacognition.

**Cognitive Reflection Test (CRT-2).** The CRT-2 is a questionnaire designed to measure the ability to overrule a prepotent response tendency that is incorrect in favor of further reflection to a correct conclusion (Thomson & Oppenheimer, 2016). Specifically, higher scores on the CRT are indicative of a lower ability to engage in effortful thinking. Scores on the CRT have been previously found to correlate strongly with a variety of rational thinking tasks (Toplak, West & Stanovich, 2014), systematic biases in confidence (Hoppe & Kusterer, 2011) and decision-making heuristics (Oechssle et al., 2009; Toplak, West & Stanovich, 2011). Additionally, the CRT has been widely used on Amazon Mechanical Turk, which makes the CRT-2 a more attractive option since previous exposure to the questions is likely to inflate scores (Bialek & Pennycook, 2018).

**Community Assessment of Psychic Experiences (CAPE).** The CAPE was adopted as a general measure of psychiatric illness and psychotic-like experiences (Konings et al., 2006). The questionnaire provides two scores of metacognitive awareness; the frequency and the level of distress associated with positive and negative experiences measured across the 42 questions. The CAPE has been found to reliably estimate psychotic and depressive symptoms in the general population (Konings et al., 2006; Mossaheb et al., 2012; Vermeiden et al., 2019). Additionally, psychotic experiences have been found to substantially alter a variety of cognitive processes. For instance, belief updating (Evans, Averbeck & Furl, 2015) and sensitivity to cognitive biases (Freeman et al, 2008; Moritz et al., 2015). Moreover, metacognitive control and monitoring have been found to be substantially altered in schizophrenia (Nelson, Stuart, Howard & Crowley, 1999; Moritz et al., 2016).

**Almost Perfect Scale Revised (APS-R).** Perfectionism was assessed through combining the subscales of the APS-R into a total perfectionism score (Slaney, Mobley, Trippi, Ashby, & Johnson, 1996; Slaney et al., 2001). To our knowledge, no study has investigated the role of perfectionism, measured through the APS-R, in perceptual decision-making and metacognition. However, studies investigating the role of perfectionism in probabilistic learning and performance monitoring have suggested this trait plays an important role in learning and error detection by heightening awareness and concerns over mistakes (Stahl et al. 2015; Brand et al., 2008).

**Life Orientation Test (LOT-R).** The LOT-R was used to assess levels of optimism versus pessimism (Scheier, Carver & Bridges, 1994). The LOT-R provides a continuous measure of trait optimism with filler questions designed to catch inattentive subjects. The questionnaire scores have been found to be associated with altered emotional salience (Sharot et al.2007) and belief updating (Sharon, Korn & Dolan, 2011). In research on metacognitive experiences, Hilton and colleagues (2011) observed no significant relationship between LOT-R scores and overconfidence. A substantial
limitation of this study is that choice certainty was only assessed through a single global confidence rating after participants completed a general knowledge questionnaire, making it possible for trial-by-trial confidence ratings to display a systematic relationship with trait optimism. This is supported by a recent study of Ais and colleagues (2016), who observed a strong positive association between confidence on a contrast change discrimination task and trait optimism.

**Baratt Impulsivity Scale (BIS).** Impulsivity was quantified through the total scores of the BIS (Patton, Stanford & Barratt, 1995), where higher scores indicate higher rates of impulsivity. This questionnaire has previously been utilised as a tool to assess trait impulsivity in both clinical groups and the general population (for a review see, Stanford et al. 2009). Moreover, BIS scores have shown strong relations to perceptual decision-making (Burnett Heyes et al., 2012; Reckless et al., 2013), memory (Hinson, Jameson & Whitney, 2003; Minear et al. 2013), attentional lapses (Sonuga-Barke, 2002; Levine, Waite & Bowman, 2013), insensitivity to punishment in reinforcement learning (Potts, George, Martin & Barratt, 2006) and metacognition (Ermis, 2016, although see Rouault et al., 2018).

**Beck Cognitive Insight Scale (BCIS).** The BCIS is a short self-report measure of levels of self-reflection and the confidence experienced in these operations (Beck et al., 2004). A Composite score on the scale is obtained when subtracting scores obtained for self-reflectiveness and self-certainty, which functions as an indicator of the willingness of introspection. BCIS has previously been used across clinical populations, however recently has been applied in healthy populations (Riggs et al., 2012). Moreover, links have previously been found between scores on the BCIS and clinical insight (Warman & Martin, 2006; Ekinci et al., 2012) and memory (Lepage et al. 2008), although no relationships were observed between confidence on a face discrimination task and BCIS scores (Fleming, Huijgen & Dolan, 2012).

**Metacognitions Questionnaire (MCQ).** Individual differences in metacognitive beliefs and monitoring strategies were assessed through MCQ (Wells & Hatton, 2004), with higher scores generally reflecting a lower level of trust in metacognitive operations. The MCQ has previously been correlated with dysfunctional metacognitive beliefs in populations with obsessive-compulsive disorder and body dysmorphia (Hermans et al., 2008; Davenport et al., 2015). However, there is some evidence to suggest this questionnaire is a valid measure for metacognitive traits in healthy adults, despite the relatively scarce nature of research on the MCQ in the general population (Sanger & Dorjee, 2016).

### 4.2.4 Drift Diffusion Model

The drift-diffusion model (DDM) was fitted to accuracy and RT data of the dot motion task of every subject. Parameters included in the DDM were drift rate \((d)\), measuring the mean strength of the evidence entering the diffusion process, decision bound \((zb)\), the level of evidence required for the
decision process to terminate, and non-decision time ($Ter$), a parameter accounting for all non-decision processes (see Figure 4.1 B). Normally distributed trial-by-trial variability in drift rate ($\sigma^2_d$), uniformly distributed non-decision time ($\sigma^2_{Ter}$) and starting point variability ($\sigma^2_z$) were also added to the model, allowing the DDM to fully capture differences in correct and error RT (Ratcliff & Rouder, 1998). The starting point ($z$) was fixed at $zb/2$ since no evidence for a significant response bias was found across the sample ($t(467) = 1.17, p = 0.24$). Finally, within-trial noise was fixed at 0.1 for all subjects and functions as the scaling parameter of the DDM (Ratcliff, 2006; Voss, Nagler & Lerche, 2013). In total, the model has six free parameters and two fixed parameters.

