Author:
Clark, Rosie

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The effect of probability and reward on saccadic and manual responses

The effect of probability and reward on saccadic and manual responses

By

Rosanne Clark

School of Experimental Psychology

University of Bristol

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Abstract

In exploration of the environment, intrinsic and extrinsic factors such as the probability and the reward value associated with stimuli can modulate behaviour. Response times are decreased to stimuli that are more rewarding or more likely to appear, and increased to those less rewarding or less likely. It is unclear how these effects interact and how similar the effects are across response modalities. In this thesis these effects were investigated first separately and then concurrently, and across both saccadic and manual responses. The effect of probability was found to be sensitive to the temporal features of the paradigm; an effect on manual responses was seen with longer inter-stimulus intervals (ISI), compared to the saccadic effect with shorter ISIs. The effect of reward was stronger in manual responses than saccadic responses – possibly a result of slower dopaminergic activation within the reward system. The temporal dynamics are postulated to be the reason there is no evidence for a correlation between saccadic and manual responses across the experiments. When manipulations of reward and probability were combined, the probability modulations dominated the effect on responses. It is suggested that this is due to the nature of probabilistic information being an intrinsic feature of the environment that is not affected by the individual observer utility or internal state. Furthermore, no effect of reward was found in healthy older adults with the same paradigm. No correlation between reward and probability effects across participants was found, suggesting that these factors affect different accumulators within a decision-making model framework. The paradigm developed in this thesis provides a feasible way in which to study reward and probability effects in Parkinson's patients with deep-brain stimulators to the subthalamic nucleus.

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Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

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CHAPTER 1

This thesis is about how the reward associated with a stimulus and the probability of a stimulus occurring in a particular place affects behaviour.

In order to support survival, animal behaviour should not be random but rather should be shaped by properties of the animal's environment and by the goals of the animal. One way to operationalise the 'goals' of the animal is to study the reward associated with a particular response. The reward is not an intrinsic property of the environment but rather is a combined property of the environment and the organism, after all a stimulus does not have a reward associated with it if there is no organism. However some properties of the environment exist independent of the presence of the organism: they are a physical property of the environment. One such example is the probability of a stimulus being in a particular place. Despite these two types of information being very different they must be combined and coordinated to shape action. To illustrate this imagine the task faced by honey bees (*Apis mellifera*) hunting for a new nest. Nest-site scouts will search for a potential new nest in different patches of the environment (Seeley et al., 2012). Two distinct factors affect the scout's chances of being able to find a new nest site and recruit the rest of the swarm. First, the probability of there being a place to nest at all in a particular patch is intrinsic to the environment, regardless of whether the scout investigates the area. Prior knowledge of the probability could be gained from other nest-site scouts recruiting to the swarm, or from previous visits to the area. Second, once a potential nest has been found the reward and quality associated with the nest site is ascertained by the scout. But this factor is not intrinsic to the environment: it depends on the attributes deemed most rewarding to the bee and is relative to the previous nest sites encountered. Additionally, when the nest-scout returns to advertise their potential nest site to the rest of the swarm by means of the waggle dance, the rewarding attributes of the nest site conveyed in the

dance could be judged relatively to the nest sites being advertised by other scouts (Seeley et al., 2012). As a result, in searching for a new nest-site a scout has to combine information about the probability of there being a potential nest-site in an area and the rewarding attributes of the nest-site or the area it is located in. This is important in terms of reducing the amount of time and energetic cost associated with the search.

In this thesis I investigate these issues using simple visual stimuli and simple manual and eye movement responses in humans. In a series of experiments I investigate the effect of probability on both manual and saccadic responses and then I investigate the effect of reward on manual and saccadic responses. In a final experimental chapter I investigate how these two factors interact. This introductory chapter follows this same format. In the first section I discuss the previous literature on probability effects. In the second section I discuss effects of reward and in a final section I discuss the neural basis of these effects with a particular focus on Parkinson's disease, as one of the aims of this thesis was to develop a paradigm that would be suitable for testing this particular population.

