Waiting Time as a Behavioural Correlate for Decision Confidence in a Carrion Crow

Thesis submitted in
partial fulfillment of the requirements for the degree

Master of Science

Graduate School of Neural and Behavioural Sciences

Faculty of Science
Faculty of Medicine

Eberhard Karls Universität Tübingen

by

Shweta Prasad
from Thrissur in Kerala, India

Tübingen, 28 October 2024

Thesis Advisor: **Prof. Dr. Andreas Nieder**
Institute of Neurobiology
University of Tübingen

Second Reader: **Dr. Felix Moll**
Institute of Neurobiology
University of Tübingen

Disclosures:

- I affirm that I have written the dissertation myself and have not used any sources and aids other than those indicated.

- I affirm that I have not included data generated in one of my laboratory rotations and already presented in the respective laboratory report.

Date / Signature: _____

Acknowledgements

Abstract

The statistical notion of decision confidence defines it as the probability that one's prediction of the outcome of a decision i.e., belief, is correct. Animals navigate ever changing uncertainty landscapes of survival, and they must use the sample of information available to them to make decisions such as predicting the quality of a food patch, or for how long it should exploit a particular patch before exploring a new one, or in choosing a mate. In this regard, having accurate confidence estimates about each available option is a crucial guiding force for optimal behaviour in relation to the animal's environment. Here, we employ a temporal post-decision wagering paradigm to study decision confidence in a carrion crow. The crow was first presented with a random dot kinetogram and asked to make a perceptual decision. If he made the correct choice, reward was delivered after a variable delay in the majority of trials. In a small proportion of correct trials, reward never arrived, and how long he waited in such trials was used as a behavioural correlate of confidence in his preceding perceptual decision. We hypothesised that the more confident he was that his decision was correct, the longer he would be willing to wait for the reward to arrive. Our results present a first line of evidence that the crow can use confidence judgements to guide his waiting behaviour. The effects found were significant but small, indicating that directed modification of the task paradigm used here is necessary to establish that waiting time is an informative behavioural correlate for decision confidence in the crow.

Contents

List of Figures

Chapter 1

Introduction

Faced with myriad uncertainties in an environment in constant flux, a decision-maker benefits from being able to flexibly update its policies of what actions it can take when moving from one environmental state to another. An update of this type would require that the decision-maker has a prior set of beliefs about how the world works based on experience interacting with its environment. A confidence judgement is such an evaluation of the goodness of ones beliefs. More precisely, we define confidence as the decision-maker's estimate of the probability that a decision is correct given the available evidence (Pouget et al., 2016; Hangya et al., 2016). Confidence is critical for learning decision policy improvements in the face of reinforcement via feedback (e.g. Drugowitsch et al., 2012; Lak et al., 2020), for deciding when to stop gathering information before acting (e.g. Drugowitsch et al., 2019), and for determining how long to keep waiting for an expected outcome before leaving the current trial and initiating a new one (Kepecs et al., 2008; Lak et al., 2014). The move away from reliance on self-reports of confidence measures, to using indirect behavioural reports such as wagers on expected reward on the trial-by-trial basis has been a major methodological improvement in how we query confidence in humans (Kunimoto et al., 2001; Persaud et al., 2007) . Furthermore, it has facilitated the study of decision confidence in non-human animals, which has bootstrapped progress towards better understanding of the neural underpinnings of confidence, primarily in mammalian model systems such as rodents (e.g: Kepecs et al., 2008) and non-human primates (e.g: Kiani and Shadlen, 2009). The subject of this study is the adaption of a paradigm that allows the study of confidence in non-human animals, here, the crow, to further our comparative understanding of principles of decision-making across the animal kingdom

In this chapter, we first introduce our notion of confidence and briefly trace how it has been studied in human and non-human animals, and their various successes and failures. Then, we present a task paradigm that has had great success in the study of mechanisms underlying confidence in rodents, and discuss the key findings therein. We then distil what qualifies a correlate of confidence as sufficient, and lay out what we expect to find when adapting the aforementioned task paradigm to study confidence in the crow.

1.1   Decision confidence

Consider the example of a dot-motion direction discrimination task. You as a subject are shown randomly moving dots and asked to determine if the global motion direction is towards the left or the right, a binary choice. Based on the evidence you collect in a trial, you

make a choice – left. Choice certainty in this setting is the probability of your answer being correct given the evidence. As visual information and the stimulus itself are stochastic and ambiguous, there is a distribution of choices that could have formed from the same evidence. The width of this distribution is a measure of the uncertainty within the choice. However, this probability distribution is independent of you choice being correct, rather, the distribution is over the set of sensory evidence that could lead to your answer. This is different from confidence.

Confidence is defined here as the subjective estimate of a choice being correct (Pouget et al., 2016). There is no notion of confidence independent of choice, although the choice may be covert. We view confidence as a type of certainty, and treat it as the posterior distribution over a binary random variable that can take only two values – correct, or incorrect. This latter posterior distribution of predictions of outcome based on choice is commonly called the belief distribution, and confidence is the probability of a particular belief or hypothesis being correct. Confidence and choice uncertainty can be shown to be inversely related.

1.2   Confidence in non-human animals

Confidence has long been treated as a metacognitive judgement, the insistence being on its highly subjective, self–reflective, higher–order level of operation. Studying metacognitive functions such as confidence or metamemory have traditionally relied on self–reports, such as via questionnaires or a confidence–rating request in sequence with a choice (Vickers, 2014; Dienes, 2007), which in turn restrictively relied on the human capacity for language. The veracity of these subjective reports have been called into question – why should we assume that human subjects are always honest in their reports? (Eriksen, 1960). Thus began a move towards non-reliance on self-reports, where following studies (e.g: Kunimoto et al., 2001) began to use proxy behaviours in the form of wagers contingent upon accuracy. Their argument was that if metacognitive reports bore any relation to task performance, one could expect significant non-zero correlation between them (Altmann et al., 1995; Fleming and Dolan, 2012). This change in methodology combined with the recent shift towards viewing confidence as a fundamental statistical computation that neurons are capable of doing as a matter of their construction (Pouget et al., 2016, Li and Wang, 2021), opened up the possibility of studying it in non-humans.

The earliest studies on confidence in non-human animals used an 'uncertain' option task. Smith and colleagues showed that capuchins, rhesus macaques (Smith et al., 1995; Smith et al., 2012) and a dolphin (Smith et al., 1997) could perform just as well as humans on this paradigm, which was a modification of the 2–choice categorization paradigm. An additional, 'uncertain' option was introduced wherein the different options were associated with different reward probabilities. The correct option in a trial always gave the highest reward, the incorrect option gave no reward, and the uncertain option gave a small but certain reward. The subjects were hypothesised to choose this option more frequently when they were unsure about their answer, in the interest of maximizing expected reward. However, they failed to show that rats could perform confidence judgements, bringing into question whether it was the animal or the task that was the limiting factor (Smith et al., 2003). A detriment of such studies was that one could not prove that the resultant behaviour was not just stimulus–outcome association: the parsimonious view posits this as a three–alternative choice task, where the uncertain option was the middle option that corresponded to the

stimuli closer to the decision boundary, effectively forming a third category. Therefore, it remained unclear whether any metacognitive abilities needed to be invoked at all in the task.

Another paradigm introduced by Hampton et al., (2004) used a 'decline' option. Here, macaque monkeys were required to perform a delayed match-to-sample task, where after the delay, they were given the option to decline to take the matching test. The idea here was that the frequency of availing the 'decline' option would correlate with confidence in prospective gains, based on a retrospective judgement about the quality of their memory. Performance of the animal on this task was compared to that in the forced choice case, where no 'decline' option was presented. The expected signature of confidence modulated behaviour here was that the performance of the animal when they are given and avail the option to decline the memory test, would supersede that when forced to make a choice, and this difference would be all the more pertinent when the task was hard – here – as the delay was increased. Macaques showed results consistent with this expectation (Hampton et al., 2004). A slight variant of the task (Kiani and Shadlen, 2009) supported the finding further, extending it to neural correlates of confidence in macaques.

While the methods so far were unable to find evidence for the use of confidence judgements in rats, Foote and Crystal, 2007 used the 'decline' option task paradigm sans the delay, that is, the memory component, and presented the first line of evidence that rats could use confidence in decision–making. This further supported the notion that it was not the animal, but the testing paradigm that was insufficient: how we query confidence judgements in animals matters (Shettleworth and Sutton, 2003). This view is also backed by the statistical notion of confidence (Kepecs and Mainen, 2012; Pouget et al., 2016; Hangya et al., 2016).

1.2.1   Task paradigm: Post-decision wagering

A major shortcoming of the decline or opt–out task paradigms is that they do not allow the measurement of choice accuracy and confidence in the choice on the same trial. Trials where animals chose to decline a memory test or opted out of giving a response were informative about the animal's level of confidence, but no information about the actual choice outcome is available. On the other hand, when the animal did not decline or opt–out of the trial, their choice accuracy was available but no confidence measure could be obtained. This lack of pair-wise correlations between choice and confidence on a trial–by–trial basis made searching for neural signatures of confidence difficult.

Kunimoto et al., 2001 and Persaud et al., 2007 used post–decision gambling tasks to characterise awareness in humans using the relationship between accuracy and confidence. Kepecs et al., 2008 modified this paradigm to study decision confidence in rats. Here, they used an odour discrimination task and rewarded the rats after a variable delay. The correlate of confidence here was the probability of trial re–initiation before reward was actually delivered. They argued that in the interest of maximizing reward, the rats would only wait for the whole reward delay if they were certain about their choice being correct, and leave a trial early to restart another the less confident they were in their preceding choice, so as to get another opportunity to win reward. Every trial therein gave a measure of the rat's choice accuracy and certainty in their choice, allowing for a straightforward characterization of the correlation between the two quantities. They found that on correct trials, the probability of trial restarts decreased with ease of task. On error trials, the rats restarted more

trials as the ease of task increased. Moreover, they found neurons in the rat orbitofrontal cortex (OFC) modulating their firing rates in a similar fashion. This finding could not be explained as a simple stimulus–outcome association, but they showed that it was perfectly in line with the predictions of a model that used comparisons between sampled stimuli and an underlying subjective belief distribution, in other words, subjective probability estimates about the outcome of a decision.

In a later study, Lak et al., 2014 modified the task slightly to allow for the measurement of a graded behavioural correlate of confidence, wherein instead of measuring the probability of restarts, they used leaving decisions, characterised as the time the rats waited at the decision port before choosing to leave (**Fig. 1.1**(a)). In this scenario, rewarded trials yielded only a measure of choice accuracy. Therefore, a small proportion of trials were baits, or 'catch' trials, wherein no reward arrived even if they made the right choice. Thus, waiting time on both correct and error trials could be measured.

Briefly, studies on confidence and its neural underpinnings in the rat brain by Kepecs and colleagues paved the way to identifying signatures of continuous–variable correlates of confidence, be it behavioural (for e.g: Lak et al., 2014) or neuronal activity corresponding to an abstract decision variable (Masset et al., 2020). Since confidence is a type of certainty forecast over the certainty of an outcome, that is, accuracy, it is first necessary to establish the agent of interest's accuracy as a function of task difficulty. Premised by the notion of an 'optimal' decision–maker that maximizes expected reward, a correlate of confidence would be modulated by what outcome leads to more certain reward. (Lak et al., 2014; McNamara and Houston, 1985; Stephens and Krebs, 1986; Middlebrooks and Sommer, 2012). This necessitates that accuracy as a function of the correlate of interest (behavioural, neural, etc.) be characterised as well. With these two functions, one is equipped to forecast the correlate as a function of task difficulty. The latter is also empirically measurable. This view effectively posits confidence as a transformation between perceptual decisions and behavioural output.

Waiting time characterised as a behavioural correlate for confidence in rats, as in Masset et al., 2020 for example, neatly demonstrates the above. In the temporal post–decision wagering task they found that the rats' accuracy increased with odour contrast, and therefore task ease (**Fig. 1.1**(b)). Next, they characterised the rat's accuracy on the task as a function of waiting time (**Fig. 1.1**(b)). They showed that the rats' accuracy was higher when they waited longer, in accordance with the notion of the optimal agent previously described (Stephens and Krebs, 1986, Middlebrooks and Sommer, 2012). This function was called the calibration curve. Lastly, they characterised the rats' waiting time as a function of task difficulty in what they called the vevaiometric curve (**Fig. 1.1**(c)). Here, they found that as the task got easier, the rats waited longer when they made the correct choice and left earlier when they made the erroneous choice.