In order to explore individual differences in decision formation, the DDM was fitted for every participant separately. All models were fit to the single-subject data using iterative simulation methods with a bounded simplex algorithm in the fminsearchbnd function in Matlab (Nelder & Mead, 1965), minimising the $G^2$ error statistic. $G^2$ indicates the goodness of fit between simulated and real data for every subject, represented by the RT quantiles [0.1 0.3 0.5 0.7 0.9] and the response probabilities. Smaller values for $G^2$ reflect the model more accurately capturing subject’s behavioural data (Ratcliff & Smith, 2004). The best subject-specific parameters estimates were selected from 50 fits initiated with alternative starting parameters. The 50 initial parameter sets were identified first, by iteratively fitting a DDM to the group-averaged RT quantiles with parameters randomly selected from a wide range until 50 sets were found that provided reasonably similar average RT’s, accuracy and misses compared to the subject’s real data. Second, the fit of the model was measured by minimizing a $G^2$ error statistic with fminsearch. This method ensured drift-diffusion parameter estimates were independently obtained for every subject, allowing further analyses with task-related variables and questionnaire measures. The set of parameters with the best fit to the group-averaged data were furthermore used to simulate 1000 trials and illustrate the model RT quantiles compared to the subject-averaged data (see figure 4.1 C).
Figure 4.1 A) Schematic depiction of a leftward motion trial in the random dot motion task. Trials started when participants pressed the spacebar, causing a fixation point to appear on the screen for 500ms. Afterwards stimulus presentation began with a proportion of dots moving coherently left or rightward, which was achieved through dots sliding along the x-axis on each frame. All other dots moved to random positions on each frame. Every 15 frames of stimulus presentation a new portion of dots was selected to move coherently. Participants were asked to indicate the overall motion of the cloud of dots. Following motion judgements, a 7-point confidence scale appeared on the screen after a short delay of 250ms. Participants were required to indicate their level of certainty in the original decision. A response deadline of 5000ms was applied to the metacognitive judgements, measured relative to the onset of the confidence scale. B) Schematic representation of the drift-diffusion model, where sensory evidence accumulates over time into a decision variable. The rate of accumulation is measured as the drift rate \(d\), which was normally distributed across trials. Accumulation continues until a decision bound \(b\) for the correct or incorrect choice is reached. Non-decision time \(T_{\text{nd}}\) measured all processes not captured in decision formation. For instance, response execution or sensory encoding of the stimulus. The starting point and the non-decision time were assumed to be uniformly distributed across trials. C) Predicted and observed reaction time (RT) quantiles of the subject-average behavioural data. Predicted RT quantiles were generated for 1000 trials from the set of drift-diffusion parameters that provided the best fit to the subject-average data.

4.2.5 Metacognitive Efficiency

Individual differences in metacognitive abilities in perceptual decision-making were assessed through two metacognitive measures. Firstly, the average level of confidence in the coherent motion
paradigm functions as an indicator of metacognitive bias. Specifically, this means individual differences in confidence are not driven by variability in the first-order accuracy, since the latter was kept constant across subjects with the continuous staircase procedure. Secondly, metacognitive efficiency was computed as $meta-d'/d'$. This measure is computed by obtaining a ratio of $d'$, reflecting a subject’s ability to reliably discriminate between stimuli, and $meta-d'$, an estimation of a person’s ability to accurately indicate choice certainty (Maniscalco & Lau, 2012; Fleming & Lau, 2014). Metacognitive efficiency can take values from 0 to $\infty$, with values between 0 and 1 indicating suboptimal estimation of confidence since $d' > meta-d'$. Conversely, when metacognitive efficiency scores are $> 1$, subjects are better at estimating confidence compared to the initial task performance since $d' < meta-d'$. This has previously been shown to reflect additional information processing, which influences the choice certainty ratings and improves subject’s ability to estimate their own performance (Charles et al., 2013; Fleming & Daw, 2017; Fleming, 2017).

Metacognitive efficiency values were computed for each participant through the HMeta-d toolbox in Matlab (Fleming, 2018). The main advantage of the HMeta-d toolbox is that it fits a hierarchical Bayesian model to the confidence scale counts of each participant, combining within- and between-subject uncertainty when $d'$, $meta-d'$ and metacognitive efficiencies are estimated. Moreover, the hierarchical Bayesian model is more robust to zero counts of certain cells on the confidence, such as the absence of high confidence errors, and requires no edge corrections found in other methods of estimation (Lee, 2008).

4.2.6 Behavioural Analysis

The relationships between summary behavioural metrics, DDM parameters, metacognitive indicators and questionnaire scores were examined through linear regressions in Matlab (Mathworks, Natick, MA) with the fitlm function. Trials with outlier response times were removed (>3 SD in either direction of the subjects mean reaction time). Behavioural indicators included first-order reaction times (RT) measured as the time elapsed from the onset of the dot motion stimulus. First-order accuracy was defined as the proportion of correct responses in the dot motion task and included misses. Confidence was obtained by averaging across all second-order judgements (with values ranging from -3 to 3). Second-order RT was measured as the time elapsed relative to the onset of the metacognitive response cue.

Metacognitive efficiency scores were computed by using the HMeta-d toolbox in Matlab, which implements a hierarchical Bayesian meta-d model (Fleming, 2017). All parameters were estimated using Markov-Chain Monte-Carlo (MCMC) methods, using 3 chains of 10000 samples with a burn-in of 1000 samples. The convergence of all parameters was assessed by visual inspection of the
MCMC chains and assessment of the convergence measures ($\hat{R} < 1.1$). Drift-diffusion parameters were obtained by fitting the drift-diffusion model to the random dot motion data, using custom routines in Matlab (see ‘Drift Diffusion Model’ above). The parameters included in the model were drift rate, starting point bias, decision threshold, non-decision time as well as variability parameters for the drift rate, starting point and non-decision time.

Questionnaire measures were obtained by summing the scores of every item, with the exception of the LOT-R, where filler items were removed from the overall score, the BCIS, where composite scores are computed by subtracting two main subscales of this questionnaire, and the CRT-2. The responses on this measure were scored manually and separate scores were computed for the number of correct, intuitive incorrect and incorrect responses. Only the total score for intuitive incorrect responses was considered for analysis as recommended in previous research (Thomson & Oppenheimer, 2016).

All regressors were z-scored in order to facilitate direct comparison between the regression coefficients of different analyses. Linear regression models additionally controlled for the covariates gender and age, resulting in the following regression model:

$$Dependent\ Variable = Questionnaire\ Measure + Age + Gender$$

The full effect of both variables, independent of the questionnaire measures, was further examined in a separate analysis. A final set of analyses examined the relationship between behavioural, metacognitive variables and DDM parameters. Similarly, behavioural and metacognitive variables displayed significant correlations. Therefore, these analyses followed an identical procedure as the questionnaire measures with z-scoring and separate regressions across all dependent variables.

4.2.7 Statistical Analysis

Like previous chapters, in every regression model the data were tested for suitability for parametric analysis. The normality assumption was assessed through examination of the outliers in the standardised residuals. Whenever the assumptions were violated the Greenhouse-Geisser or the Huynh-Feldt corrected degrees of freedom and p-values are reported (the correction applied was contingent on the degree of violation). Additionally, all post-hoc paired-sample t-tests and the p-values of linear regressions reported were corrected for multiple comparison based on the number of dependent variables tested using the Bonferroni-Holm correction method (Holm, 1979). In all subsequently reported results, correct p-values are mentioned.
4.3 Results

4.3.1 Behavioural Results on the Dot Motion Task

To verify the quality of the first- and second-order motion judgement data we conducted a number of analyses to test for the presence of a number of very well-established behavioural phenomena.

Firstly, first-order reaction time (RT) and confidence were examined as a function of accuracy. In line with previous chapters and the existing literature, RTs were significantly slower (Figure 4.2 A; \( t(467) = 30.26; p < 0.001 \)), and confidence ratings significantly lower (Figure 4.2 B; \( t(467) = 32.57; p < 0.001 \)) on erroneous compared to correct choices. Second, a within-subject median-split was performed on the coherence level across trials in order to explore the impact of small fluctuations in the stimulus evidence on first-order reaction time, confidence and accuracy. As would be expected, lower coherence trials were associated with significantly slower reaction times (Figure 4.2 C; \( t(466) = 29.93, p < 0.001 \)), significantly lower confidence (Figure 4.2 D; \( t(466) = 24.14, p < 0.001 \)) and significant decreases in first-order task performance (Figure 4.2 E; \( t(466) = 85.54, p < 0.001 \)). These results demonstrate that the data were of sufficient quality to clearly identify a number of canonical choice behaviour effects.