1.1 Probability

1.1.1 Saccades

Humans (and other animals) make eye movements to stabilise the retinal image or to point the fovea (the primary axis of the eye) to a region of 'interest' (Gilchrist, 2011). Retinal stability is maintained by the vestibulo-ocular reflex which moves the eye to compensate for head movements (Gilchrist, 2011). One class of movements made by the eye are saccades, where the eye jumps to point the fovea to a region of 'interest' (Gilchrist, 2011). There is a dramatic reduction in visual ability at locations away from the fovea so saccadic eye

movements are made very frequently across a wide range of tasks (Gilchrist, 2011). The metabolic costs of making saccadic eye movements frequently are low, due to their being generated by six extraocular muscles and the eyeball being light and mobile: thus the costs are balanced by the benefits of minimal time to make saccades and maximising the number of fixation locations (Gilchrist, 2011). There are additional costs associated with moving the head rather than the eyes, so the frequent use of saccades may be optimal for the visual system (Gilchrist, 2011).

One way to conceptualise this saccadic behaviour is as a decision-making process, which can be regarded as an internal process which produces behaviour that manifests in the motor output of a human or animal (Ludwig, 2011). In the case of saccades in response to sensory stimulation, the eye movement response may be direct (e.g. in a visually guided saccade task) or more arbitrary and symbolic (Ludwig, 2011). Whatever the complexity of the sensory-motor mapping, we make decisions to move the eyes and where/when to move them (Ludwig, 2011). One of the primary parameters of saccades is the latency: the time taken to initiate a saccade. Often in experimental studies this is taken to be the time between the onset of the event being responded to (e.g. appearance of a target) and the start of the eye movement in response (Gilchrist, 2011). Studying saccade latencies is useful tool to study saccadic decision-making as they can be thought of as a composite of the time to process the visual stimulus, the accumulation of a decision process, and the final motor execution (Gilchrist, 2011). The affect of modulating several decision-related variables (such as strength of sensory evidence, prior probability and reward value) can be manifested in the saccadic latencies. However, even when the stimulus and response are constant, latencies vary on a trial-by-trial level (Gilchrist, 2011; Ludwig, 2011).

1.1.2 Saccades and attention

Saccadic eye movements are important for directing the eye to an area in the environment, and are therefore tightly coupled to the cognitive necessity to improve the processing of sensory information from a specific location in space. More generally this process of improving the processing of some part of the sensory information is known as spatial attention and is one of the cornerstone processes of psychology (James, 1890; Posner, 1980). The relationship between attention generally and saccadic eye movements specifically remains controversial (Kristjánsson, 2011), however, in normal behaviour the two are clearly linked. This link is perhaps most strongly argued for in the 'premotor theory of attention' which postulates that spatial attention does not result from a dedicated control mechanism, but comes from a weaker activation of the same frontal-parietal circuits that determine motor behaviour toward specific spatial locations (Rizzolatti & Craighero, 2010). Support for this position comes from experiments showing that when unexpected imperative stimuli were located in the opposite hemifield to where attention was located, reaction times were longer than when attention and the stimuli were in the same hemifield (Rizzolatti & Craighero, 2010). This so called 'meridian effect', can be easily accounted for by the premotor theory of attention: attention derives from preparation to move the eyes towards the cued location and reprogramming an eye movement is more complex than reprogramming an eye movement in the same hemifield (Rizzolatti & Craighero, 2010). Evidence for a causal relationship between eye movements and attention was further corroborated by experiments with individuals who could not make saccades towards a cued position because of a constrained extreme eye deviation or a peripheral palsy (Rizzolatti & Craighero, 2010). The modification in the eye movement abilities were paralleled by a modification in the ability to orient visuospatial attention; when the eyes cannot move to a particular location the attention cannot shift either (Rizzolatti & Craighero, 2010).

1.1.3 Saccades and Hicks Law

The uncertainty of where we need to attend and move our eyes to in the environment is increased by the number of possible locations there are. This is formalised in Hick's law which states that manual reaction times increase logarithmically with the number of alternative stimuli (Hick, 1952). This effect has been found in saccadic reaction times but only when there is a transformation between the stimulus and the response (Kveraga, Boucher,& Hughes, 2002; Lee, Keller, & Heinen, 2005; Ludwig, 2011). In an experiment by Kveraga et al. (2002), they found only antisaccades (saccades directed away from a target) and not prosaccades (directed towards a target) followed Hick's law. This finding suggests that saccades made under response uncertainty must not require the process of response selection (Kveraga et al., 2002). However, Lee and colleagues (2005) argued that the task used in this experiment was not similar to that used by Hick and others where a particular key on a keyboard was associated with the location of a particular visual stimulus, requiring a stimulus-response transformation. They found that Hick's law held in their experiment where participants were required to make a saccade to the remembered location of a visual target whose colour was specified by a central cue, thus requiring a stimulus-response transformation (Lee et al., 2005).