Not only did these studies establish that rats are capable of making confidence judgements, they characterised the neuronal mechanisms underlying decision confidence. The temporal post–decision wagering paradigm allowed for querying a subjective measure such as confidence reliably, and without being constrained by language.
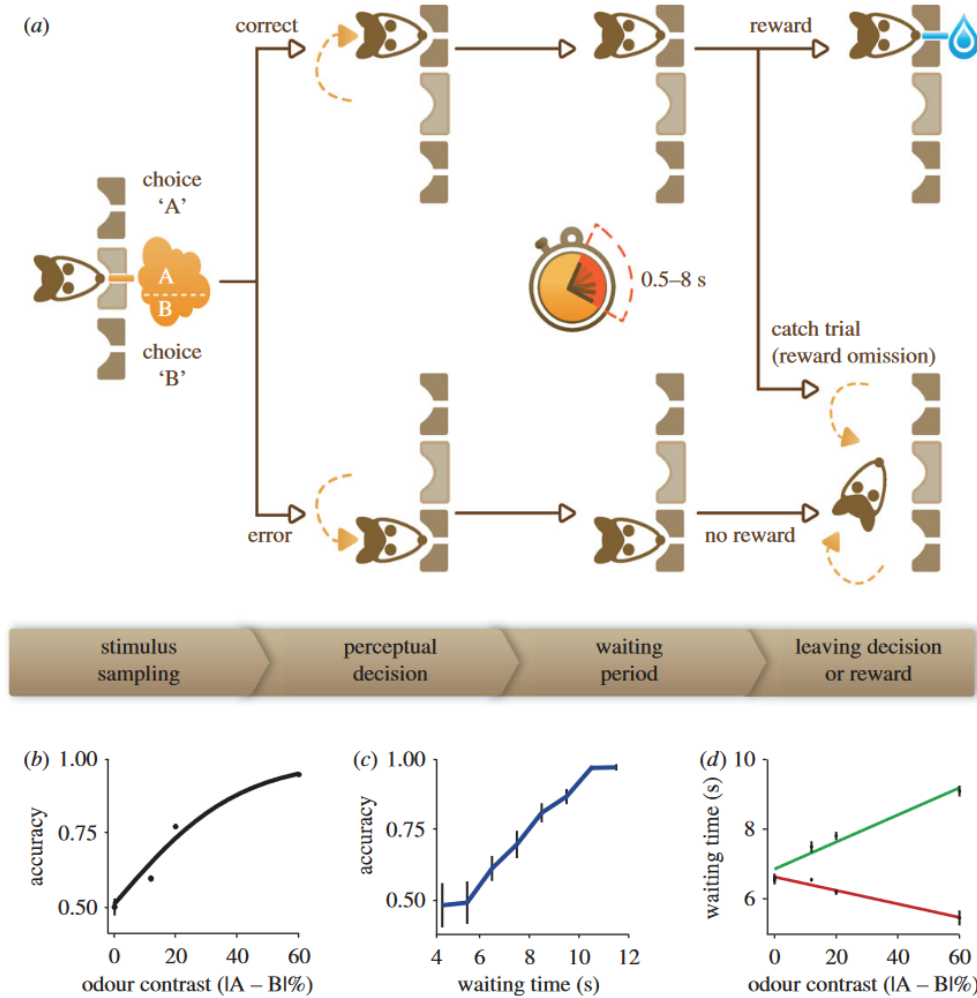
Figure 1.1: **A leaving decision task to study confidence in animals:** Figure from Kepecs and Mainen, 2012. *(a)* The rat initiates a trial by entering the central odor port. After a pseudorandom delay of 0.2–0.5 s, a mixture of two odours is delivered and they have to respond by moving to either choice port A or B to indicate which odour dominated the mixture. A drop of water is delivered after a 0.5 - 8 s (exponentially distributed) waiting period for correct decisions. In approximately 10% of correct trials, reward was withheld, and no feedback provided. Waiting time was measured on these catch trials and on all error trials as the time from entry into a choice port until withdrawal. *(b)* Psychometric function for an example rat. *(c)* Choice accuracy as a function of waiting time, called the **calibration curve**. *(d)* Mean waiting time as a function of task difficulty for an example rat, called the **vevaiometric curve**. Catch trials in green, error trials in red.

1.2.2 Confidence in birds

Thus far, we discussed findings in mammals such as rats (Lak et al., 2014), a dolphin (Smith et al., 1995), macaques and humans (Smith et al., 2003; Smith et al., 2012). But what about in birds? Various birds such as pigeons and corvids have been shown to have cognitive capabilities comparable to primates (Nieder, 2018; Jarvis et al., 2005). However, there are very few studies on decision–making and specifically, decision confidence in birds. Over the last two decades, pigeons have been a popular model system (Clayton and Emery, 2015; Güntürkün et al., 2017), and previously employed task paradigms failed to show any signs of their using confidence judgements. For example, Sole et al., 2003 and Nakamura et al., 2011 made use of 'uncertain' option tasks; Inman and Shettleworth, 1999 and Sutton and Shettleworth, 2008 made use of metamemory tasks; Both camps found no conclusive evidence of behavioural signatures of confidence in the pigeon. They suggested that while it was possible that the absence of evidence of metacognitive abilities in pigeons (and bantams – see Nakamura et al., 2011) is a result of insufficient testing paradigms (Shettleworth and Sutton, 2003; Kepecs and Mainen, 2012), they did not rule out that the insufficiency might be rooted in the species being tested. In this vein, they also suggested that perhaps, the family of corvids is a promising avenue.

Corvids are known to possess high-level cognitive capabilities such as object permanence (Hoffmann et al., 2011), numerical competence (Nieder, 2018), can plan for future events (Raby et al., 2007) and perform mental time-travel (Clayton and Dickinson, 1998). We therefore set out to test carrion crows on their ability to use confidence judgements in decision–making. Previous studies on carrion crows have shown that they possess the ability to perform analogical reasoning (Smirnova et al., 2015) and statistical inference (Johnston et al., 2023), laying groundwork that their cognitive abilities are supplemented by the basic statistical scaffolding needed to use abstract confidence. Carrion crows have the ability to perform flexible rule–switching tasks (Veit and Nieder, 2013; Moll and Nieder, 2014; Veit et al., 2014, Nieder et al., 2020) and have been shown to possess a wide range of spatio–numerical competences (Kirschhock and Nieder, 2022), including a concept of zero (Kirschhock et al., 2021). Moreover, they have been shown to possess sensory consciousness (Nieder et al., 2020), setting the grounds for testing their metacognitive abilities further.

The success of the post–decision wagering paradigm in the study of animal confidence inspired us to ask whether we could adapt it to show that the crow – a bird – also uses confidence judgements to guide its behaviour.

1.3 Aims of this study

To show that waiting time is a reliable behavioural correlate of decision confidence in the crow, we need to establish the animal's performance on the decision-making task, and find a monotonically increasing trend in the relationship between decision accuracy and waiting time (the calibration curve). If the latter trend is not found, we discard waiting time as an informative correlate for decision confidence.

Here, we adapted the previously discussed temporal post–decision wagering paradigm to study confidence in the crow. In this pilot study, we aim to test if waiting time is indeed a reliable report of confidence in the crow. Based on findings in rats performing similar tem-

poral post-decision wagering tasks (Lak et al., 2014; Ott et al., 2018; Masset et al., 2020), we hypothesised that first, the crow would wait for longer on catch trials than on error trials. Second, waiting times would increase with coherence on catch trials, and decrease with coherence on error trials. Third, the crow's choice accuracy would increase monotonically as a function of waiting time.

This study is a novel test of avian cognitive abilities, and earnestly probes whether a corvid songbird can use confidence judgements to guide their behaviour. If our findings are consistent with the above posited hypotheses, we would have a preliminary line of evidence for the use of decision–confidence amongst birds.

Chapter 2

Methods

2.1 Subject

One hand–raised male carrion crow (*Corvus corone corone*) 11 years of age was trained on a temporal post–decision wagering task. The crow was housed in an indoor facility in a social group (group aviary dimensions: length 360 cm, width 240 cm, height 300 cm; using guidelines specified in Hoffmann et al., 2011). Food was controlled during the training and testing periods. Water was provided *ad libitum* in the aviary and during training/testing. He was weighed before and after every session.

All experiments were carried out in accordance with the national animal experimentation regulations and were authorised by the Regierungspräsidium Tübingen, Germany.

2.2 Experimental set-up

A custom–built darkened operant conditioning chamber was used to train and test the crow on the task. The crow was tethered to a wooden perch by means of custom–made leather jesses, and perches facing a touch-screen (15" 3M Microtouch, 60 Hz refresh rate) 14 cm away. The screen was used to present stimuli and collect the crow's response pecks. The chamber is equipped with speakers, an automatic crow feeder atop which the screen is placed, an infrared beam emitter facing down on the crow from the chamber ceiling and a camera on the side along the horizontal plane of the crow's head, used to monitor the crow from the outside. A reflective surface was attached to a small headpost fastened to the crow's head – the infrared beam emitted from the ceiling forms a light barrier which is 'broken' when the reflector is no longer in its path, allowing us to keep track of the subject's head position. The crow was trained to maintain fixation by staying within the light barrier unless it is to respond to the task in an appropriate manner. Barrier breaks and reentry are accompanied by distinct acoustic feedback. During training, every correct trial is rewarded and accompanied by 'correct' auditory and visual feedback. Every incorrect trial during training leads to no reward, no visual feedback and 'incorrect' auditory feedback. Visual stimuli were presented on the touch-screen monitor and the crow was trained to peck on appropriate targets to register their responses. Audio stimuli are played back via speakers placed behind the screen.

For every correct sequence of actions corresponding to the behavioural protocol at hand, the crow was given one mealworm (*Tenebrio molitor* larvae) or one crow seed pellet, dis-

pensed by means of an automated feeder built in-house. The subject was not water restricted in the aviary, and was provided with water breaks after every 60 rewarded trials during training/testing sessions. The ratio of mealworms to seed pellets in one disk is calibrated according to the expected number of trials per session and the required intake to maintain the crow's weight at least at 80% its weight while not in training, since the seed pellets are more nutritious than the mealworms, and can satiate the crows faster.

2.3 Task

We adapted a temporal post-decision wagering task from Kepecs et al., 2008, and Lak et al., 2014 to study confidence-guided decision making in crows. Briefly, the crow first makes a perceptual decision, and then waits for a variable interval for reward delivery, contingent on the outcome of the decision. In a small fraction of trials where the crow made a correct decision, and in all trials where he did not, reward delivery is omitted and we treat the time the crow waits as the temporal cost he is willing to pay to obtain reward, based on how certain he was about the outcome of his decision. The temporal wager (i.e waiting time in unrewarded trials) is the behavioural measure of interest. We now describe the details of the task.

The first phase of the task is a perceptual decision (**Fig.2.1**, **decision**). The crow is presented with a random dot kinetogram (RDK) and asked to discriminate whether the majority of dots are moving to the left or to the right. The global motion direction of the stimulus is represented as an arrow corresponding to global motion direction in the task schematic **Fig.2.1**. After a short delay of 500 ms, a set of targets corresponding to one of two rules appears to cue response: if the targets are white, they must respond by pecking on the congruent target, i.e the target corresponding to the direction of global dot motion; on the other hand, if the targets are red, they must respond by pecking on the incongruent target, i.e the target opposite to the direction of global motion. Each rule was presented with equal probability. The crow had a maximum of 2000 ms to respond, and the time between response cue presentation and response registration, wherein he leaves the light barrier to peck the target on screen, is his reaction–time on the perceptual decision. Once the decision is made, they enter the temporal wager phase of the task (**Fig.2.1**, **investment**), where reward delivery T_R is delayed by 1.5 - 7s (drawn from a uniform distribution, inclusive), and the probability of reward delivery is set to 80%. That is, in 80% of trials where they made the correct perceptual decision, they are rewarded if they successfully wait for the whole interval ('correct' trials). In the other 20% of trials ('catch' trials), and in all trials where they made the erroneous choice ('error' trials), they receive no reward or feedback. How long the crow waits in anticipation of the reward a in catch or error trial is considered here as a behavioural correlate of their decision confidence in that trial. Waiting time T_w on such trials is defined as the time between barrier reentry after the decision peck, signalled by the flash of the white square, and the following light barrier break.