Finally, while single-trial confidence reports reliably reflected the individual’s accuracy in the random dot motion task (median within-subject correlation: \( \rho = 0.27, p < 0.001 \); ranging from \( \rho = -0.09 \) to \( \rho = 0.69 \)), a between-subject correlation showed objective performance only accounted for approximately 1% of the variance in confidence judgements (between-subject correlation: \( \rho = -0.08, p = 0.1 \)). Taken together, these correlation patterns demonstrate that the titration method was successful in parcelling out the effect of individual differences in accuracy on the average confidence in the dot motion task, while leaving intact the relationship between confidence and first-order accuracy on a within-subject level.
Figure 4.2 Behavioural effects in the random dot motion task. Asterisks indicate the level of significance after Bonferroni-Holm correction for multiple comparisons based on the number of statistical tests, with $p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: ***. A) Group reaction time (RT) histogram for error and correct trials. Vertical lines indicate the average response time for error and correct trials. B) Choice confidence was significantly higher on correct compared to error trials. C) Mean RT as a function of coherence level (based on a within-subject median split). RT is significantly higher when coherence levels are low. D) Average confidence plotted as a function of coherence level, showing significantly higher confidence on trials where stimulus evidence is stronger. E) Accuracy plotted as a function of coherence level, showing significantly higher task performance on trials when stimulus evidence is relatively stronger.

4.3.2 Exploring the Relationship between Perceptual Decision-Making Performance in the Laboratory and Real-World Behaviour

In a first step, the relationship between questionnaire measures and behavioural indicators of decision-formation on the primary task were examined through linear regressions, while controlling for the effects of gender and age (Figure 4.4 A-H). Individual differences in reaction times (RT) on motion judgements were negatively associated with scores on BIS (Figure 4.4 A; $\beta = 0.11$, $t(467) = -2.55$, $p = 0.025$), indicating that faster RTs were found when people scored higher on trait impulsivity. None of
the other questionnaires approached significance in linear regressions with first-order reaction time (p = 0.139). Similarly, none of the questionnaire measures showed a relationship with the average accuracy on the random dot motion task (Figure 4.4 B; p = 0.108).

Next, the individual subject parameter estimates of the drift-diffusion model (DDM) were separately regressed against all questionnaire measures in order to examine the relationship between the mechanistic underpinnings of decision formation and self-report measures of cognitive functioning. In line with results from Rouault et al. (2018), BIS scores did not show a significant relationship with decision threshold (Figure 4.4 E; β = -0.06; t(460) = -1.51, p = 0.529). Interestingly, trait impulsivity did exhibit a strong negative association with non-decision time (Figure 4.4 C; BIS: β = 0.17, t(465) = -3.9, p < 0.001). Therefore, while higher impulsivity scores are associated with lowered non-decision time, the exact nature of this association is unclear since the non-decision time parameter reflects processing delays occurring before (e.g. sensory encoding) and after (motor execution) the decision process. Additionally, previous studies have suggested perfectionism is associated with more cautious response strategies, which in the modelling literature traditionally has been associated with increases in the decision bound (Stahl et al., 2015; Thapar et al., 2003). However, the results indicated no significant relationship between APS scores and the decision boundary (Figure 4.4 E; β = 0.01, t(456) = 0.33, p = 0.742). Similarly, while positive valence has been correlated with both drift rate and starting point bias (Gesiarz et al., 2019), analyses indicated no significant relationships between either drift rate or starting point variability and LOT scores (Figure 4.4 H & D; d: β = -0.01, t(460) = -0.38, p = 0.707; σ²: β = 0.03, t(463) = 0.77, p = 0.439). Contrary to expectations, scores on the CRT-2 were not associated with lowered decision bounds across subjects (Figure 4.4 E; β = 0.01, t(460) = 0.01, p = 0.836). Instead a significant positive association between CRT-2 scores and the drift rate parameter were observed (Figure 4.4 D; β = 0.10, t(458) = 2.78, p = 0.045), indicating that a higher strength of sensory evidence was associated with a lowered willingness to engage in effortful thinking. Finally, BCIS scores showed a positive association with drift rate (Figure 4.4 ; β = 0.10; t(458) = 2.77, p = 0.038), indicating that a higher willingness to engage in introspection was associated with a stronger representation of the evidence. None of the other linear regression coefficients across all analyses approached significance (Figure 4.4 A-H, p = 0.086).
Figure 4.3 Standardised regression coefficients obtained in linear regressions with the behavioural outcomes on the primary task and the latent structure of perceptual decision formation as dependent variables and questionnaire measures as independent variables. Linear regression were conducted separately for every questionnaire measure while controlling for the effects of gender and age. Black bars indicate the standard error of the mean. Asterisks indicate the level of significance after Bonferroni-Holm correction for multiple comparisons based on the number of dependent variables across analyses, with $p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: ***. **Behaviour variables**: A) Standardised regression coefficients showing the relationship between average dot motion reaction time (RT) and questionnaire measures. Results indicate a significant positive association between trait impulsivity and RT. B) Standardised regression coefficients showing the relationship between average accuracy on the dot motion task and questionnaire measures. None of the self-report measures included showed a significant association with accuracy. **Model Parameters**: C) Relationship between non-decision time and all questionnaire measures. Impulsivity shows a significant positive association with non-
decision time. D) Relationship between drift rate and all questionnaire measures. Cognitive reflection and insight show a significant positive association with drift rate. E) Relationship between decision bound and all questionnaire measures. None of the self-report measures included showed a significant association with decision bound. F) Relationship between non-decision time variability and all questionnaire measures. None of the self-report measures included showed a significant association with non-decision time variability. G) Relationship between drift rate variability and all questionnaire measures. None of the self-report measures included showed a significant association with drift rate variability. H) Relationship between starting point variability and all questionnaire measures. None of the self-report measures included showed a significant association with starting point variability.

4.3.3 Individual Differences in Metacognition are Associated with Different Measures of Cognitive Awareness

The relationships between metacognitive behaviour on the random dot motion task and questionnaire measures was examined through linear regressions, which controlled for the effects of gender and age (Figure 4.3 A-C).

A first set of analyses investigated the relationship between the average level of confidence and all measured constructs. In line with expectations, individual differences in the total scores on the CRT-2, MCQ and CAPE were found to be positively related with the average confidence level in the laboratory task (Figure 4.3 A; CRT-2: $\beta = 0.21$, $t(463) = 4.85$, $p < 0.001$; MCQ: $\beta = 0.12$, $t(462) = 2.67$, $p = 0.032$; CAPE: $\beta = 0.12$, $t(463) = 2.64$, $p = 0.035$). This indicates that a higher confidence, or a tendency towards overconfidence, across subjects is associated with a lowered ability to engage in effortful thinking (CRT-2), a higher distrust in metacognitive operations (MCQ) and more frequent psychotic-like experiences (CAPE). Furthermore, contrary to previous research (Ais et al., 2016), the current study observed no significant relationship between the average level of confidence and optimism (LOT) scores (Figure 4.5; $\beta = -0.02$, $t(464) = -0.53$, $p = 0.599$). In a second set of analyses we found that second-order RTs positively associated with the scores on the BCIS (Figure 4.3 B; $\beta = 0.15$, $t(464) = 3.36$, $p = 0.003$), showing slower metacognitive responses were associated with a higher willingness for introspection. None of the other questionnaire measures showed a significant relationship with metacognitive RT ($p = 0.371$). Similarly, metacognitive efficiency scores did not display a significant association with any of the questionnaires in the test battery (Figure 4.3 C; $p = 0.203$).

Taken together, these results reveal a diverging pattern of relationships between metacognitive behavioural variables in the random dot motion task and measures of different real-world metacognitive experiences. Specifically, individual differences in average confidence and second-order
RT are associated with aspects of cognitive awareness, while metacognitive efficiency did not show any significant relationships (Figure 4.3 A-C). Additionally, the pattern of associations with confidence suggests that a tendency towards overconfidence on simple perceptual decisions is associated with more negative real-world metacognitive outcomes.