1.1.4 Saccades and target probability

In addition to the number of possible alternative stimuli in our environment changing, the relative probability of those alternatives occurring can also change. A non-saccadic example of this would be in the framework of receiving a medical diagnosis, where the various alternative causes for a set of symptoms are each associated with relative probabilities of those causes (Ludwig, 2011). This is formalised in Bayes' rule, which combines the current evidence (likelihood) with the prior probability of some event (Ludwig, 2011). In the same way that the

number of alternatives can affect behaviour, the probabilities also have an effect. Lamb and Kaufman (1965) found that Hick's law does not hold for unequally likely alternatives and across different response modalities it has been demonstrated that more frequently occurring stimuli are responded to faster (Carpenter & Williams, 1995; Kaufman & Levy, 1966; Lamb & Kaufman, 1965; Mowbray, 1964). The probability effect is particularly well established for a saccadic response (Basso & Wurtz, 1997; Carpenter & Williams, 1995; Dorris & Munoz, 1998; Jóhannesson, Haraldsson, & Kristjánsson, 2013; Koval, Ford, & Everling, 2004; Liu et al., 2010, 2011; Noorani & Carpenter, 2013). For example, it has been shown that for two target locations, decreasing the prior probability of a target occurring in a location increases the saccadic reaction time (Carpenter & Williams, 1995). This experiment was conducted using a range of relative probabilities from .95 to .05, and a linear relationship was found between the logarithm of the prior probability and the median saccadic response times. As is common in psychophysical experiments, data were collected from only two participants with very large numbers of trials. Additionally, it should be noted that the effect of prior probability on saccadic response times was not instantaneous; Carpenter and Williams (1995) reported hours of practice for the participants in the experiment before the modulations in saccadic reaction time were complete and stable.

1.1.5 Complex studies of probability effect

A number of studies further investigated the probability effect with more complex tasks. It has been found that both absolute and relative target position are affected by probability manipulations (Miller, 1998). For a spatially occurring visual target, Miller (1998) found that a change in both relative and absolute target position produced the same effect of the probability of alternatives, where one location in a sequence of four letters had a higher

probability of containing the target letter, and the sequence itself was occasionally offset (Liu et al., 2010). Several studies have used a pro and antisaccade task alongside a probability manipulation (Koval et al., 2004; Liu et al., 2010). In a prosaccade task, participants are told to look from a fixation point to a target as soon as it appears. In contrast in an antisaccade task participants are asked to look in the opposite direction from the stimulus, suppressing the automatic response of looking towards it (Munoz & Everling, 2004; Noorani & Carpenter, 2013). Antisaccades have longer latencies, are prone to errors, and may employ different cognitive processes. This combination of effects has been referred to as the antisaccade cost (Liu et al., 2010). Although the probability effect was documented in these studies in the prosaccade conditions, it was not seen in the antisaccade conditions (Koval et al., 2004; Liu et al., 2010). In Koval and colleagues (2004) study, more prosaccade errors were made when the participant was required to make an antisaccade away from the high probability location, supporting the hypothesis that errors in antisaccade tasks are a result of an increased level of motor preparation. However, Liu and colleagues (2010) found that the antisaccade cost was only present in antisaccades away from the high probability location. They proposed that higher location probability demands more attention, creating increased difficulty in inhibiting the automatic prosaccades (Liu et al., 2010). This also provides an explanation as to why prosaccades to lower probability locations take longer to be executed. Researchers have argued that inhibition plays a crucial role in the suppression of a prosaccade in an antisaccade task (Everling & Fischer, 1998; Liu et al., 2010). It should be noted however that Liu and colleagues' (2010) task was not a typical antisaccade task but involved target uncertainty; the correct location had to be determined with an odd-one-out visual search task (Jóhannesson et al., 2013).