RDK stimuli of 4 motion strengths (coherences) were generated anew for every session of data collected. Coherence refers to the proportion of dots moving in the same direction. The ease of direction discrimination increases with the coherence of dot motion. For this task, we generated RDKs of 10%, 20%, 40% and 80% coherence separately for leftwards and rightwards motion using a custom MATLAB script. Each kinetogram consisted of white dots of radius 0.24 degrees of visual angle (dva; 1 dva = 33.4 pixels) moving at 16 dva per second on a black background of diameter 16 dva. 20 consecutive frames were displayed at
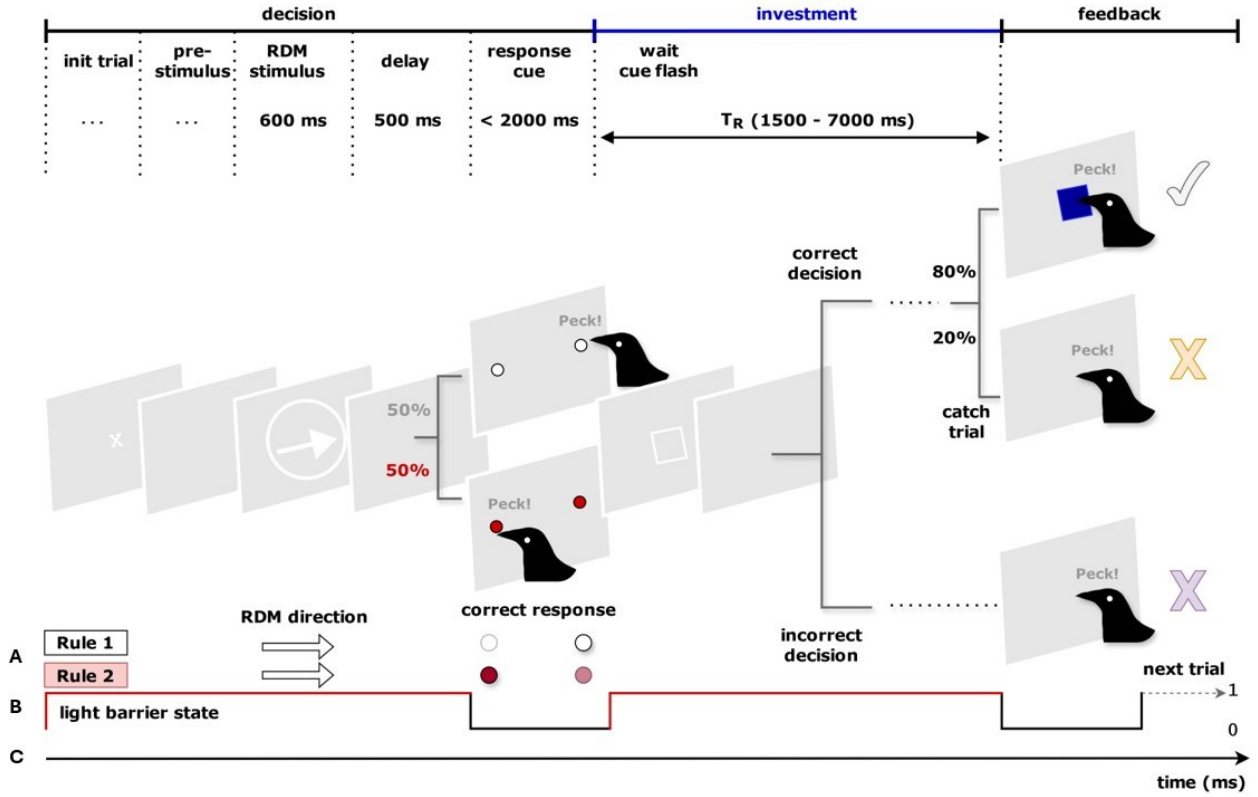
Figure 2.1: **A temporal post–decision wagering task.** The task has two distinct phases, one where the crow makes a perceptual decision, and the second where he makes a time investment which [we want to show] is based on the decision outcome. **Decision phase:** The crow initiated a trial by entering the light barrier and fixating on the screen. Trial initiation was indicated to the crow by a brief flash of a white '×', followed by a 600 ms stimulus presentation period wherein a random-dot kinetogram (RDK) is played to the crow. This was followed by a 500 ms delay where the crow maintains his decision in working memory. Next, a response was cued by colored target pairs corresponding to one of two rules: white targets for congruent responses, and red targets for incongruent responses. The crow had a maximum of 2000 ms to respond. **Investment phase:** After the decision peck was registered, the crow had to re-enter the light barrier to continue the trial so as to be rewarded. The beginning of the investment phase was indicated to the crow as a flash of a white square the instant he re-enters the barrier. If he made the correct choice and successfully waited for $T_R \sim U[1.5, 7]$ seconds, he was rewarded 80% of the time. In these trials, a blue square appeared on the screen, and pecking it dispensed reward, along with auditory and visual feedback. No reward was delivered in case he left early in these trials. In the other 20% of correct trials ('catch trials'), and in all error trials, reward was withheld indefinitely. The orange and lilac crosses in the feedback phase indicates that no feedback was given to the crow in such trials. The tick–mark indicates he gets rewarded, and is given multimodal feedback for his success. **At the bottom of the schematic: A.** The two rule contexts and their corresponding correct responses are indicated for a rightwards RDK stimulus as shown on the corresponding gray panel in the decision phase. Rule 1: white targets cue a congruent response (right target). Rule 2: red targets cue an incongruent response (left target). **B.** Light barrier state 1 (or 'up', in red) indicates that the crow is in the barrier; Light barrier state 0 (or 'down', in black) indicates barrier break. **C.** Solid black arrow indicates the passage of time in milliseconds.

60 frames per second to produce the dot movement. The RDKs had a net dot-density of 4 dots per dva^2, and each kinetogram was 1 second long. The stimuli were placed at the centre of the screen along the horizontal of the crow's eyes. The subjects were shown the stimuli on the screen against a black background, so that only the white dots were salient. These parameters were set based on previous work studying global motion encoding in the crow nidopallium caudolaterale (Wagener and Nieder, 2017). The dots moved either to the left (180°) or to the right (0°).

The RDK was shown for 600 ms, and after a 500 ms delay wherein the crow had to maintain his decision in working memory, diametrically opposite targets appeared to cue the crow's response. The targets were either both white or both red to cue different rules: white targets cue a congruent response; red targets cue an incongruent response. For example, if white targets appeared, rightwards motion must be reported on the right target, whereas if red targets appeared, it should be reported at the left target. The combination of the 2 rule contexts (white, red), 2 directions of motion (left, right) and 4 coherences (10%, 20%, 40% and 80%) produces 16 unique stimulus conditions. Blocks of 80 rewarded trials were balanced to guarantee 1 catch trial of each of the 16 conditions. In this way, every condition had at least 120 catch trials at the end of 10 sessions, which guaranteed the minimum requirement assuming 480 rewarded trials every session. The CORTEX scheduler guaranteed that the conditions were randomised and uniformly distributed in frequency. Test sessions were run till at least 480 rewarded trials were completed, with the exception of two sessions.

Stimulus presentation and behavioural data collection is mediated by a custom written COR-TEX (National Institute of Mental Health, Bethesda, Maryland) programme. The CORTEX software handles scheduling and balancing of all experimental conditions, and automates the appropriate sequence of events depending on the crow's behaviour, such as dispensing a reward (i.e controlling the feeder) and associated stimuli. Its primary input signals are (a) light barrier breaks (i.e the crow is no longer fixated on the stimulus on screen), (b) touch-screen pecks, and (c) time between events of interest, as control signals.

2.4   Training

The crow was previously trained on various paradigms including reaction-time versions of the random dot-motion direction discrimination task, an interval timing task, rule-switching tasks and various delayed match-to-sample tasks. Pertaining to the task here, the testing phase began only after the subject performed consistently above 65% on the perceptual decision-making part of the task, and successfully waited for the reward cue to appear in over 85% of correct trials.

Training on the temporal post-decision wagering task involved the following distinct phases. First, the crow was trained to respond as soon as the stimulus sample period ended. Second, a small delay was introduced between sample presentation and target appearance. At this point, no red targets were introduced. After this was successful, he was introduced to two sets of target cues corresponding to the two rules. The crow was trained to associate white targets with congruent responses, and red targets with incongruent responses, initially by presenting blocks of trials involving only one rule type, and eventually blocks where the rules were presented in random order. No additional changes were introduced until the crows performed reliably at at least 70% overall accuracy for each phase of training described thus far.

It was of utmost importance that they performed reliably in the perceptual decision-making phase of the task, since we planned to ultimately introduce catch trials in the test phase, which meant a lowering of the 100% probability of reward delivery to 80%. As previously mentioned, the crows have performed left–vs–right random dot-motion discrimination tasks before, but only in the congruent context. The crows are thus trained for a relatively shorter period of time on the incongruent rule. However, we only proceeded to the next step once the performance on both rules were above the 70% threshold.

Next, we introduced a delay between response registration and reward delivery. This was done in gradual steps, since two discrete cues demarcated the start and end of the waiting phase: a white square outline was flashed at the centre of the screen for 60 ms to indicate the start of the waiting period, and a filled blue square appeared after the waiting period, pecking on which delivered reward. The blue square stayed on screen until it was pecked, so that the crow was forced to explore where pecking it led. First, both the flashing of the white square and the blue reward request cue were shown in instantaneous sequence after the decision response was registered. Once they learnt reliably that only the additional step of pecking the blue square led to a reward, the interval between the white square flash and the appearance of the blue square was gradually increased. The crow was expected to stay in the light barrier without breaking it for the whole waiting period. Light barrier breaks led to trial re–initiation, which also meant that correct trials went unrewarded. This could potentially confuse the crow about what it is doing wrong, and lead to reversal of intended training outcomes. Therefore, training this phase of the task was tracked using the difference between the number of correct trials and the number of rewarded trials. The smaller this difference, the better the crow had grasped the task. For our subject, this metric quickly converged to values lower than 50, on training sessions that went over 420 rewarded trials, indicating he understood that he had to wait for the reward to be delivered after making a decision.

Catch trials were introduced only in the test sessions. In test sessions, the crow entered the waiting phase (white square flash) on all trials regardless of whether they made the correct or incorrect choice in the previous phase. All catch trials and error trials entered the waiting phase, allowing us to get a trial–by–trial measure of both choice and confidence in it. No feedback was provided in either case. Waiting ended when the crow broke the light barrier to initiate a new trial.

2.5   Analysis of behavioral data

All analyses were carried out in MATLAB (v.R2024a, MathWorks Inc.) using custom written programmes. Behavioural data collected using CORTEX was converted from the default storage format to MATLAB readable `.spk` format using SpikeTools (toolbox version 7.0; W. Asaad, G. Rainer & M. Histed, Massachusetts Institute of Technology). Decision reaction times were measured as the time passed between targets appearing, and the light barrier break before the decision peck is made. Waiting time was measured as the time passed between re-entry into the light barrier after the decision peck which triggered the cue demarcating the start of the waiting period, and the following light barrier break, which signalled trial re-initiation.

Performance on direction discrimination was characterised as the proportion of correct tri-

als out of all completed trials, calculated by pooling trials of each coherence. Performance was similarly calculated after pooling trials by rule. Session-wise means per group were calculated, and averaged across 12 sessions, reported along with the standard error of means (SEM). Perceptual thresholds were estimated by fitting a second degree polynomial to each empirical performance curve.

To analyse reaction time distributions on the task, we first pooled all correct trials and error trials and then separated them by coherence. Median reaction times per group of interest were calculated per session, and then averaged across 12 sessions in the reported plots. Similar treatment was applied on trials pooled by rule type. One-sided Kolmogorov-Smirnov tests were used to test individual distributions for normality. Wilcoxon rank sum tests were used to test for differences between error and correct trial groups thus pooled since they did not follow normal distributions. Kruskal-Wallis tests with Dunn-Sidak correction for post-hoc comparisons were performed on coherence–wise groups within and between trial types.

Waiting times were similarly treated after pooling trials into catch and error trials. Where appropriate, the distribution medians were used as the measure of central tendency, and calculated for each relevant group session-wise, and then averaged across all sessions. χ^2 goodness-of-fit tests were carried out on the cumulative distribution functions of catch and error trials to test whether normal or gamma distributions fit the data better. Since the waiting times were not normally distributed, non-parametric statistical tests (Kruskal-Wallis rank tests) were used for further analyses. Post-hoc comparisons were made after applying the Dunn-Sidak correction. Effect size of difference between catch and error trial distributions were characterised using Cohen's d statistic.

The relationship between waiting times and task difficulty in terms of coherence is referred to here as the *vevaiometric curve*. Waiting times on catch and error trials were separately pooled into coherence conditions (10%, 20%, 40%, 80%), session-wise medians were calculated and averaged across all sessions for the reported curve. Vevaiometric curves were also calculated after splitting the trials into rule-wise pools. Kruskal-Wallis rank tests were used to test for differences between groups and post-hoc comparisons were carried out after applying the Dunn-Sidak correction to p-values.

The error associated with every session-averaged data point in both reaction time and waiting time measures is a slight modification of the SEM: here, we use median absolute deviation (MAD) in place of standard deviation (SD) as a measure of dispersion of reaction/waiting times at a condition across sessions to accommodate the fact that neither are normally distributed in any subset under consideration here. Moreover, MAD is more robust to outliers than SD, and is more appropriate here.