Figure 4.4 Standardised regression coefficients for the behavioural indicators of metacognitive decision formation obtained through linear regressions with every questionnaire measure as independent variables. Linear regressions were conducted separately for every questionnaire measure while controlling for the effects of gender and age. Black bars indicate the standard error of the mean. Asterisks indicate the level of significance after Bonferroni-Holm correction for multiple comparisons based on the number of dependent variables across
analyses, with $p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: ***.  

A) Linear regression coefficients exploring the relationship between confidence and questionnaire measures. A significant positive association was observed between cognitive reflection, daily-life metacognition, insight into symptoms and the overall level of confidence.  

B) Linear regression coefficients exploring the relationship between questionnaire measures and metacognitive response times, indicating a significant positive effect of cognitive insight on confidence reaction time.  

C) Linear regression coefficients exploring the association between metacognitive efficiency and questionnaire measures. None of the questionnaire measures displayed a significant association with metacognitive efficiency scores, as indicated by the absence of asterisks.

4.3.4 Individual Differences in the Mechanistic Underpinnings of First-Order Decision Predict Metacognitive Decision Formation

A final set of analyses aimed to examine the relationship between the latent structure of perceptual decision-formation and the metacognitive experience of these decisions. This was done through separate linear regressions with each parameter of the drift-diffusion model (DDM) as independent variables while controlling for the effects of gender and age.

Firstly, average confidence ratings were significantly negatively associated with non-decision time and non-decision time variability (Figure 4.5 A; $\text{Ter}: \beta = -0.33, t(465) = -8.41, p < 0.001; \sigma_{\text{Ter}}^2: \beta = -0.14, t(460) = -3.58, p = 0.002$). This suggests that higher levels of variability and longer durations of non-decisional processes adversely influence the average level of confidence experienced in these choices.

Secondly, average second-order RT were significantly associated with non-decision time, non-decision time variability, drift rate, bound and starting point variability (Figure 4.4 B; $\text{Ter}: \beta = 0.33, t(464) = 8.01, p < 0.001; \sigma_{\text{Ter}}^2: \beta = 0.26, t(459) = 6.39, p < 0.001; d: \beta = 0.32, t(460) = 9.05, p < 0.001; b: \beta = -0.12, t(459) = -2.96, p = 0.013; \sigma_d^2: \beta = 0.13, t(463) = 3.10, p = 0.008$). Only drift rate variability did not significantly predict second-order RT (Figure 4.5 B, $\beta = -0.08, t(459) = -1.79, p = 0.074$). Interestingly, the direction of all regression coefficients in the previous analyses mirrors the results observed when examining the relationship between the DDM parameters and the first-order RT ($\text{Ter}: \beta = 0.87, t(465) = 44.52, p < 0.001; \sigma_{\text{Ter}}^2: \beta = 0.65, t(462) = 20.57, p < 0.001; d: \beta = 0.32, t(460) = 9.05, p < 0.001; \sigma_d^2: \beta = -0.20, t(458) = -4.82, p < 0.001; b: \beta = -0.20, t(461) = -4.66, p < 0.001; \sigma_b^2: \beta = 0.17, t(462) = 4.00, p < 0.001$). Unsurprisingly, a moderately strong correlation was found between the average motion RT and confidence RT across subjects ($\rho = 0.43, p < 0.001$), which further demonstrates the tight coupling between first- and second-order decision reaction times. These results corroborate with neural results from Chapter 3, which showed a strong modulation of the CPP prior to the first-order decision by confidence.
Finally, metacognitive efficiency scores across subjects were not significantly related to any of the DDM parameters (all p > 0.05), which suggests that the ability to correctly distinguish one’s own performance might be functionally distinct from the evidence accumulation process that governs the first-order decision.

Figure 4.5 Standardised regression coefficients for metacognitive variables obtained through linear regressions with drift-diffusion model (DDM) parameters as independent variables. Linear regressions were conducted separately for every parameter of the DDM while controlling for the effects of gender and age. Black bars indicate the standard error of the mean. Asterisks indicate the level of significance after Bonferroni-Holm correction for multiple comparisons for the number of dependent variables across analyses, with p < 0.05: *, p < 0.01: **, p < 0.001: ***. A) Relationship between confidence and DDM parameters. Non-decision time and non-decision time variability shows a significant negative relation with average level confidence, which suggest that higher confidence is associated with shorter and less variable non-decision processes. B) Relationship between confidence reaction time (RT) and DDM parameters. Non-decision time, non-decision time variability, drift rate, bound and starting point variability show a significant positive relation with average confidence RT in the
coherent motion task. C) Relationship between metacognitive efficiency and DDM parameters across subjects, none of the associations approached significance, as indicated by the absence of asterisks.
4.4 Discussion

In order to function optimally in daily-life situations, humans must develop stable patterns of behaviour and cognition to be able to respond to changes in their sensory environment. In experimental settings, perceptual decision-making paradigms aim to investigate these cognitive and behavioural trends, relying on simplified and more controlled sensory discrimination tasks. It is often assumed that these simple perceptual choices tap into the same patterns of cognition that underlie real-world decision-making and metacognition. However, laboratory experiments that investigated this assumption have yielded inconsistent results (Duckworth & Kern, 2011; Saunders et al., 2018). Therefore, the current chapter aimed to provide a more definitive test of this assumption by, capitalising on recent technological advancements in online testing procedures to collect data from a large naturalistic sample (Crump, McDonnell & Gureckis, 2013; Gillan et al. 2016; Rouault et al., 2018; Moses-Payne et al., 2019; Rollwage, Dolan & Fleming, 2018). Furthermore, this was combined with computational modelling approaches that parse the latent structure of perceptual decision formation (Ratcliff, Smith, Brown & McKoon, 2016; Forstmann et al., 2016) along with novel metrics of metacognitive function derived from type-II signal detection theory (Fleming & Lau, 2014; Fleming, 2017).

Online testing presents considerable challenges, such as the variability in technical equipment and subjects’ abilities to understand the instructions (Chandler, Mueller & Paolacci, 2012; Paolacci & Chandler, 2014). Considerable attention was given to experimental checks that aimed to maximise the data quality. For instance, participants were required to run the task in a specific frame rate and resolution, which allowed standardising stimulus presentation, and additionally were required to pass a quiz about the dot motion task before participating in the study. Despite this, a considerable level of data attrition still occurred across the sample. However, analyses on the behavioural data from the final sample does show canonical effects, such as lowered confidence on errors compared to correct decision, which indicate the reliability of these subjects.

Examinations of the relationships between the parameters of the DDM and self-report measures revealed significant associations between impulsivity and non-decision time, as well as correlations between drift rate and the willingness to introspect (BCIS) and the ability to engage in effortful thinking (CRT-2). Although, CRT-2 scores were not related to the decision bound as theorized. Additionally, while previous research indicated impulsivity and perfectionism might have a systematic relationships to the decision bound (Barke et al.,2017; Stahl et al., 2015; Schrijvers et al., 2010; Kim & Lee, 2011), the current study found no evidence to support these predictions (see also, Rouault et al., 2018). Furthermore, while associations were expected between optimism score (LOT) and drift rate or starting point variability with (Gesiarz et al., 2019), no such significant relationships
were found. In summary, while the current study did observe some significant associations between DDM parameters and the self-report measures of daily-life cognitive functions, the predicted relationships did not materialise. It is possible this might reflect the limited ecological validity of the computational models or the measured constructs in this particular study. For instance, research on impulsivity has shown distinguishable components underlie this trait (Green & Myerson, 2013; Logan, van Zandt, Verbruggen & Wagenmakers, 2014), which have previously been found to poorly correlate and in some cases completely dissociate from each other (Dalley & Robbins, 2017). However, multiple alternative explanations can be given for the absence of effects, which highlights the particular challenges of the application of computational models in the study of inter-individual differences.