It is interesting that parallels have been drawn between the influence of prior probability and spatial attention (Liu et al., 2010). Prior probability can be categorised as a form of

expectation, which facilitates visual perception by biasing interpretation on the basis of known probabilistic information (Summerfield & Egner, 2009). Learned perceptual expectation about the environment such as spatial probability can guide attention towards a likely location of a relevant item, and the violation of expectation can be employed as a signal for attracting attention towards a potentially significant event (Summerfield & Egner, 2009). This often means that expectation and attention interact, and generally the behavioural effects of expectation and attention are similar; both attended and expected stimuli are detected and recognised more readily than unexpected or unattended (Summerfield & Egner, 2009). It is important to note however, that these similarities are not reflected in the neural activity in visual regions representing the stimulus, suggesting that despite interaction they are still governed by different processes (Summerfield & Egner, 2009). This will be further explored later in this introduction.

1.1.6 Cueing

One of the primary behavioural tasks used for measuring shifts in attention is also related to the effects of prior probability: the Posner cueing task. This task involves the use of a cue to attract participants' attention to a location in space that contains a response target (Hayward & Ristic, 2013; Posner, 1980). It has been found that participant responses are faster when the cue indicates the side that the target is then presented on (Druker & Anderson, 2010). This has been called 'probabilistic cueing', as it is providing information about the likelihood of the target appearing in a certain spatial location on a trial-by-trial basis (Druker & Anderson, 2010). These experiments involving cues constitute another temporal probability effect similar to that seen in simpler paradigms such as Carpenter and Williams' (1995) study. Traditionally 80% of the cues are valid and 20% of the cues are invalid; in effect this is very similar to a

simple probability manipulation of two targets either side of fixation being associated with 0.8 and 0.2 prior probability (Posner, 1980). However, it is possible that the effect of probability is more local than global in paradigms where a cue is provided on a trial-by-trial basis.

This leads to the consideration of generally whether the probability effect is a short-term process updated on the basis of recent sensory information, or is a long-term global process that happens over the course of experiments (Druker & Anderson, 2010; Walthew & Gilchrist, 2006). Sometimes even without manipulations of prior probability, humans (Anderson, Yadav & Carpenter, 2008; Carpenter, 2001) and monkeys (Fecteau & Munoz, 2003) develop idiosyncratic motor biases to favour a particular response (Ludwig, 2011). For example, in Anderson et al. (2008) it is a preference for successive movements in the same direction (Ludwig, 2011). However, this can be interpreted as internally generated and misguided estimates of prior probability (Ludwig, 2011). Walthew and Gilchrist (2006) suggested that the search benefits for more probable locations resulted from short-term target location repetitions ('repetition priming'), rather than learning of a spatial probability distribution (Druker & Anderson, 2010). They showed that when short-term target repetitions were restricted, there was no statistical learning effect (Druker & Anderson, 2010; Walthew & Gilchrist, 2006). However, Druker & Anderson (2010) found that if targets were near previous target locations (repetition priming) then responses were faster, and if they were near a high-probability region (probability cueing) then responses were also faster. They used probability distributions that were continuous across the display rather than a few arbitrary locations, thus producing fewer spatial repeats and allowing dissociation between the effects of high-probability location from that of repetition priming (Druker & Anderson, 2010). This suggests that statistical learning about the probabilities of stimuli can produce the probability effect, and this is supported by Liu (2010) and colleagues who showed that the probability effect was not simply repetition

priming but rather suggested that it was due to a long-term global process accumulating across trials.

1.1.7 Robustness of these probability effects

Despite being well established in the literature, there has been some discussion over whether the probability effect seen in some of the aforementioned studies is a reliable and robust effect. Jóhannesson and colleagues (2013) found no effects of probability on several simple pro and antisaccade tasks, and they only found a probability effect in more complex tasks when decisions based on visual search had to be made. Thus they hypothesised that probability manipulations affect the time taken to discern which stimulus is the target and which saccade type should be made, rather than a global effect on saccadic latency (Jóhannesson et al., 2013). This is supported by the observation that the task in Liu and colleagues (2010) experiment where probability effects on antisaccade cost were found was not a typical antisaccade task but involved target uncertainty (Jóhannesson et al., 2013).