To show that time investment is a correlate for decision confidence in this task, it is necessary to characterise the relationship between performance and waiting time. We call this the *calibration curve*. To this end, we calculate performance versus waiting time only on catch trials, assuming that the performance in this subset reflects overall performance. This assumption is justified since catch trials are predefined in any given block and lead to appropriate treatment based on decision outcome. Waiting times on catch trials were sorted and binned into 1s bins. Performance was calculated per bin for every session, and the bin

was accepted if it had a minimum of 3 trials. Performance in a time bin was averaged across sessions if at least 8 sessions had numerical values in the bin. This was done to account for noise due to very few trials in the bin. A line was fit to session-wise data, and the average line is plotted on the final curve. The slopes of the lines regressed were tested against 0 (one-sided Kolmogorov-Smirnov) to quantify the significance of the trend.

All curve fitting and statistical analyses were carried out using MATLAB's Curve Fitting and Statistical & Machine Learning toolboxes.

Chapter 3

Results

3.1 Overall behaviour

3.1.1 Performance

The first phase of the task involved a perceptual decision. A 600 ms RDK of 10%, 20%, 40% or 80% coherence was shown to the crow, and then a left–right target pair appeared after a 600 ms delay. The crow completed a total of 9469 trials (of which, 7111 were hits) across 12 sessions. Each session totalled at around 600 trials, including 60 - 120 practice trials before testing commenced. The crow had an overall accuracy of 75.60 ± 1.72% across the

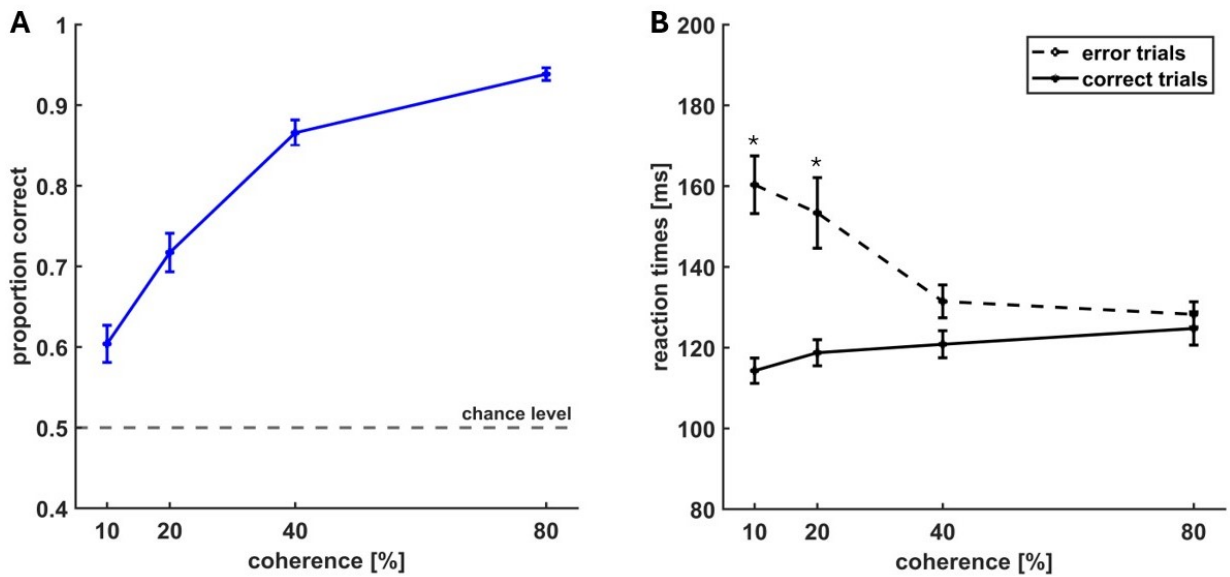Figure 3.1: **Performance of one crow on a delayed dot-motion direction discrimination task: A.** Session-averaged performance curve (n = 12); The proportion of correct choices out of all choices at a coherence is reported at 4 coherence values. Error bars represent SEM. The dotted line represents chance discrimination performance (0.5). **B.** Session-averaged median reaction times (in milliseconds) at 4 coherence values, separated by correct trials (solid line) and error trials (dashed line). Error bars represent modified SEM (refer to **Section 2.5**); '*' demarcates significant difference between the curves at the respective coherence value (p < 0.01, Wilcoxon rank sum test).

12 sessions, and he performed above chance (50%) at all motion strengths. The crow's performance increased with motion strength but did not reach a 100% on the easiest presented coherence condition. His perceptual threshold (coherence corresponding to 70% accuracy)

for left–right direction discrimination was at 17.9% (derived from overall empirical performance curve).

Reaction times decrease with coherence on error trials but not on correct trials (**Fig. 3.1B**). The crow has significantly higher latencies on error trials than correct trials ($p < 0.05$, 2-way Kolmogorov-Smirnov); The medians for correct trials and error trials were 127 ms and 135 ms, respectively. Latency on error trials is significantly higher than that on correct trials at coherence 10% ($p < 0.01$, Wilcoxon rank sum) and 20% ($p < 0.001$, Wilcoxon rank sum) but not at the others. This is different from what one expects out of purely reaction-time based perceptual decision-making paradigms, wherein latencies decrease with ease of discrimination and saturates asymptotically on both correct and error trials, and one can expect a faster drop in latency on correct trials. The data here only partially aligns with our expectations: reaction times decrease with ease of discrimination only on error trials and stay flat on correct trials. This is interesting on its own, but is not further probed here.

3.1.2   Waiting times

After the perceptual decision, the crow was rewarded on 80% of correct trials following a variable delay T_R, drawn from a uniform random distribution between 1.5s and 7s (mean $T_R = 4.25$s). Rewarded trials did not yield waiting time measurements, so reward was withheld in 20% of correct trials (catch trials), and on all error trials. The waiting times (T_w) were not normally distributed. This was tested using the χ^2 goodness-of-fit test; a gamma distribution fit significantly better than a normal distribution to the data on catch trials and error trials. $p <<< 0.001$ for both catch trials and error trials, in favor of the gamma distribution. Overall, the crow waited for longer on catch trials than error trials (**Fig. 3.2**). The median waiting time on catch trials was greater than that on error trials (median error $T_w = 8.07$s, median catch $T_w = 8.45$s; Wilcoxon rank sum test, $p << 0.001$). This finding supports our first hypothesis, that the crow would wait for significantly longer on catch trials than on error trials.
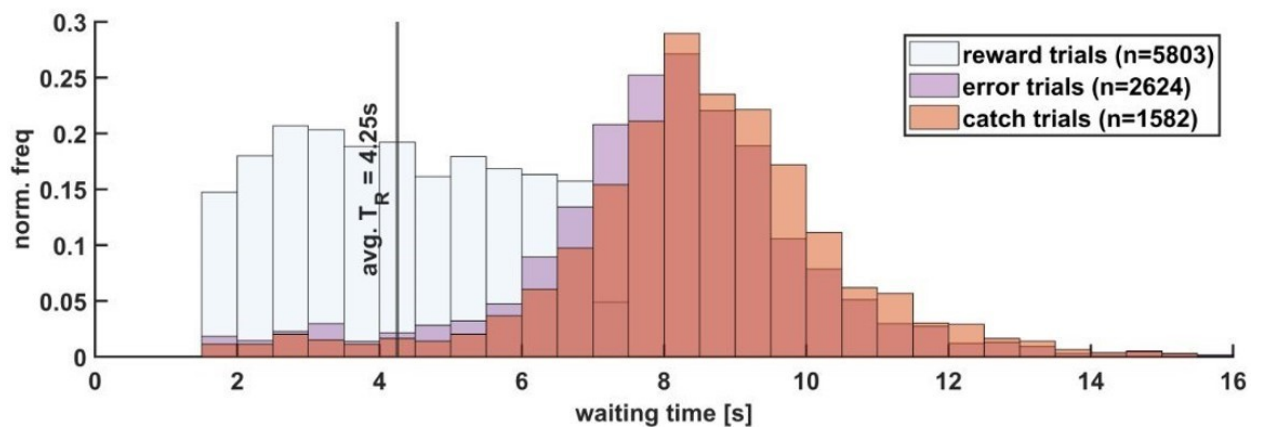
Figure 3.2: **A crow's time investment in a temporal post-decision wagering paradigm:** Distributions of the crow's waiting time on catch trials (orange) and error trials (lilac). The distribution of T_R (delay in reward delivery) on rewarded trials is also shown (pale blue). Histogram bins have been normalised by area under the curve. Only $1.5 \leq T_w \leq 16$ (s) are shown here.

While the effect was significant, it was in the small-medium range (Cohen's d = 0.4, 95% CI = [0.25, 0.5]), and all within a 1s window, as opposed to the several seconds reported

in rats (Ott et al., 2018; Masset et al., 2020). To note here, waiting times longer than 16s comes primarily from the earlier sessions, and fewer trials led to such long waiting times as the sessions progressed, indicating a learning effect may be at play here; Consequently, we restrict the distributions at 16s. A preliminary look into the catch and error trial waiting time distributions separated by coherence supports our second hypothesis (**Fig. 3.3**). This is further explored in the following.
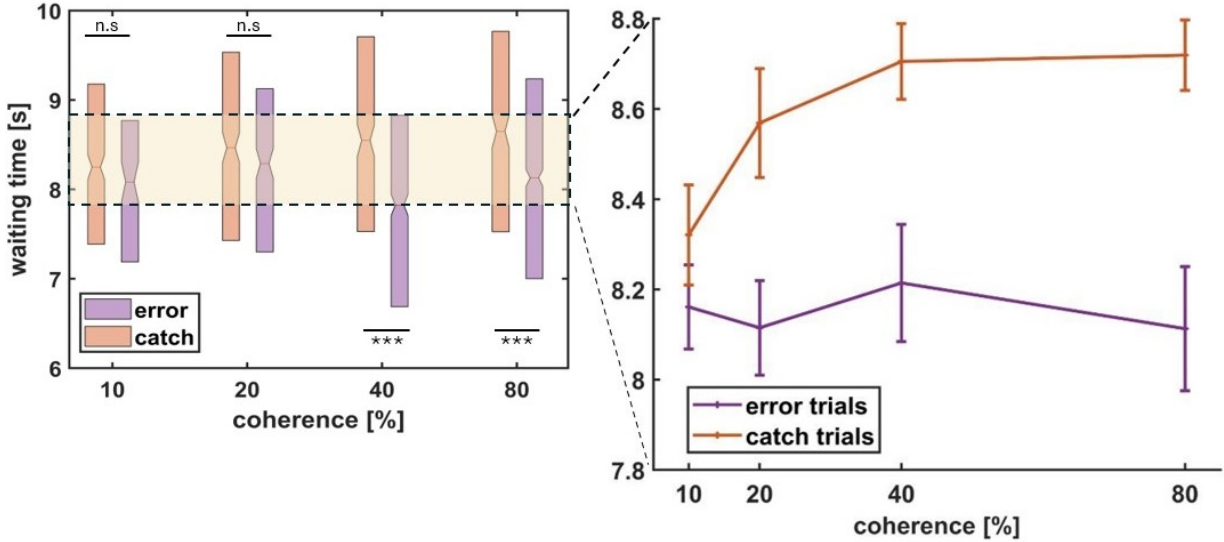

Figure 3.3: **Overall vevaiometric curves:** The left panel shows waiting time distributions separated by trial type at each coherence tested. The boxes show the 25th and 75th percentiles; The notch corresponds to the distribution median. The region indicated by the pale yellow box is expanded upon in the right panel, which shows the crow's vevaiometric curves – session-averaged ($n = 12$) median waiting times separated by trial type (lilac for error, orange for catch), against coherence condition. Error bars correspond to modified SEM. '*': $p < 0.05$; '***': $p < 0.001$; 'n.s': p-value not significant;

Waiting times on catch trials and error trials were separated by coherence conditions, pooling leftwards and rightwards decisions together (**Fig. 3.3**). The distributions of median waiting times on catch and error trials were significantly different from each other at all coherences (Kruskal-Wallis tests within coherence groups, all p-values < 0.05). However, when taking the whole distributions of catch and error trials at a given coherence into consideration, significant differences only persisted at the higher two coherences (**Fig. 3.3**, left panel). Next, we computed the crow's vevaiometric function as session-averaged median waiting times against against coherence (**Fig. 3.3**, right panel). We found that waiting time increased with coherence on catch trials (orange curve), where the crow had made the correct decision. This supports our hypothesis that the easier the decision, the longer the crow would be willing to wait for reward. While we expected the inverse trend to exist on error trials (lilac curve), we found that the difficulty of the perceptual discrimination held no bearing on waiting time when he made the erroneous decision: on error trials, the waiting times remained largely constant with increasing coherence.