Firstly, many of the previous experiments did not employ a continuous staircase procedure (for instance, Barke et al., 2017; Stahl et al., 2015; Schrijvers et al., 2010; Gesiarz et al., 2019). While this method ensured accuracy remained constant across subjects and allowed for the interpretation of the average confidence as metacognitive bias, constraining participants to achieve highly similar accuracy levels might have led to a different pattern of DDM parameters to those that would have been observed if the participants had been presented with identical stimuli and permitted to select their own decision making strategies. For instance, inter-individual differences in bound setting could mean that certain subjects needed stronger coherent motion to hit the desired level of accuracy, which in turn could drive differences in the drift rate parameter. Furthermore, all parameters in the DDM were obtained through a standard model fitting procedure, which required fixing the within-trial noise as a scaling parameter (Ratcliff and Rouder, 1998; Ratcliff, 2006; Voss, Nagler & Lerche, 2013). While this method is conventionally used to estimate parameters, recent studies have started to question the assumption of equal within-trial noise. In particular, in the context of comparing individuals and groups there is compelling evidence that factors such as psychological disorders and ageing directly impact the neural level of noise (Garett et al., 2013; O’Connell et al, 2018; Dully et al, 2017). The assumption that within-trial noise is identical across subjects is unlikely to be realistic in the current sample, given the wide range of ages and scores on the CAPE. This in turn might have contributed to the inter-individual differences arising from variations in within-trial noise being attributed to other DDM parameters, potentially causing some relationships to be obscured. Finally, recent studies have highlighted that behavioural measures traditional experimental paradigms have limited between-subject variability, which limits the reliability of these tasks when investigating individual differences (Hedge, Powell & Sumner, 2018; Dang, King & Inzlicht, 2020). In a recent study, Lerche & Voss (2017) observed that the test-retest reliability of the DDM parameters was similar to behavioural measures in a variety of experimental paradigms. Therefore, it is likely that the limited between-subject variability might have
contributed to the absence of the predicted relationships between decision formation and the questionnaire measures.

A second set of analyses explored the association between metacognitive outcomes and self-report measures. In line with expectations, associations were observed between the metacognitive behavioural variables and multiple questionnaire measures of daily-life metacognition. Specifically, higher confidence was associated with a lowered disposition to engage in effortful thinking (CRT-2), higher distrust of metacognitive beliefs (MCQ) and higher self-reports of psychotic-like symptoms (CAPE). Additionally, second-order reaction times showed a positive relation with the inclination to introspection. However, the present data did not exhibit any correlations between optimism (LOT) and the average level of confidence, which has been reported previously (Ais et al., 2016; although see, Hilton et al., 2011). In fact, the tendency towards overconfidence across subjects was specifically related to more negative daily-life cognitive functioning. A pattern corroborates with earlier experiments that have linked overconfidence to heuristic decision-making (Tversky & Kahneman, 1974; Johnson & Fowler, 2011) and delusional beliefs and psychotic experiences in schizophrenia (Moritz et al., 2014; Klein, Altinyazar & Metz, 2013). However, the failure to replicate the relationship between confidence and optimism scores might have multiple reasons. It is possible this association in previous studies was coincidental and related to smaller sample size (N = 18; Ais et al., 2016). Alternatively, this absence of a correlation might be an unintentional aspect of the experimental structure in this study. Specifically, the questionnaire reports were always administered after the behavioural paradigm. Hence, the continuous titration, which disables behavioural improvements during the dot motion task, might have influenced the overall optimism experienced by subjects.

A final group of linear regressions aimed to elucidate the relationship between the DDM-derived parameters of perceptual decision formation and subsequent metacognitive judgements. Results indicate individual differences in average confidence and second-order response times are significantly related to the DDM parameters. Interestingly, the results of the linear regression with confidence reaction time closely resembled the effects observed between first-order reaction time and mechanistic underpinning of decision formation. Additionally, a moderately strong correlation between first- and second-order reaction times was found, which further suggests a tight coupling between both decision-making stages. These findings are in line with the neural observations from the previous Chapter 2 & 3, where the CPP amplitude prior to the first-order decision in showed a direct scaling with the delayed confidence ratings. Furthermore, the observed relationship between non-decision time and confidence conform with the results from a recent experiment of Gajdos and colleagues (2019), which showed that the level of subthreshold muscle activation prior to the first-order decision was positively related to confidence. In the current study the opposite pattern is observed, which might
indicate that slower and more variable motor execution is related to lower choice certainty. However, further research would be required to investigate the directionality of this association and rule out alternative non-decisional processes captured in this parameter.

Aside from the drawbacks mentioned earlier, other considerations must be made when interpreting the results from this experiment. Firstly, evidence suggests confidence ratings are sensitive to variability in stimulus information, which suggests that inter-individual variability in within-trial noise could be a key influence on subsequent metacognitive judgements (De Gardelle & Summerfield, 2011; De Gardelle & Mamassian, 2015; Zylberberg, Fetsch & Shadlen, 2016; Boldt, De Gardelle & Yeung, 2017; Bang, Shekhar & Rahnev, 2018, 2019). Second, the current paradigm ensured that the subjective task difficulty remained constant throughout and across subjects by implementing a continuous staircase procedure. However, a recent study from Rahnev & Fleming (2019) suggests that the staircase procedures might inflate metacognitive efficiency estimates. Future studies could remedy this limitation by adopting more extensive staircase procedures prior to running the experiment, allowing only for one level of difficulty throughout behavioural tasks or separately estimate efficiency scores in every level of difficulty and average across them. Thirdly, the ability of the current experiment to detect associations between metacognitive efficiency and questionnaire scores might have been attenuated by model fitting procedure. In particular, the Bayesian hierarchical model for estimating meta-\(d^\prime\) considers both the subject- and group-level uncertainty, which can limit subject-level variability. One solution to this problem that could be adopted in future research would be to include more empirical driven priors in the linear regression models (Moutouniss et al., 2018).

In conclusion, the current experiment aimed to investigate the relationship between behavioural indicators from perceptual decision-making task with confidence ratings and measures of daily-life cognition, metacognitive experiences and personality. Data was collected from a large group of subjects, taking advantage of recent methodological and technological advances in online testing procedures. Analyses indicated that individual differences in metacognitive indicators and the parameters of the DDM were associated with multiple questionnaires that measured different aspects of real-world cognitive functioning. Furthermore, associations were observed between decision formation variables and subsequent metacognitive behaviour. Despite this, the current study failed to observe many of the predicted associations between DDM parameters and questionnaire measures. This might, at least in part, reflect some of the limitations of current computational models of perceptual decision-making in the study of individual differences. Nevertheless, this experiment provided tentative evidence for the assumption that metrics of perceptual decision-making and metacognition obtained in laboratory experiments tap into the same processes that govern real-world cognitive functions, while also highlighting the potential of online studies as an exciting new avenue to explore this question.
Chapter Five
General Discussion

5.1 Thesis Overview

Metacognitive experiences are a pervasive feature of perceptual decision-making and play a key role in supporting and enabling adaptive behaviour. However, despite the ubiquitous nature of this process, the exact neural mechanisms that govern the emergence of metacognitive representations has remained unclear. In recent years, computational modelling studies have played an increasingly pivotal role in generating empirically testable predictions about these mechanisms (Forstmann et al., 2016). In particular, the adoption of sequential-sampling models has fuelled neurophysiological research examining the proposal that our metacognitive judgments are based on a read-out of the same evidence accumulating decision variable that determines our first-order choices (Pleskac & Busemeyer, 2010; Yu, Pleskac & Zeigenfuse, 2015). While this work has provided compelling support for the involvement of evidence accumulation processes in metacognitive evaluations (Desender et al., 2016; Tagliaabue et al., 2019, Fleming, van der Putten & Daw, 2018; Boldt & Yeung, 2015; Murphy et al., 2015; Desender et al., 2019), many questions regarding the relationship of the decision-related neural signals in the construction of representations of graded confidence remained. For instance, it remains unclear in what form the decision-variable is read-out for metacognitive judgements, at what point relative to the first-order choice this read-out occurs and what potential other sources of information might contribute to confidence outside of the cumulative evidence.