1.1.8 Probability and manual reaction times

In humans, manual responses are also ubiquitously used to study behaviour, for example the in the previous discussion of Hick's Law where manual reaction times increase logarithmically with the number of alternative stimuli (Hick, 1952). Much of the early literature showing the probability effect was conducted using manual responses: collecting data from simple button press responses is straightforward and effective (Kaufman & Levy, 1966; Lamb and Kaufman, 1965; Mowbray, 1964). However, given that many studies investigating the effect of prior probability on behaviour focus on either saccadic or manual responses, it is

important to address how far the results can be generalised by examining how similar these processes are and how they might interact.

The premotor theory of attention postulates that processes involved in spatial attention and selection of motor responses share a common neural substrate (Eimer, Van Velzen, Gherri & Press, 2006; Rizzolatti, Riggio & Sheliga, 1994). It suggests that response-induced attentional shifts would be initiated both in the oculomotor system and when hand movements are being prepared (Eimer et al., 2006; Rizzolatti et al., 1994). Decision-making models for visuomotor behaviour generally propose that a visual event produces an internal response, rising with time until a decision threshold is reached and a motor response is initiated (Bompas & Sumner, 2008). From the pre-motor theory of attention, it could be postulated that a common source of information is used for all types of motor responses and that the same decision threshold would apply to all responses: response time would then be the sum of stimulus processing time and motor latency where the latter is the only source of difference between response types (Bompas & Sumner, 2008).

However, behavioural data from both response modalities are needed to investigate the support for this theory. There have been some studies that directly compare responses to stimuli across the two modalities. Some of these studies have shown support for this theory, for example Taylor, Carpenter and Anderson (2006) found similar parameters in manual and saccadic response times for visual processing of contrast, supporting a common target detection stage preceding each type of reaction. However, there is not a clear result across the scope of the literature. A classic debate in the literature concerns the relationship between motor and perceptual responses, rather than specifically saccadic responses (Bompas & Sumner, 2008; Tappe, Niepel & Neumann, 1994). One particular study by Tappe and colleagues (1994) compared a temporal order judgement task (TOJ) with a simple manual reaction time task. The TOJ task involved the participants lifting their index finger on either hand from two sensor

surfaces to indicate which stimulus they had perceived as the first one (Tappe et al., 1994). These types of task have been traditionally regarded as a valid measure for visual latency, as it refers to an event that is purely visual (until subjective sensation is generated) whereas reaction time tasks encompasses decision and motor processes in addition to sensory processing (Tappe et al., 1994). They found that TOJ responses were less affected than direct manual reaction times by spatial frequency of stimuli, leading to the conclusion that motor and perceptual responses share only partial processing (Bompas & Sumner, 2008; Tappe et al., 1994). Research by Bompas and Sumner (2008) partially supports these differences between processes, but specifically investigating manual and saccadic reaction times. They found that the difference in reaction times to S-cone (blue cone) and luminance signals was larger for saccade latencies than for manual responses (Bompas & Sumner, 2008). This could suggest that saccadic responses can take better advantage of fast signals when they are available (Bompas & Sumner, 2008). This result is not compatible with the suggestion in Taylor et al. (2006) that the same target detection stage is used for manual and saccadic responses, but a less parsimonious decision-making model could maintain the hypothesis of a common collector stage where signals across all pathways are brought together but have different decision thresholds for different responses (Bompas & Sumner, 2008). However, aspects of their results violate other predictions proposed by this kind of model: for example, they found no evidence for a correlation between saccadic and manual reaction times, which would be expected if they both relied on the same combination of signals (Bompas & Sumner, 2008). Together these results suggest a more complex explanation beyond the premotor theory of attention for the similarities and differences between manual and saccadic responses, but do provide a strong rational for further investigation in this area.

1.2 Reward

Rewards of different forms are an important motivation for the decisions we make in our lives. Given that rewards can be presented in various ways for multiple options, our brain has to integrate and compare rewards to come to a decision associated with the highest subjective value (Dreher & Tremblay, 2009). Rewards can differ in their form and are often grouped into the categories of primary (e.g. food, liquid) and secondary rewards (e.g. money) (Dreher & Tremblay, 2009). There can also be differences in reward attributes: often we have to trade off magnitude of reward, delay in receiving reward, and the probability of receiving the reward (Dreher & Tremblay, 2009).