Our third hypothesis was that accuracy would increase with waiting time; The more certain the crow was about its decision outcome, the longer it would be willing to wait for reward to arrive. If this is the case, a monotonically increasing trend must exist between the crow's decision accuracy and time investment. In lieu of this, we constructed a calibration curve using only catch trials, assuming that the distribution of waiting times for correct trials is a
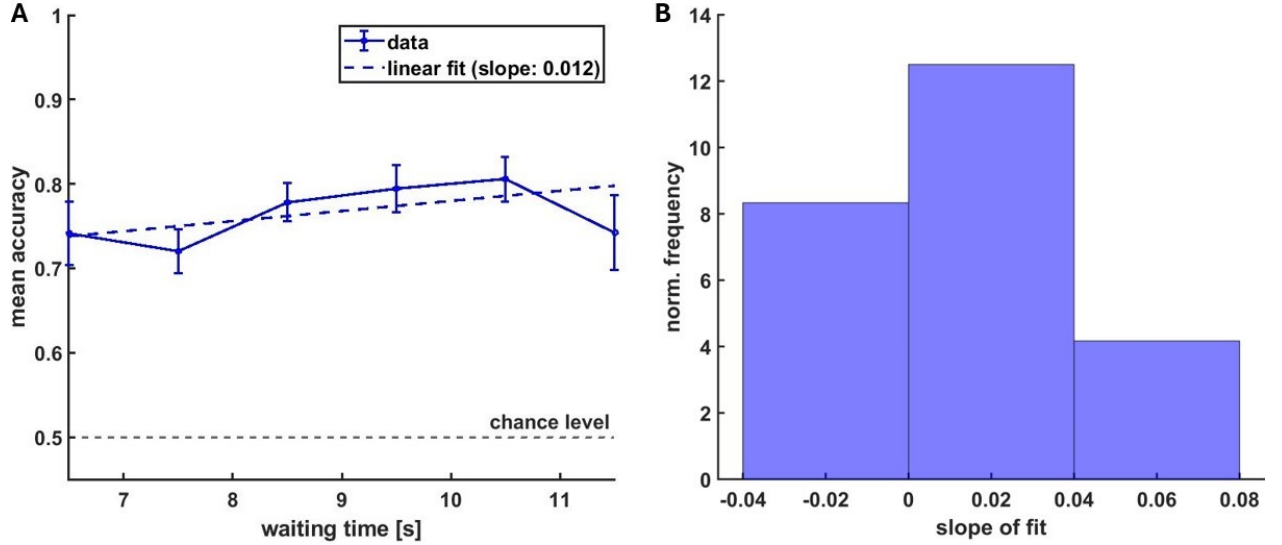
Figure 3.4: **Relationship between choice accuracy and waiting time: A. Calibration curve;** The solid blue line shows the crow's session averaged (n = 12) accuracy as a function of his waiting time in a given time–bin. The blue dashed line is the average linear fit to these points. Error bars represent SEM. **B.** Histogram of slopes of session-wise calibration curves.

representative sample of the correct waiting time distribution. We found a positive, linear trend (slope = 0.0120 ± 0.018) in the overall calibration curve (**Fig. 3.4A**). The slope of the trend, while significantly greater than 0, is small. This was confirmed by testing if the distribution of slopes per session were greater than 0 (**Fig. 3.4B**, $p < 0.01$, Kolmogorov-Smirnov test against 0). Notwithstanding the above result, the curve shows waiting times in the range 6 - 12s, and what can be noticed is that at 11.5s, the accuracy falls. That is, the calibration curve is not strictly monotonic. This may be due to opposing effects of the two rules that have been pooled together in every analysis thus far. Moreover, notice that the mean accuracies in each time bin are very close to the crow's overall average accuracy (75.6%). In sum, we have found a roughly monotonically increasing trend, which however, looks to be a jitter around the mean overall accuracy. The implications and probable causes of this are discussed later on. The rule-specific aspects of the task are discussed next.

3.2 Rule-wise behaviour

The task had two rule contexts: white targets indicated to the crow that it had to respond congruently to the direction of dot motion; on the other hand, red targets indicated to the crow that it had to flip its response. The two rules (and the delay before their appearance) were introduced in order to help disentangle motor preparatory activity from the more abstract neural representations of decision confidence that we are after. While this work does not delve into neural data, it is pertinent to study what additional effects this could introduce in the crow's behaviour. Thus far, we have looked at data pooling both rule contexts. Perhaps, one rule was harder than the other to perform correctly, and pooling the data may be inappropriate. To investigate if the rules lead to different effects, we next group the data into rule-wise pools, and perform similar analyses to **Section 3.1**.

Ideally, with the purpose for which this modification was introduced in mind, there should

be no differences in the crow's ability to perform the task in different rule contexts. However, given the relatively short training on the incongruent rule, it can be expected that performance on this rule is lower than that on the congruent rule, and effects more pronounced in the harder coherence conditions. Moreover, we expect that if differences in the vevaiometric and calibration curves do emerge between the rules, it may be a consequence of the outcome of one rule being more difficult than the other at present.

3.2.1 Performance

The crow shows similar performance on the congruent and incongruent rule contexts (**Fig. 3.5A**). The crow performed roughly the same number of trials in both rule contexts, and had similar ratios of hits:misses. On the congruent rule (white), he performed 3556 out of
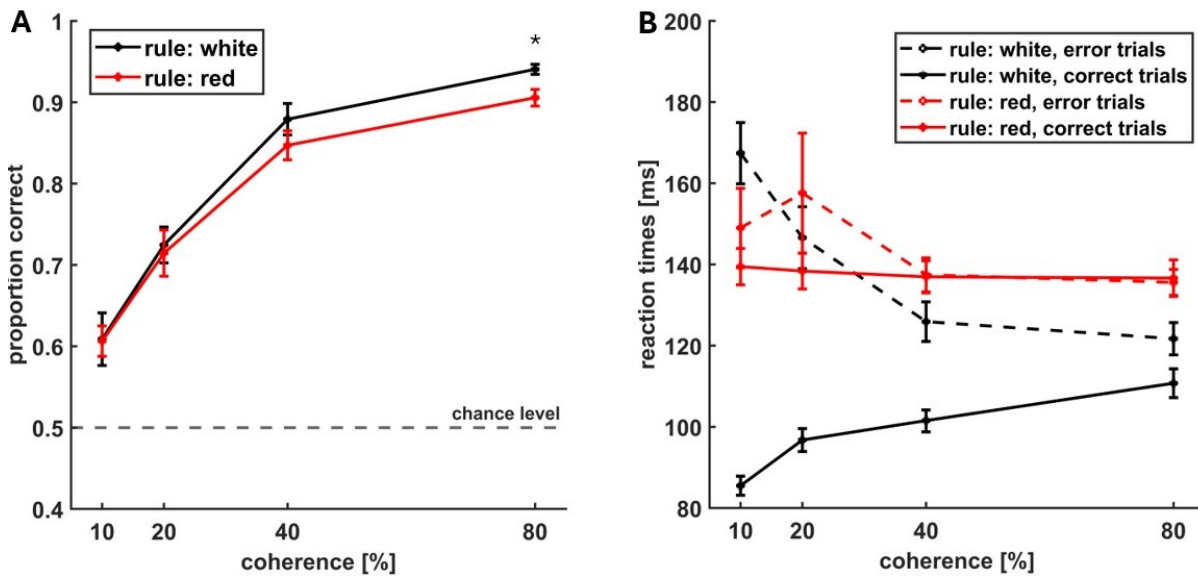

Figure 3.5: **Rule-wise performance of one crow on a delayed dot-motion direction discrimination task: A.** Session-averaged (n = 12) performance curves on rule white (solid black) and rule red (solid red). Dashed line represents chance level performance (50%). Error bars represent SEM. '*': p < 0.05 (Wilcoxon rank sum test). **B.** Session-averaged median reaction times (in milliseconds) of the crow in rule context white (solid black line for correct trials, dashed black line for error trials); and in rule context red (solid red line for correct trials, dashed red line for error trials). Error bars represent modified SEM.

4689 correctly, giving an average accuracy of 75.84 ± 2% across sessions. On the incongruent rule (red), he performed 3555 out of 4780 trials correctly, with an average accuracy of 74.37 ± 2% across sessions. There were no significant differences in the performance of the crow at each coherence condition considered rule-wise (refer to **Fig. 3.5A**), except at the easiest motion strength of 80%, where the performance on rule white was significantly greater than that on rule red (p = 0.0179, Wilcoxon rank sum test). In both rule contexts, we found that performance increased with coherence, and the perceptual threshold for rule red (18.5%) was slightly greater than for rule white (17.8%).

Next, we found a significant difference between the reaction time (RT) distributions on the two rules (p << 0.001, Wilcoxon rank sum test). The median RT on rule white was 112.25 ms, and that on rule red was 137.5 ms. First, on rule white, reaction times on error trials are significantly greater than those on correct trials (p < 10^{-12} Wilcoxon rank sum

test). The median RT on error trials was 136.5 ms, and the median RT on correct trials was 98.25 ms, which is in line with our expectations. As the task gets easier, the reaction times on error trials decrease (**Fig. 3.5B**, dashed black line). However, we observed that reaction times decreased with decreasing coherence on correct trials (**Fig. 3.5B**, solid black line), the inverse of the expected trend based on what we know from the purely reaction-time version of the dot-motion direction discrimination task employed in macaques (Roitman and Shadlen, 2002).

Second, on rule red, there was no significant difference between the crow's reaction times on correct and error trials ($p > 0.5$, Wilcoxon rank sum test). The median RT on error trials was 136.5 ms, and the median RT correct trials was 137.5 ms). There was no difference between coherence conditions ($p > 0.5$, Kruskal-Wallis tests with Dunn-Sidak correction), on both correct (**Fig. 3.5B**, solid red line) and error trials (**Fig. 3.5B**, dashed red line).

In summary, while there was no difference between the overall average performances on the two rules, the perceptual threshold on rule red was slightly higher than on rule white. Furthermore, the performance of the crow was significantly lower in rule red at the easiest coherence condition presented, and the reaction times on rule red were greater than that on rule white. All of this indicates that rule red was harder for the crow than rule white. We speculate that these differences may be a consequence of the relatively shorter training period on the incongruent (red) rule condition as opposed to the congruent one (white), and the task structure, particularly the delay before the targets appear. We next inspect whether these differences, however small they may be, hold any bearing on the observed waiting behaviour.

3.2.2 Waiting times

The crow performed 788 catch and 1263 error trials in the context of rule white, and 794 catch and 1361 error trials in the context of rule red.
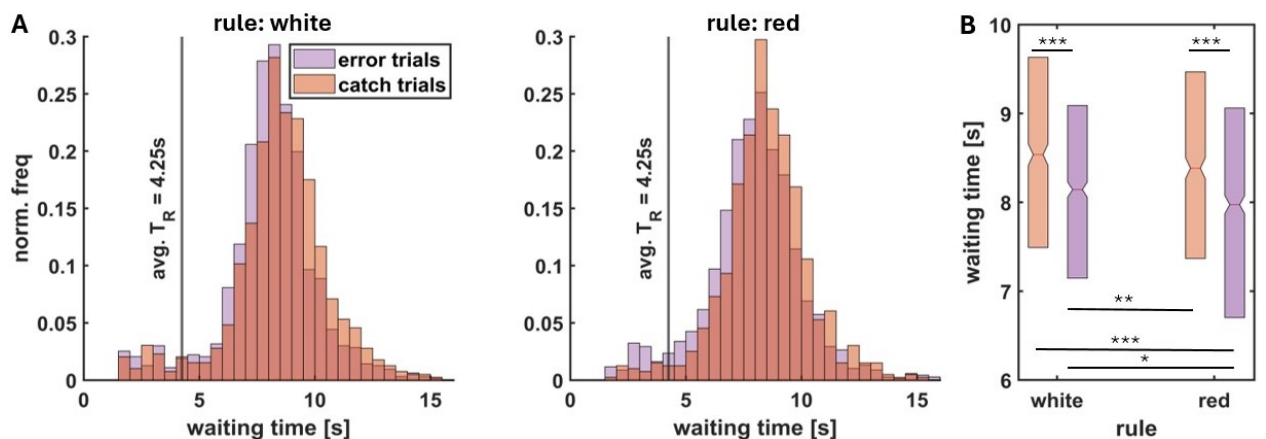
Figure 3.6: **Rule-wise waiting time distributions on catch and error trials: A.** Waiting time distributions on catch trials and error trials shown for $1.5 \leq T_w \leq 16$ (s). Left panel shows the distributions for rule white, right panel for rule red. The average reward delay (avg. $T_R = 4.25$s) is indicated as a black line in both panels. **B.** Waiting time distributions separated by trial type (lilac for error, orange for catch), for each rule context. The boxes show the 25th and 75th percentiles; The notch corresponds to the distribution median. '*': $p < 0.05$; '**': $p < 0.01$; '***': $p < 0.001$; Kruskal-Wallis tests, with Dunn-Sidak correction for post-hoc comparisons.