The current thesis aimed to capitalise on recent advancements in the development of EEG paradigms that permit the separation and measurement of the distinct stages of perceptual decision-making in the human brain (O’Connell et al., 2012; Kelly & O’Connell, 2013). Specifically, the parsing of both domain-general and effector-specific decision-related signals allowed the current thesis to address key questions about the unique contributions of each level of processing in the emergence of choice confidence. In Chapter 2, the effects of uncertainty in evidence durations and stimulus-response mapping on the dynamics of perceptual decision-making were investigated, which influenced the emergence of confidence in these signals. These further employed a task with simultaneous first- and second-order judgements. Furthermore, to our knowledge, this is the first study to employ confidence ratings to study the temporal dynamics of the sensory evidence accumulation. These manipulations allowed Chapter 2 to explore outstanding questions about the nature of response conflict and its
contributions to metacognition. The experiment reported in Chapter 3 was a natural progression from
the work conducted in Chapter 2 and utilised a behavioural paradigm that separated first-order
perceptual choices and second-order confidence judgements in time. The presence or absence of
additional stimulus information after the initial first-order decision was varied across trials, which
allowed for a formal investigation of the extent to which post-decisional accumulation processes
contribute to retrospective metacognitive reports. Finally, Chapter 4 sought to investigate the
fundamental assumption that lab-based behavioural metrics of decision-making and metacognition are
indicative of the same processes that govern real-world cognitive functions.

This Chapter will review the main contributions of the experiments conducted in this thesis. To
this end, three general themes were identified which will be discussed separately in the following
sections. A first general theme is the functional role of domain-general evidence accumulation signals,
which comprises the examination of the impact of temporal uncertainty on the accumulation process
and how this interacts with the emergence of confidence (Chapter 2), as well as the extent to which
post-decisional evidence accumulation occurs in this signal (Chapter 3). A second theme discussed is
the involvement of motor level processes in the construction of metacognitive judgements and
highlights the role of motor preparation signals in the expression of response conflict (Chapter 2) and
the resetting of decision bounds on trials where changes of mind occur (Chapter 3). A final theme
concerns the validity of perceptual decision-making and metacognitive tasks and how these are related
to self-report measures of daily-life cognitive functions (Chapter 4).

5.2 The temporal Dynamics of Domain-General Evidence
Accumulation in the Emergence of Choice Confidence

Recent mathematical models have proposed that the evidence accumulation process that
governs perceptual decisions might also influence the emergence of metacognitive judgements
(Pleskac & Busemeyer, 2010; Yu, Pleskac & Zeigenfuse, 2015; Resulaj et al., 2009; Merkle & van
Zandt, 2006; Moran et al., 2015; Fleming & Daw, 2017). This suggests a common neural currency
might underlie both first- and second-order decisions. Support for this account comes from single-cell
recordings in primates, which have shown that the same neural populations that encode perceptual
decisions also exhibit attenuated firing rates when monkeys opted-out of the decision process in favour
of a sure, but smaller reward (Kiani & Shadlen, 2009). In humans, explorations have centred on a
domain-general evidence accumulation signal known as the centroparietal positivity or the CPP, which
forms a pure index of the sensory evidence accumulation (Steinemann, O’Connell & Kelly,
2018). Therefore, the CPP is a particularly strong candidate neural signature to inform metacognitive
judgements since its amplitude would not require additional transformations in the read-out for a specific level of confidence. Indeed, previous studies have linked the CPP amplitude to a variety of metacognitive evaluations, such as subjective visibility ratings (Tagliabue et al., 2019), the subjective experience of conflict (Desender et al., 2016), error awareness (Murphy et al., 2015; Boldt & Yeung, 2015) and the decision to opt-out in favour of a sure reward (Gherman & Philiastedes, 2015). However, this work did not address a number of important issues. Firstly, most studies only conducted stimulus-locked analyses (Tagliabue et al., 2019; Desender et al., 2016; Gherman & Philiastedes, 2015), which is problematic since reaction time variability will obscure the temporal dynamics of the emergence of confidence in the CPP upon averaging across trials. Secondly, while experiments have started to investigate the role of post-decisional processes in the context of error awareness (Murphy et al., 2015; Boldt & Yeung, 2015), to date no study has directly investigated the extent to which these post-choice processes trace the external stimulus presentation. Experiments conducted in both Chapters 2 and 3 were designed to overcome these issues, which permitted for novel insights and deeper understanding of the relationship between the neural signatures of perceptual decision-making and confidence.

5.2.1 Uncertainty in Evidence Duration and Stimulus-Response Mapping Influences Evidence Accumulation and the Emergence of Confidence

A first key insight is that both uncertainty in evidence durations and response requirements substantially influence perceptual decision formation and the emergence of subjective confidence. This was shown in Chapter 2 across experiments with two random-delay random dot motion tasks, which manipulated the duration of stimulus presentation and foreknowledge about stimulus-response mapping. Results from both studies indicate people strategically adjusted to the temporal uncertainty in the external stimulus. Specifically, domain-general evidence accumulation in the CPP was found to peak at the average stimulus duration. This neural signature was also predictive of the final level of confidence, exhibiting a faster build-up rate and higher peak amplitude with increased choice certainty in both studies. This relationship remained visible at the single-trial level, where CPP amplitudes predicted small variations in the continuous confidence scale irrespective of other task-related variables (Fleming et al., 2010; Kiani, Corthell & Shadlen, 2014). Further examination of the domain-general evidence accumulation traces by confidence providing insight into the impact of foreknowledge about motor requirements across both experiments. In the longest stimulus duration, a modulation of the CPP by confidence immediately prior to the response cue was absent when motor commands varied. However, when aligning the measurement window of the amplitude to the peak of the CPP, a strong modulation of was observed by the final level choice certainty. This suggested participants disengaged
from the evidence in favour of preparing for the non-trivial saccadic response. Further support for this interpretation comes from the similar peak latencies of the CPP across different levels of confidence, which suggests the decision process was terminated regardless of the level of accumulated evidence at the time of the average motion duration.

This builds on previous studies of the CPP, which have demonstrated strategic adjustments in the evidence accumulation process occur in response to temporal uncertainty in the onset of external stimulus information. Chapter 2 complements these findings by showing that participants can calibrate not only the onset but also decision termination in order to pursue optimal performance outcomes. Moreover, to our knowledge this is the first study to use a confidence scale to directly investigate the relationship between decision formation and confidence. This extends on the previous literature that has utilised other metacognitive evaluations (Tagliabue et al., 2019; Desender et al., 2016; Gherman & Philiastides, 2015), which have been shown to target subtly distinct processes to confidence rating scales (Rausch, Hellman & Zehetleitner, 2018; Rausch & Zehetleitner, 2016). Furthermore, the finding that a modulation of the CPP by confidence can only be observed around the peak amplitude and not at the response cue has important methodological implications for future studies. Namely, researchers have to carefully consider the temporal characteristics of the decision process when measuring the CPP to test hypotheses, since experimental manipulations alter how this signal evolves over time.

5.2.2 Confidence Relies on both Pre- and Post-Decisional Evidence Accumulation

A second key insight relates to the continuation of evidence accumulation after the first-order perceptual decision. A first indicator of the continued accumulation was observed in Chapter 2, where the build-up of the CPP continued after the disappearance of external stimulus information up to response execution. This possibility was formally explored in Chapter 3, where participants performed a difficult contrast change detection task followed by confidence judgements. Crucially, this paradigm manipulated the occurrence of stimulus presentation after the first-order contrast discrimination, which allowed for an exploration of the extent to which post-decisional sensory evidence accumulation signals reflected the external stimulus information. Results indicated the presence or absence of external stimulus information did not significantly influence the post-decisional evidence accumulation process, which indicates continued deliberation can occur even in the absence of new external information in line with the findings of Chapter 2.

Furthermore, the results from Chapter 3 indicated CPP was comprised of two qualitatively distinct phases that partially overlapped in time. Specifically, prior to the first-order perceptual decision
the CPP amplitude was significantly elevated on correct choices, high confidence judgements and trials where subjects did not change their mind. Afterwards, the CPP returned toward baseline before resuming a second build-up that peaked prior to the onset of the confidence scale. Interestingly, the opposite pattern of activations were observed during this time window, with larger CPP amplitudes prior to low confidence ratings, changes of mind and after erroneous first-order decisions. These observations of distinctive stages in the CPP pose serious challenges to some computational models of metacognitive decision formation, which assume post-decisional evidence accumulation with respect to the choice alternatives simply continues after the first-order decision bound is crossed (Moran et al., 2015; Pleskac & Busemeyer, 2010; Resulaj, et al., 2009; van der Berg et al., 2016; Zylberberg et al., 2016; Yu, Pleskac & Zeigenfuse, 2015). In contrast, the pattern of results in Chapter 3 is more in line with more recent proposals that of post-decisional evidence is mapped to an evaluation of the correctness of the first-order choice (Fleming & Daw, 2018; Fleming, van der Putten & Daw, 2018).

5.2.3 Outstanding Questions

The occurrence of qualitatively distinct stages in the CPP across the experiments in Chapters 2 and 3 has important implications about the nature of the processes that underlie sensory evidence accumulation in general. In particular, it is possible that separate neural populations encode the evidence that informs first- and second-order decisions. However, little is known about the intracranial generators of the CPP, some studies have pointed to the involvement of the parietal cortex as the origin of domain-general evidence accumulation (see for instance, Desender et al., 2016). There is evidence that suggests sub-populations of neurons in this cortical area encode different stimulus categories (Raposo, Kaufman & Churchland, 2014), which supports the interpretation of distinct neurons encoding both first- and second-order decisions. However, formal explorations of this hypothesis would require more research that triangulates the precise neural origins of the CPP. One potential avenue is an approach that combines non-invasive recording techniques in humans, such as simultaneous EEG and fMRI recordings (Philiastides et al., 2011; Ostwald et al., 2012). Once the neural generators of the CPP have been elucidated single-cell recording could directly assess the representation of stimulus information in neural firing rates (Kiani & Shadlen, 2013).

Another outstanding question is whether or not the partial overlap between the first- and second-order CPPs in Chapter 3 is a reflection of the averaging procedure. In particular, it is possible that at the single-trial level first- and second-order evidence accumulation stages are completely dissociable but that there is variability in the timing of when the first-order CPP returns to baseline. This, upon averaging across trials, might lead to the partial overlap observed in the waveforms. While this complicates a more detailed investigation into the timing of the second-order accumulation
process, an investigation of the difference waves in Chapter 3 provides an indicator that the nature of the evidence accumulation process in the CPP after the first-order decision shifted to a different type of evaluation almost immediately. Future studies could aim to further tease apart these evidence accumulation stages in order to gain a deeper understanding of the mechanics that underlie the second-order CPP. For instance, by adopting longer time intervals in between the first-order decision and the metacognitive judgements that would allow the first-order evidence accumulation process to fully return to baseline.

5.3 Motor level Processes Influence the Emergence of Confidence

A third and crucial insight is the demonstration of the involvement of motor level processes in the emergence of confidence. While previous research has suggested that motor preparation stages might play a role in metacognitive evaluations (Siedlecka et al., 2019; Gajdos et al., 2019; Palser et al., 2018; Fleming et al., 2015; although see, Wokke et al., 2017; Herding et al., 2019), these studies did not investigate the specific nature of this relationship or the temporal dynamics over which these signals might influence confidence. The current thesis aimed to address this gap in the literature by investigations of effector-specific mu/beta motor preparation, which measures the level of motor activation over the contra- and ipsilateral hemispheres. Results in Chapters 2 and 3 demonstrated that stronger motor preparation over the ipsilateral hemisphere was associated with lowered choice confidence prior to response execution. In contrast, contralateral mu/beta band activity reached a stereotyped amplitude irrespective of the level of confidence, similar to previous observations with respect to the first-order decision (Kelly & O’Connell, 2013). While it is possible motor level processes directly influence metacognitive judgements, computational models have suggested the relative difference between these signals is a more likely indicator of the final level of confidence (Davelaar, 2009; Merkle & van Zandt, 2006; Vickers, 1979). This suggests these signals might instead signal response conflict, which can be measured through theta band activity over the mid frontal areas of the brain (Cohen & Cavanagh, 2011, Cohen & Donner, 2013; Cavanagh et al., 2012). Theta power has previously been associated with metacognitive judgements, although the precise nature of this association was unclear (Wokke et al., 2017; Murphy et al., 2015). Results from Chapter 2 build on these findings by demonstrating that increased theta band activity was associated with lower confidence prior response execution.

The results from Chapter 2 also have broader implications about the nature of theta power. In particular, to date it has remained unclear if this signature reflected a conflict between two competing evidence accumulators (Merkle & van Zandt, 2006; Vickers, 1979) or reflects differences in the coactivation of the motor response (Yeung et al., 2004; Yeung, 2014; Botvinick et al., 2001). No
differences were observed in theta-band activity prior to the response cue in Chapter 2, while clear modulations were observed prior to the first-order response execution. This aligns more with the idea of theta as an index of response conflict. This account is further supported by the observations that both theta- and beta-band activity index confidence in similar time windows prior to the response. However, it is possible the absence of a modulation in theta prior to the response cue is a reflection of the relatively short stimulus presentation, which is suboptimal to reliably estimate power in the lower frequencies. This issue is further compounded by the natural loss of temporal precision in the lower frequency bands, which means it is difficult to assess the temporal dynamics of theta band activity. Future studies could aim to address these issues with paradigms that are specifically tailored to investigate the relationship between theta- and beta-band activity, for instance by adopting longer stimulus presentation durations. Furthermore, more research is required to investigate to what extent these signals contribute to the emergence of confidence independently of the cumulative evidence in the CPP.