In both rule contexts, the crow waited for longer on catch trials than in error trials (**Fig. 3.6A**; p << 0.001 for both rules, Wilcoxon rank sum tests). For rule white, the median catch T_w was 8.54 s, median error T_w was 8.14 s. For rule red, the median catch T_w was 8.39 s, and median error T_w was 7.97s. The difference between median catch T_w and median error T_w for rule red was greater than for rule white (420 ms in red, 400 ms in white) and the respective effect sizes were 0.41 and 0.39 (Cohen's d).

Comparing between the rule conditions, catch trial waiting times were significantly greater than error trial waiting times irrespective of rule contexts (**Fig. 3.6B**). Furthermore, the error trial waiting times in rule white were greater than in rule red, with a 17 ms difference between medians.

However, the catch trial waiting times in both conditions had similar distributions (p > 0.1, Kruskal-Wallis test) although the difference between medians was 15 ms, which is very close to the earlier reported differences between medians. The small effects prompt us to be very careful in our interpretation of differences between conditions, especially because waiting times are in the order of seconds while the differences between them are in the order of milliseconds.
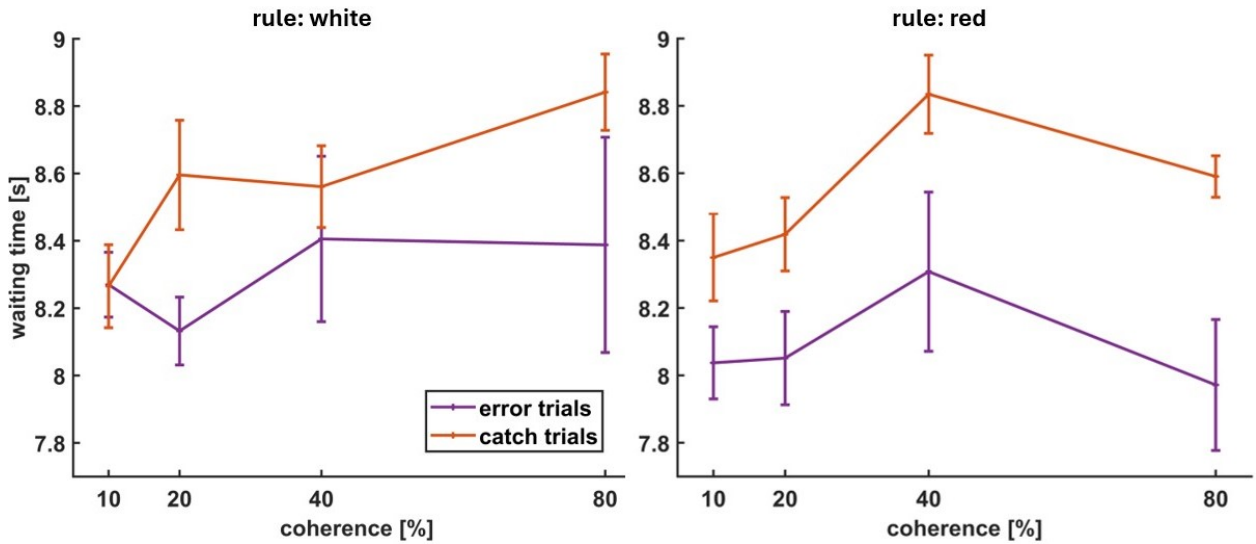

Figure 3.7: **Rule-wise vevaiometric curves:** Session-averaged (n = 12) median waiting times versus coherence for rule white (left panel) and rule red (right panel); Curves for error trials are in lilac and for catch trials, in orange. Error bars represent modified SEM.

Next, we look at the rule-wise vevaiometric functions of the crow to better characterise any differences between the rules and their respective contributions to the overall observed behaviour. In both rule contexts (**Fig. 3.7**), we find that the crow waited for longer on catch trials as the coherence increases (orange curves in both panels). This is consistent with our second hypothesis about the relationship between waiting times and ease of task. Moreover, it is consistent with what is observed in the overall vevaiometric curve (**Fig. 3.3C**).

Next, we characterised the vevaiometric functions for error trials in the two rule contexts (lilac curves in both panels, **Fig. 3.7**). On rule white, the curve did not decrease with increasing coherence as we hypothesised. Instead, waiting time on error trials showed a step-like increase after the perceptual threshold, between coherence values 20% and 40% (refer to **Fig. 3.7A**). However, was this really a step function? We found that there were
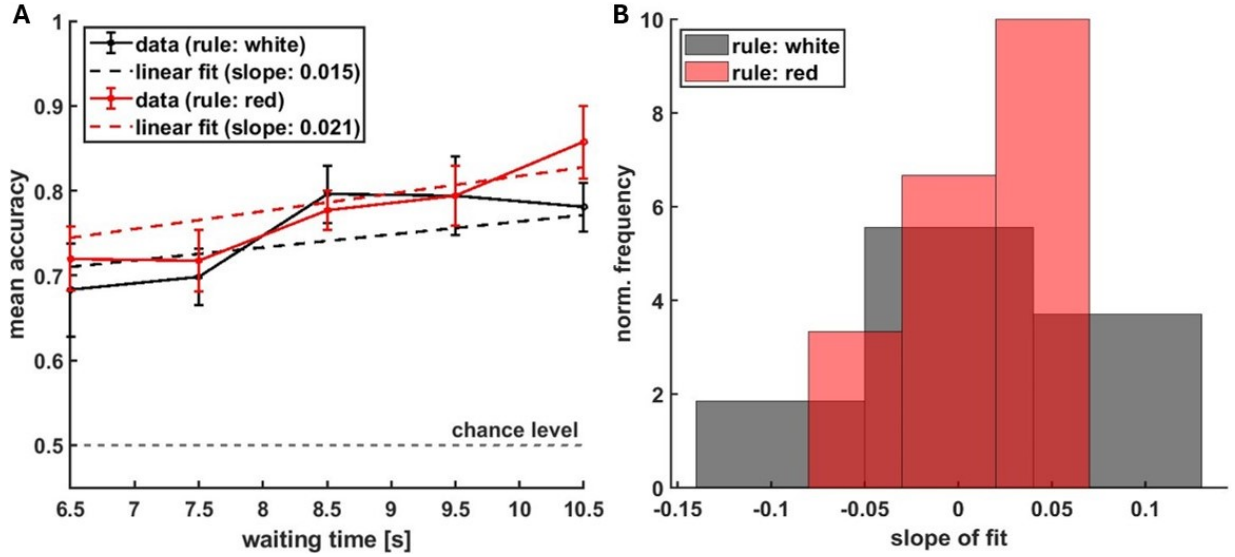
Figure 3.8: **Rule-wise calibration curves: A.** Session-averaged (n = 12) mean accuracy as a function of waiting time on catch trials, and significance of the trend in the context of rule white (black lines) and rule red (red lines). Solid lines correspond to data, dashed lines correspond to linear fit to data, and error bars represent SEM. **B.** Normalised histograms of session-wise calibration curves.

no significant differences between overall waiting time distributions of different coherence groups on error trials in this rule context (all p-values > 0.05, Kruskal-Wallis tests with correction for multiple comparisons), indicating that the error trial waiting times remained more–or–less constant as a function of task difficulty.

On rule red, the vevaiometric function for error trials appeared to show a decreasing trend. However, similar to rule white, comparing coherence-wise overall distributions indicated that they were not significantly different (all p-values > 0.05, Kruskal-Wallis tests with correction for multiple comparisons). The medians tell a slightly different story than the entire distributions. Furthermore, the main difference between the error trial distributions between the rules appeared at coherences 40% and 80% (p-values < 0.05 for both; Kruskal-Wallis tests). One could ask whether differences arise primarily at the easier conditions as a consequence of the delay before responding, leading to different strategies when the task is relatively hard versus easy, and perhaps, modifications to the task in this direction would be beneficial when trying to show that waiting time can be a useful correlate to confidence.

In summary, upon inspecting individual vevaiometric curves for each rule context (**Fig. 3.7**), we did not find inconsistencies with what the overall vevaiometric curves (**Fig. 3.3**, right pane) for error and catch trials report. This supports the conclusion that the rules did not have a confounding effect on the observed overall behavior. To further test this, we also inspected the crow's rule-wise calibration curves in the following section.

Do the two rules have different effects on the relationship between the crow's accuracy and waiting times? Calibration curves were plotted individually for each rule context, using only catch trials of the respective rule type (**Fig. 3.8**). The curves for both rules (**Fig. 3.8A**, solid lines) showed small but significant linear increasing trends (**Fig. 3.8A**, dashed lines), with the respective slopes being significantly greater than 0 (p_w = 0.007 for rule white, p_r = 0.0052 for rule red; 1-way Kolmogorov-Smirnov tests). The histograms of session-wise slopes

corroborate this for both rules (**Fig. 3.8B**). The trend was strictly monotonically increasing for rule red but not so on rule white, and the effects slightly more significant in the context of rule red ($p_w/p_r = 1.35$). However, the size of the effects were too small to make any further comment and necessitates further experimentation. The increase in accuracy with waiting time was significant but small for both rules, and moreover, the slopes were not different between the rules (both roughly 0.01). They were also similar to what we found in the overall case (**Fig. 3.4A**). This prompts us to conclude that the rules did not have confounding effects on the overall calibration curve.

In sum, the crow had overall longer waiting times on catch trials than error trials, and waiting time increased with ease of direction discrimination on catch trials. Waiting time was not modulated as a function of task difficulty on error trials. Most importantly, we found that the crow's choice accuracy showed an increasing trend with waiting time, indicating waiting time can be used as a correlate for confidence in his choice. However, the effect was small. We next investigated if the effect was in anyway diminished as a result of interaction between the two rule conditions, but we found the same trends persisted individually in both rule contexts, in terms of their vevaiometric and calibration curves. Consequently, we concluded that the rules did not introduce a confound in the observed overall effect.

Chapter 4

Discussion

In this work, we present results combining data from 12 sessions in one carrion crow who was trained to perform a temporal post–decision wagering task. Our goal was to investigate if waiting time (or time investment) in this task paradigm is a good correlate for decision confidence in the crow. To our knowledge, there are presently no other studies on decision confidence in the crow, and previous studies in birds did not show conclusively that they have the ability to use confidence to guide behaviour. However, this could be the result of insufficiency in testing paradigms (Shettleworth and Sutton, 2003), uninformative behavioural correlates for decision confidence (Sutton and Shettleworth, 2008) or perhaps, related to specific avian families (Sole et al., 2003). Recent studies in rats (Kepecs et al., 2008; Lak et al., 2014; Masset et al., 2020) have shown the temporal post–decision wagering paradigm to be a successful way to query rodent decision confidence, and we took inspiration from the paradigm in these studies to design a task to study confidence–guided behaviour in our corvid.

For waiting time to be a useful correlate for decision confidence in any animal, it should show a monotonically increasing trend with the animal's certainty about the outcome of their decision. This is in agreement with optimal foraging theory for a risk sensitive forager (Charnov, 1976; Drugowitsch et al., 2019; Stephens and Krebs, 1986). In light of the paradigm at hand, we can say that waiting time is a good correlate for the crow's confidence if it shows substantial increases with ease of task – it is well established that choice accuracy increases with the ease of perceptual decision–making;Roitman and Shadlen, 2002; Shadlen and Newsome, 1996). A good correlate of confidence would increase with ease of task as a consequence.

In **Section 3.1**, we presented evidence that waiting time positively and significantly correlated with ease of task and decision accuracy in one crow. The crow waited for longer when he made the correct decision (on catch trials) than when he made the erroneous one (on error trials). Waiting times increased with dot–motion coherence on catch trials, but stayed constant on error trials. However, the effects found are too small to allow us to make superlative claims about the quality of the behavioural correlate. Furthermore, we find indications that features of the task at hand, such as the delay before response registration, may have had a role to play in weakening the effect observed. In **Section 3.2**, we ruled out the introduction of two rules as a possible confound for the small effect size. In sum, we have here a preliminary line of evidence for decision confidence in corvids, and perhaps, improving upon the paradigm used here can provide more insight into corvid cognition.