Finally, Chapter 3 highlighted one additional feature of effector-specific motor preparation signals in relation to confidence. Specifically, by allowing participants to indicate changes of mind when rating their confidence, this experiment could provide the first exploration of this phenomenon at the motor level. Results indicated these trials were associated with a crossover of ipsilateral and contralateral traces after the initial decision, which reflects a resetting of the decision bound in favour of the final choice alternative. This demonstrates a novel means to investigate the temporal dynamics of changes of mind at the neural level. Future research should utilise a similar procedure to further investigate the dynamics of the rebound and crossover effects observed in the post-decision time window in Chapter 3. For instance, the current study could not fully examine the relationship between changes of mind and confidence due to the low trial count in the high confidence bin. Nevertheless, one prediction would be that a high confidence change of mind requires more evidence in comparison to a lower confidence change of mind, which should be translated a stronger crossover in the former. Furthermore, Moran and colleagues (2015) suggested a computational model of second-order RT, where the post-choice evidence accumulation requires a collapsing boundary to capture RT effects. At the neural level, previous studies have suggested collapsing boundaries might be expressed through urgency at the motor level (Steinemann et al., 2018; Murphy, Boonstra & Nieuwenhuis 2016; see also Chapter 2), as such this collapsing bound mechanism might be traceable in the effector-specific mu/beta traces after the first-order decision.
5.4 Are Computational Models of Decision-Making, Metacognition Associated with Real-World Cognitive Function?

Whereas the previous sections of the discussion centred on the neural processes that shape the emergence of metacognitive judgements, Chapter 4 of this thesis aimed to investigate the fundamental assumption that lab-based metrics of perceptual decision-making and metacognition are governed by the same processes that govern daily-life cognitive functions. The experiment devised in this chapter builds on recent advancements in online data collection and testing procedures (Rouault et al., 2018). Online testing has considerable challenges with respect to experimental control and data quality (Chandler, Mueller & Paolacci, 2012, 2014), yet previous research has demonstrated that careful study design can make online experiments a powerful tool to test hypotheses in more representative samples (see for instance, Gillan et al., 2016). Despite this, previous research has largely focused on the relationship between lab-based variables and clinical symptoms (Hauser et al., 2017; Rouault et al., 2018, Moses-Payne et al., 2019). Therefore, the main contribution of Chapter 4 was to add to the emerging body of literature by investigating the relationship between the latent structure of perceptual decision formation, metacognitive behavioural variables and self-report measures of daily-life cognition and metacognition.

The results from this study indicated that individual differences in metacognitive bias were largely in line with the previous research (Moritz et al., 2014; Tversky & Kahneman, 1974; Johnson & Fowler, 2011), showing associations between overconfidence and heuristic cognitive processes and reports of more frequent psychotic-like experiences. Similarly, both metacognitive bias and second-order RT showed a strong relationship with the decision formation parameters, which is in line with the neural results of Chapter 3 that show the evidence accumulation in the CPP prior to the first-order decision is a strong predictor of the final level of confidence. However, investigations of the individual differences in the parameters of perceptual decision formation with questionnaire measures did not confirm any predictions based on previous research (for instance. Gersiaz et al., 2019; Kim & Lee, 2011). This might indicate that the mathematical model of perceptual decision formation that was adopted for this study has a limited ecological validity.

Another possibility is that the absence of significant effects highlights the inherent difficulties when applying computational models to the study of individual differences. A first issue arises during the standard model fitting procedure. Namely, in order to obtain the optimal set of parameters in each subject, a scaling parameter (i.e. a parameter that is fixed to an arbitrary value) must be selected so that the model can settle on one solution. By convention, the within-trial noise parameter is typically selected for this purpose (Ratcliff, 2006; Voss, Nagler & Lerche, 2013). However, this approach has
recently been called into question since there is compelling evidence that noise levels are different across age and in clinical groups (Garett et al., 2013; O’Connell et al, 2018; Dully et al, 2017). This could obscure relationships between parameters and self-reports, since the variability that would normally be attributed to the within-trial noise is instead spread over the other parameters in the model. Moreover, the within-noise parameter would be interesting to investigate in relation to metacognitive since research has shown confidence judgements are particularly susceptible to both noise in the external environment and internal noise along the sensorimotor hierarchy (De Gardelle & Summerfield, 2011; De Gardelle & Mamassian, 2015; Zylberberg, Fetsch & Shadlen, 2016; Boldt, De Gardelle & Yeung, 2017; Bang, Shekhar & Rahnev, 2018, 2019).

A final contributing factor is that the current study adopted a continuous staircase procedure, which allowed this study to interpret variability in confidence across subjects as a metacognitive bias (Fleming & Lau, 2014). However, this unintentionally might have similarly obscured variability in the parameters of the model, since participants were no longer able to devise their own behavioural strategies and were instead fixed to perform at a certain level of accuracy. Moreover, in a recent paper, Fleming & Rahnev (2019) demonstrated that adopting a continuous staircase also has a substantial effect on the metacognitive efficiency scores. Namely, this causes inflation in the scores of this metric that is proportional to the variability in the stimulus. In line with recommendations from these researchers, one solution to this issue that future studies could adopt is to apply a more exhaustive staircase procedure prior to the experiment that results in a singular difficulty level. Alternatively, future experiments could adopt multiple difficulty levels and compute metacognitive efficiency scores in each separately, subsequently averaging these scores to obtain a single unbiased estimate for each subject (Fleming & Rahnev, 2019).

In summary, Chapter 4 has aimed highlighted some of the particular challenges associated with the application of computational models of perceptual decision-making in the study of individual differences. While the issues of continuous titration could be readily addressed in future studies. The implication of the scaling parameter is seemingly more inherent to the model fitting procedures and therefore the solution is not obvious. One alternative could be that researchers select the scaling parameter in every study based on the predictions and research questions of interest. For instance, in a recent study Afacan-Seref and colleagues (2018) fixed the bound parameter and left the within-trial noise free to vary, in order to investigate the mechanisms that govern the formation of decision and value biases. These researchers theorized that fixing the bound would place a natural limit on the parameters they were interested in, starting point bias and drift rate variability, which could enhance the ability of the fitting procedure to find the optimal set of parameters. However, more systematic research on the impact of different scaling parameters is required to fully understand how this would
change the interpretation and outcomes of mathematical models. Another solution is to isolate neural measurements of within-trial noise, which could be used to determine each subject’s within-trial noise parameter. This would keep within-trial noise as the scaling parameter but allow researchers to account for individual differences in the noise parameter by setting each individual’s parameter to the value that corresponds to their internal neural noise level.

5.5 Concluding Remarks

At the start of his thesis, the recent advancements in the field of computational modeling of metacognitive decision formation were highlighted, which have suggested that the evidence accumulation mechanisms that govern perceptual decision making might also be involved in the emergence of metacognitive representations. This account has recently gathered compelling support from both neurophysiological recordings in primates as well as imaging and electrophysiological studies in humans. However, many questions remain about the functional role of the evidence accumulation process in the emergence of confidence. For instance, little is known about how strategic adjustments in perceptual decision formation might influence metacognitive experiences, to what extent post-decisional evidence accumulation is dependent on external stimulus information or what the role of motor level processes in the emergence of a graded representation of confidence is. By investigating these questions, the current thesis made a number of important insights. Firstly, Chapter 2 showed the construction of confidence in perceptual decision-making signals is indirectly influenced by both uncertainty in the stimulus duration and response requirements. Secondly, Chapter 3 demonstrated that post-decisional accumulation occurs independent of external stimulus presentation and might reflect a distinctive evidence accumulation process compared to the processes that govern the first-order decision. Thirdly, Chapter 2 further suggested that motor preparation signals influence confidence judgements by signalling response conflict. While Chapter 3 further shows that these signals were also found to implement the change in decision bound that occurs after the first-order decision when people change their mind about the initial choice. Fourthly, Chapter 4 contributed to the growing body of literature that investigates the relationship between lab-based behaviour and daily-life cognitive functions, showing the challenging nature and some of the potential limitations of computational models of perceptual decision-making in the study of individual differences. Finally, this thesis highlighted some outstanding questions that could be addressed in future research, such as further examination of the hypothesis that the post-decisional accumulation in the CPP reflects a qualitatively distinct stage and what time scale this accumulation occurs on.
References


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