How do the results presented here compare with those from rats performing an analogous task? The behaviour of the rats showed clear alignment with the predictions of a normative temporal wagering model (Lak et al., 2014; Masset et al., 2020). Overall, the rats waited longer on catch trials than on error trials, similarly to the distributions reported here. However, the effects of choice and task difficulty were much more pronounced in the rat. For one, the vevaiometric curves showed that their waiting times increased with task ease on catch trials, and decreased with task ease on error trials, regardless of the modality of the perceptual decision. In the crow, waiting times increased with task ease on catch trials, but did not decrease with task ease on error trials, as would be predicted by a normative model of the task. Furthermore, the extent of median waiting times as reported in the rat vevaiometric curves was two to three times that in the crow here; from end–to–end, the median waiting times tiled 3 - 7 s in Masset et al., 2020, as opposed to the 8 - 9 s observed here (**Fig. 3.3**). Second, rats showed a pronounced and monotonic increase in accuracy with increasing waiting time (for example, as in **Fig. 1.1**(c)), as opposed to the small overall positive slope of the calibration curves reported in this study. Another difference in the calibration curves is the extent of waiting times we reported. In rats, they report waiting times between 2 - 12 s. Meanwhile, although we had trials where the crow waited for less than 6 s, and more than 12 s, there were not enough trials across sessions to allow for its averaging in their respective bins. Therefore, we restricted the extent of reported waiting times in the calibration curve to between 6 and 12 s.

Comparing with Shettleworth and colleagues' studies in pigeons, the methodology used here establishes behavioural signatures of confidence that can be better delineated from simple stimulus–outcome association learning. The task designs in Inman and Shettleworth, 1999 and Sutton and Shettleworth, 2008 tested primarily metamemory using delayed match–to–sample tasks, while trying to generalize to metacognitive abilities in pigeons overall. The task belonged to the 'opt–out' class of task paradigms. A criticism of these experiments is that the birds could have been using cues such as the delay duration to make associations with the likely outcome, and therefore, still show behaviour similar to an agent employing metacognitive processes. In our study, while we employed a delay before the response was registered, the duration of the delay remained a constant. Moreover, waiting time, the measure used here, is a direct and continuous behavioural output as opposed to a binary output variable such as the choice to opt–out of a trial, which is sensitive to relative pay–off (Kepecs and Mainen, 2012). The most comparable experiment in the aforementioned studies is Experiment 4 in Sutton and Shettleworth, 2008, where they gave confidence ratings after performing a memory test. The pigeons were given two options associated with different expected rewards: if they pecked on a risky, blue target, they were choosing to gamble based on their preceding choice, for 12 seed pellets. If their choice was correct, they received all 12 pellets, otherwise, none. Their other option was a safe, yellow target, pecking which gave them an assured reward of 6 pellets regardless of the outcome of their choice. Again, an optimal agent employing metacognitive processes would avail the blue option when they were more confident, and go for the yellow option when they were not. However, no differences in frequencies of their choosing the yellow or blue target was found. This method was improved upon in Nakamura et al., 2011, which reported on bantams in addition to pigeons, and showed birds could make retrospective judgements about their choices. However, stimulus–outcome associations with confounding drivers could not be ruled out here as well.

4.1   Caveats and limitations

This study reports findings from one crow. While diminishing the generalizability of the observations made here, it does not discredit them: the more important sample size here is the number of sessions, and consequently, number of trials. Another limitation due was the relatively shorter overall training duration on the red, incongruent rule context. This is simply a result of the crow having been trained on a task similar to the congruent rule condition prior to commencing training on this paradigm. Nevertheless, we ensured that the bird attained a daily performance of over the 65% threshold on both rules.

There are some fundamental differences between the paradigm used to study decision confidence in rats versus the adaptation presented here. First, the perceptual decision is based on a visual stimulus. In rats, earlier studies (Kepecs et al., 2008; Lak et al., 2014) primarily used olfactory stimuli, and then later both auditory (Poisson clicks) and olfactory (odour mixture ratio) stimuli to find correlates of a modality–general abstract representation of confidence at the behavioural and neuronal levels (Masset et al., 2020). We chose dot–motion direction discrimination as the basis of this task for primarily three reasons: (i) it provides a rich repertoire of stimuli amenable to evidence accumulation models consistent with the suggested models in rodents; (ii) crows are highly visual animals and there is evidence that they can discern global motion in this task (Wagener and Nieder, 2017) and (iii) the subject of this study was adept at dot-motion direction discrimination as a result of previous training.

A major limitation of this study is that we did not employ a 0% coherence condition in the perceptual decision. 0% coherence of dot motion corresponds to completely random dot–motion, with no underlying global motion direction. Including this value would help us gauge the bird's performance curves more precisely, since we would be able to establish a known perceptual baseline, here, 50% accuracy, or chance–level performance. We did not include this condition taking into consideration that the relative proportion of catch trials (20%) is high. We did not know whether inclusion of the delay and two rule contexts would make the task that much more difficult, and did not want to lower the bird's expected reward further. In the same vein, coherence values can be better chosen to tile the axis of task difficulty in a more informative manner, for example, by including more conditions closer to the perceptual threshold.

Second, the paradigm this study adapts uses neither a delay nor random rule–switches before reporting decisions. Their tasks relied on the reaction–time paradigm, and therefore, the animals' decision that they had collected sufficient evidence to reach a decision. Not only did we use a fixed sample duration (600 ms), we introduced a delay and two rule–cues to remove spatial dependence of left–vs–right responses and consequent conflation of directional motor–preparatory neuronal activity with an abstract representation of decision confidence. As mentioned in earlier sections, this modification was necessary to ensure that the task was robust to the requirements of neuronal data collection. In **Section 3.2.2**, we ruled out the possibility of the rule contexts being a potential confound, so we can be confident that this modification does not have additional influence on the observed behaviour.

Fixed stimulus–presentation duration and reaction–time paradigms using RDKs have been shown to have differing effects in macaques, with respect to the window it provides into the evidence accumulation process preceding a perceptual decision (Roitman and Shadlen, 2002).

Briefly, a purely reaction–time based perceptual decision–making paradigm allows one to assume that the animal perceived (subjectively) enough to make a decision, and therefore, the well studied speed–accuracy trade–off is prominent in the observed behaviour. In fixing the sample duration, the evidence accumulation process is cut–off (Roitman and Shadlen, 2002), and perhaps enforces the use of different response strategies for coherence values above and below the animal's perceptual threshold to compensate for the quality of evidence. Perhaps, one may find a rectified linear unit–like transformation between confidence and confidence–guided behaviour; For instance, it might be optimal to rely on confidence measures at easier conditions (i.e, above the perceptual threshold), and here consequently wait proportionally longer with decision confidence, whereas fall back on a constant behavioural output independent of confidence at all hard conditions (i.e, below perceptual threshold) which here translates to leaving at a constant, early time regardless of relative ease within hard conditions. This may also explain the first mode of waiting times between 1.5 and 4.25 s, as observed in the waiting time distributions for each rule (**Fig. 3.6A**).

Given that the median waiting times on catch and error trials are less than 2 seconds longer than the maximum shown waiting time, can it be that the bird was timing the maximum possible reward delay ($T_R = 7$s) and the responses we are seeing is a floor effect? The latter is unlikely, because the distributions of waiting times on catch and error trials, while showing a sizable overlap, are significantly different to each other, and moreover, different from the reward delay distribution. Before settling on the T_R distribution used in this work, we tested a small set of variants, including fixed reward delays, wherein we could see that the bird had learnt to estimate the interval precisely, and the catch and error trial distributions were not different from each other, and their means were indistinguishable from the reward delay. This indicated that what we are seeing in the present report is not a floor effect, but a weak effect. The influence of the maximum T_R can be tested by changing the underlying distribution of T_R from a uniform distribution to an exponential distribution with an identical mean, and cut–off at 7s: this would reduce the frequency with which the longer T_Rs appear in trials, and hinder the bird's ability to learn to time that interval. If the bird was relying on timing the maximum rather than the average of the T_R distribution, then we would expect a significant shift towards the average T_R in waiting time distributions.

4.2 Future directions

Using waiting time instead of other forms of post–decision wagering as in Kiani and Shadlen, 2009 helps to give a continuous behavioural correlate of a decision variable important to understanding principles of decision–making across a variety of animal species(Kepecs and Mainen, 2012). The success of this paradigm in the rodent model (Kepecs et al., 2008; Lak et al., 2014; Ott et al., 2018; Masset et al., 2020) inspired the testing of waiting time as a correlate for decision confidence in crows. However, for a first study into corvid confidence, the task used here perhaps has too many bells and whistles. While the intention behind the inclusion of all the components was to make the task robust to the requirements of neuronal recordings, the results of the experiments indicate it is pertinent to do systematic parameter variation to indubitably establish that we are indeed looking at a measure of confidence in crows, and moreover, to find parameter combinations that magnify the effect observed in the desired direction.

As a first modification for precise examination of the bird's perceptual discrimination per-

formance, the 0% coherence condition needs to be incorporated. Moreover, inclusion of more coherence conditions that tile the perceptual space better such that not more than 2 conditions are close to the highest performance level, and more conditions tend towards the perceptual threshold from either side, would give us a clearer picture of the bird's performance on the task. This modification would also tie–in to the following point related to the influence of higher variability on interval estimation. Second, reverting to the reaction–time paradigm with one rule context is suggested. This would also allow further clarity in interpretation when varying other parameters more fundamental to this study, such as those related to the reward delay distribution, and reward probability.

Interval timing literature (Gibbon, 1977; Malapani et al., 1998; Malapani and Fairhurst, 2002; Allman et al., 2014) and other studies using variants of the current task (Miyazaki et al., 2012; Miyazaki et al., 2018; Miyazaki et al., 2020) report that scalar timing effects may be prevalent here. If this is indeed the case, we could wield it to our benefit and move the center of the T_R distribution to a longer value, or increase the variance of the currently used distribution. According to scalar timing theory, both would increase the waiting times on the task primarily as a result of introduction of noise in the crow's subjective interval estimation processes. Shifting the mean of the reward delay distribution to the right (i.e longer average T_R) would lead to longer median waiting times, and increasing the variance of the reward delay distribution (i.e, extending the range of the uniform distribution equally on either side of avg. $T_R = 4.25$s) would lead to flatter waiting time distributions. In doing either, one could expect that the difference between catch and error trial waiting time medians (and distributions) would be magnified. If after systematic parameter variation we find no convincing effect on waiting times, then other task designs such as the looking task (Kepecs and Mainen, 2012; Call and Carpenter, 2001; Hampton et al., 2004) should be employed.

The study of decision confidence is incomplete without the buttress of computational frameworks, which provide powerful theory and falsifiable hypotheses about the mechanisms underlying cognitive processes (Ott et al., 2018; Kepecs and Mainen, 2012; Hangya et al., 2016). Without going into the implementation level of analyses, Marr's algorithmic level of description is in itself, highly informative, and can tell us *what* (signatures) to look out for, and perhaps even *where* in the brain. Kepecs, Ott and colleagues' works have laid the groundwork for a computational framework within which we can study confidence in non-human animals. We did not model the behaviour observed in this study due to aforementioned limitations, particularly the effect size and the number of subject[s]: any model-based interpretation would be over-extending in nature. However, as a next step, this serves as a great comparative neuroethological starting point after further task parameter tuning: if models that sufficiently explain rodent behaviour and also generalize to primate models of decision–making fail to generalize to what we observe in corvids, it may spotlight fundamental differences in the underlying mechanisms of mammalian and avian cognition. On the other hand, its success would point to general principles of cognition realized by convergent evolution (Jarvis et al., 2005; Nieder, 2018), which warrants deeper study in itself.

References

Allman, M. J., Teki, S., Griffiths, T. D., & Meck, W. H. (2014). Properties of the internal clock: First- and second-order principles of subjective time. *Annu. Rev. Psychol.*, *65*(1), 743–771.

Altmann, G., Kwan, L., & Goode, A. (1995). Unconscious knowledge of artificial grammars is applied strategically. *Journal of Experimental Psychology-learning Memory and Cognition - J EXP PSYCHOL-LEARN MEM COGN*, *21*, 1322–1338. https://doi.org/10.1037//0278-7393.21.5.1322

Call, J., & Carpenter, M. (2001). Do apes and children know what they have seen? *Animal Cognition*, *3*(4), 207–220. https://doi.org/10.1007/s100710100078

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*(2), 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays [Publisher: Nature Publishing Group]. *Nature*, *395*(6699), 272–274. https://doi.org/10.1038/26216

Clayton, N. S., & Emery, N. J. (2015). Avian models for human cognitive neuroscience: A proposal [Publisher: Elsevier]. *Neuron*, *86*(6), 1330–1342. https://doi.org/10.1016/j.neuron.2015.04.024

Dienes, Z. (2007). Subjective measures of unconscious knowledge. In R. Banerjee & B. K. Chakrabarti (Eds.), *Models of brain and mind* (pp. 49–269, Vol. 168). Elsevier. https://doi.org/https://doi.org/10.1016/S0079-6123(07)68005-4

Drugowitsch, J., Mendonça, A. G., Mainen, Z. F., & Pouget, A. (2019). Learning optimal decisions with confidence. *Proceedings of the National Academy of Sciences*, *116*(49), 24872–24880. https://doi.org/10.1073/pnas.1906787116

Drugowitsch, J., Moreno-Bote, R., Churchland, A. K., Shadlen, M. N., & Pouget, A. (2012). The cost of accumulating evidence in perceptual decision making. *Journal of Neuroscience*, *32*(11), 3612–3628. https://doi.org/10.1523/JNEUROSCI.4010-11.2012

Eriksen, W., C. (1960). Discrimination and learning without awareness: A methodological survey and evaluation. *Psychological Review*, *67*(5), 279–300.

Fleming, S. M., & Dolan, R. J. (2012). The neural basis of metacognitive ability [Publisher: Royal Society]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1594), 1338–1349. https://doi.org/10.1098/rstb.2011.0417

Foote, A. L., & Crystal, J. D. (2007). Metacognition in the rat [Publisher: Elsevier]. *Current Biology*, *17*(6), 551–555. https://doi.org/10.1016/j.cub.2007.01.061

Gibbon, J. (1977). Scalar expectancy theory and weber's law in animal timing. *Psychol. Rev.*, *84*(3), 279–325.

Güntürkün, O., Ströckens, F., Scarf, D., & Colombo, M. (2017). Apes, feathered apes, and pigeons: Differences and similarities. *Current Opinion in Behavioral Sciences*, *16*, 35–40. https://doi.org/10.1016/j.cobeha.2017.03.003

Hampton, R. R., Zivin, A., & Murray, E. A. (2004). Rhesus monkeys (macaca mulatta) discriminate between knowing and not knowing and collect information as needed before acting. *Animal Cognition*, *7*(4), 239–246. https://doi.org/10.1007/s10071-004-0215-1

Hangya, B., Sanders, J. I., & Kepecs, A. (2016). A mathematical framework for statistical decision confidence [Publisher: Neural Comput]. *Neural computation*, *28*(9). https://doi.org/10.1162/NECO_a_00864

Hoffmann, A., Rüttler, V., & Nieder, A. (2011). Ontogeny of object permanence and object tracking in the carrion crow, *Corvus corone*. *Animal Behaviour*, *82*(2), 359–367. https://doi.org/10.1016/j.anbehav.2011.05.012

Inman, A., & Shettleworth, S. J. (1999). Detecting metamemory in nonverbal subjects: A test with pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *25*(3), 389–395. https://doi.org/10.1037/0097-7403.25.3.389

Jarvis, E. D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., Paxinos, G., Perkel, D. J., Shimizu, T., Striedter, G., Wild, J. M., Ball, G. F., Dugas-Ford, J., Durand, S. E., Hough, G. E., Husband, S., Kubikova, L., Lee, D. W., . . . Avian Brain Nomenclature Consortium. (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews. Neuroscience*, *6*(2), 151–159. https://doi.org/10.1038/nrn1606

Johnston, M., Brecht, K. F., & Nieder, A. (2023). Crows flexibly apply statistical inferences based on previous experience. *Current Biology*, *33*(15), 3238–3243.e3. https://doi.org/10.1016/j.cub.2023.06.023

Kepecs, A., & Mainen, Z. F. (2012). A computational framework for the study of confidence in humans and animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1594), 1322–1337. https://doi.org/10.1098/rstb.2012.0037

Kepecs, A., Uchida, N., Zariwala, H. A., & Mainen, Z. F. (2008). Neural correlates, computation and behavioural impact of decision confidence. *Nature*, *455*(7210), 227–231. https://doi.org/10.1038/nature07200

Kiani, R., & Shadlen, M. N. (2009). Representation of confidence associated with a decision by neurons in the parietal cortex. *Science*, *324*(5928), 759–764. https://doi.org/10.1126/science.1169405

Kirschhock, M. E., Ditz, H. M., & Nieder, A. (2021). Behavioral and neuronal representation of numerosity zero in the crow. *The Journal of Neuroscience*, *41*(22), 4889–4896. https://doi.org/10.1523/JNEUROSCI.0090-21.2021

Kirschhock, M. E., & Nieder, A. (2022). Number selective sensorimotor neurons in the crow translate perceived numerosity into number of actions [Publisher: Nature Publishing Group]. *Nature Communications*, *13*(1), 6913. https://doi.org/10.1038/s41467-022-34457-5

Kunimoto, C., Miller, J., & Pashler, H. (2001). Confidence and accuracy of near-threshold discrimination responses. *Consciousness and Cognition*, *10*(3), 294–340. https://doi.org/10.1006/ccog.2000.0494

Lak, A., Costa, G. M., Romberg, E., Koulakov, A. A., Mainen, Z. F., & Kepecs, A. (2014). Orbitofrontal cortex is required for optimal waiting based on decision confidence. *Neuron*, *84*(1), 190–201. https://doi.org/10.1016/j.neuron.2014.08.039

Lak, A., Hueske, E., Hirokawa, J., Masset, P., Ott, T., Urai, A. E., Donner, T. H., Carandini, M., Tonegawa, S., Uchida, N., & Kepecs, A. (2020). Reinforcement biases subsequent perceptual decisions when confidence is low, a widespread behavioral phenomenon. *eLife*, *9*, e49834. https://doi.org/10.7554/eLife.49834

Li, L., & Wang, D. (2021). Adaptive neurons compute confidence in a decision network [Publisher: Nature Publishing Group]. *Scientific Reports*, *11*(1), 22190. https://doi.org/10.1038/s41598-021-01523-9

Malapani, C., Rakitin, B., Levy, R., Meck, W. H., Deweer, B., Dubois, B., & Gibbon, J. (1998). Coupled temporal memories in parkinson's disease: A dopamine-related dysfunction. *J. Cogn. Neurosci.*, *10*(3), 316–331.

Malapani, C., & Fairhurst, S. (2002). Scalar timing in animals and humans. *Learn. Motiv.*, *33*(1), 156–176.

Masset, P., Ott, T., Lak, A., Hirokawa, J., & Kepecs, A. (2020). Behavior- and modality-general representation of confidence in orbitofrontal cortex. *Cell*, *182*(1), 112–126.e18. https://doi.org/10.1016/j.cell.2020.05.022

McNamara, J. M., & Houston, A. I. (1985). Optimal foraging and learning. *Journal of Theoretical Biology*, *117*(2), 231–249. https://doi.org/10.1016/S0022-5193(85)80219-8

Middlebrooks, P. G., & Sommer, M. A. (2012). Neuronal correlates of metacognition in primate frontal cortex. *Neuron*, *75*(3), 517–530. https://doi.org/10.1016/j.neuron.2012.05.028

Miyazaki, K., Miyazaki, K. W., & Doya, K. (2012). The role of serotonin in the regulation of patience and impulsivity. *Mol. Neurobiol.*, *45*(2), 213–224.

Miyazaki, K., Miyazaki, K. W., Sivori, G., Yamanaka, A., Tanaka, K. F., & Doya, K. (2020). Serotonergic projections to the orbitofrontal and medial prefrontal cortices differentially modulate waiting for future rewards. *Sci. Adv.*, *6*(48), eabc7246.

Miyazaki, K., Miyazaki, K. W., Yamanaka, A., Tokuda, T., Tanaka, K. F., & Doya, K. (2018). Reward probability and timing uncertainty alter the effect of dorsal raphe serotonin neurons on patience. *Nat. Commun.*, *9*(1).

Moll, F. W., & Nieder, A. (2014). The long and the short of it: Rule-based relative length discrimination in carrion crows, corvus corone. *Behavioural Processes*, *107*, 142–149. https://doi.org/10.1016/j.beproc.2014.08.009

Nakamura, N., Watanabe, S., Betsuyaku, T., & Fujita, K. (2011). Do birds (pigeons and bantams) know how confident they are of their perceptual decisions? *Anim Cogn*.

Nieder, A. (2018). Evolution of cognitive and neural solutions enabling numerosity judgements: Lessons from primates and corvids [Publisher: Royal Society]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1740), 20160514. https://doi.org/10.1098/rstb.2016.0514

Nieder, A., Wagener, L., & Rinnert, P. (2020). A neural correlate of sensory consciousness in a corvid bird [Publisher: American Association for the Advancement of Science]. *Science*, *369*(6511), 1626–1629. https://doi.org/10.1126/science.abb1447

Ott, T., Masset, P., & Kepecs, A. (2018). The neurobiology of confidence: From beliefs to neurons. *Cold Spring Harbor Symposia on Quantitative Biology*, *83*, 9–16. https://doi.org/10.1101/sqb.2018.83.038794

Persaud, N., McLeod, P., & Cowey, A. (2007). Post-decision wagering objectively measures awareness. *Nature Neuroscience*, *10*(2), 257–261. https://doi.org/10.1038/nn1840

Pouget, A., Drugowitsch, J., & Kepecs, A. (2016). Confidence and certainty: Distinct probabilistic quantities for different goals [Publisher: Nat Neurosci]. *Nature neuroscience*, *19*(3). https://doi.org/10.1038/nn.4240

Raby, C. R., Alexis, D. M., Dickinson, A., & Clayton, N. S. (2007). Planning for the future by western scrub-jays. *Nature*, *445*(7130), 919–921. https://doi.org/10.1038/nature05575

Roitman, J. D., & Shadlen, M. N. (2002). Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. *The Journal of Neuroscience*, *22*(21), 9475–9489. https://doi.org/10.1523/JNEUROSCI.22-21-09475.2002

Shadlen, M. N., & Newsome, W. T. (1996). Motion perception: Seeing and deciding. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(2), 628–633. Retrieved October 13, 2024, from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC40102/

Shettleworth, S. J., & Sutton, J. E. (2003). Animal metacognition? it's all in the methods. *Behavioral and Brain Sciences*, *26*(3), 353–354. https://doi.org/10.1017/S0140525X03380082

Smirnova, A., Zorina, Z., Obozova, T., & Wasserman, E. (2015). Crows spontaneously exhibit analogical reasoning [Publisher: Elsevier]. *Current Biology*, *25*(2), 256–260. https://doi.org/10.1016/j.cub.2014.11.063

Smith, J. D., Shields, W. E., Schull, J., & Washburn, D. A. (1997). The uncertain response in humans and animals. *Cognition*, *62*(1), 75–97. https://doi.org/10.1016/s0010-0277(96)00726-3

Smith, J. D., Couchman, J. J., & Beran, M. J. (2012). The highs and lows of theoretical interpretation in animal-metacognition research. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1594), 1297. https://doi.org/10.1098/rstb.2011.0366

Smith, J. D., Schull, J., Strote, J., McGee, K., Egnor, R., & Erb, L. (1995). The uncertain response in the bottlenosed dolphin (tursiops truncatus) [Place: US Publisher: American Psychological Association]. *Journal of Experimental Psychology: General*, *124*(4), 391–408. https://doi.org/10.1037/0096-3445.124.4.391

Smith, J. D., Shields, W. E., & Washburn, D. A. (2003). The comparative psychology of uncertainty monitoring and metacognition. *The Behavioral and Brain Sciences*, *26*(3), 317–339, discussion 340–373. https://doi.org/10.1017/s0140525x03000086

Sole, L., Shettleworth, S., & Bennett, P. (2003). Uncertainty in pigeons [Publisher: Psychon Bull Rev]. *Psychonomic bulletin & review*, *10*(3). https://doi.org/10.3758/bf03196540

Stephens, D. W., & Krebs, J. R. (1986). Risk-sensitive foraging. In *Foraging theory* (pp. 128–150, Vol. 1). Princeton University Press. Retrieved October 13, 2024, from http://www.jstor.org/stable/j.ctvs32s6b.10

Sutton, J. E., & Shettleworth, S. J. (2008). Memory without awareness: Pigeons do not show metamemory in delayed matching to sample.

Veit, L., Hartmann, K., & Nieder, A. (2014). Neuronal correlates of visual working memory in the corvid endbrain [Publisher: Society for Neuroscience]. *Journal of Neuroscience*, *34*(23), 7778–7786. https://doi.org/10.1523/JNEUROSCI.0612-14.2014

Veit, L., & Nieder, A. (2013). Abstract rule neurons in the endbrain support intelligent behaviour in corvid songbirds [Publisher: Nature Publishing Group]. *Nature Communications*, *4*(1), 2878. https://doi.org/10.1038/ncomms3878

Vickers, D. (2014). *Decision processes in visual perception*. Academic Press.

Wagener, L., & Nieder, A. (2017). Encoding of global visual motion in the nidopallium caudolaterale of behaving crows (D. Munoz, Ed.). *European Journal of Neuroscience*, *45*(2), 267–277. https://doi.org/10.1111/ejn.13430