Reward is fundamental to motivation, learning and decision-making; scientists have used behavioural techniques, neuroimaging and electrophysiological recordings to begin to understand the mechanisms underlying reward processing and how it affects different areas of cognition (Dreher & Tremblay, 2009). The network identified within the brain is described as the reward system, involving dopaminergic midbrain neurons, the ventral striatum, the prefrontal cortex, and the amygdala (Dreher & Tremblay, 2009). Electrophysiological data in monkeys has shown that dopaminergic neurons carry information about two parameters of reward: a reward prediction error signal (difference between expected and delivered reward) and a signal covarying with reward uncertainty (Dreher & Tremblay, 2009). This system is crucial in an unstable world as an important aspect of maximising reward in learning and tracking which options will be more profitable and how those payoffs change over time. Understanding of this system has partly arisen from neurological and psychiatric disorders (e.g. schizophrenia, Parkinson's disease, drug addiction) where processing of reward is dysfunctional (Dreher & Tremblay, 2009). The neurological basis of reward will be discussed in more detail later in this introduction.

There are different ways in which rewards can be associated with stimuli and the actions that are required to obtain them. Some of the earlier studies of reward focus on classical (Pavlovian) conditioning, where the rewarding outcome follows the conditioned stimulus regardless of the behavioural reaction; over time a representation of the outcome is evoked by the stimulus and elicits a behavioural reaction (Schultz, 2006). In contrast, studies of instrumental conditioning require the subject to execute a behavioural response to obtain the reward (Schultz, 2006). This reinforces stimulus-response links and allows participants to influence their environment and determine the rate of reward (Schultz, 2006). This theory supports the frequent use of performance-based (or at least directly task related) incentives in more recent paradigms investigating processing of reward.

1.2.1 Reward effect on reaction times

One way in which reward can affect behaviour is by modulating the time taken to respond to different stimuli in the environment. Optimisation of the reward we receive may involve diverting attentional resources to more highly rewarding stimuli, and under time constraints these same resources should be applied to those stimuli most likely to yield reward. This could manifest itself in how long we spend attending to more highly rewarding or more likely rewarding stimuli, or how quickly we react to it reappearing in our environment relative to other stimuli.

Several studies have investigated the effect of reward value on response latencies in different modalities, both in primates and human participants (Bendiksby & Platt 2006; Takikawa, Kawagoe, Itoh, Nakahara & Hikosaka, 2002; Hickey & van Zoest, 2012; Lucas et al., 2013). Experimental data from primates has shown that mean saccadic latency was shorter in rewarded trials than in non-rewarded, in a task with four possible stimuli locations

(Takikawa et al., 2002). Furthermore, error trials were higher when the monkey was not rewarded, suggesting a higher motivational state when rewarded, and longer latencies were seen in non-rewarded trials shortly after a rewarded trial (Takikawa et al., 2002). This suggests a local process governing non-stationary reward processing, such that the reward value of the current trial (and therefore reaction time) is affected by the previous trials.

Yamamoto, Kim and Hikosaka (2013) found that after training monkeys on a set of fractal objects, half of which were associated with high reward and the other with low reward, a gaze bias was developed. Even after reward was no longer delivered with the presentation of an object, first saccades were made to the highest value object and then to other high valued objects sequentially, generally avoiding fixating low valued objects (Yamamoto et al., 2013). Additionally, the objects associated with higher reward were fixated for longer than the lower valued objects (Yamamoto et al., 2013). In another primate study, Kawagoe, Takikawa and Hikosaka (1998) used a memory guided saccade task where the monkeys were required to make saccades to a remembered cue location. They found that latencies were shorter and peak velocities higher when saccades were followed by a reward than when they were not (Kawagoe et al., 1998). Saccades to the rewarded direction were also more accurate than those to the non-rewarded locations; the frequency of error saccades were higher in the non-rewarded trials (Kawagoe et al., 1998). Research by Bendiksby and Platt (2006) has shown that increasing the magnitude of reward in blocks in a peripherally-cued saccade task decreases saccadic reaction times. These studies suggest that reward has an effect on several parameters of saccades (latency, velocity), the accuracy of saccadic responses, and oculomotor capture. They also suggest that the global magnitude of reward available within the experiment has an effect on behaviour as well as the relative rewards across different options.

In human behavioural research, a visual search task was conducted where the participants had to orient to a target above or below a central fixation point, ignoring a salient distracter

presented slightly to left/right of the direct path between fixation and target (Hickey & van Zoest, 2012). Participants received a random reward magnitude for a correct response; when the distracter was associated with a rewarding outcome, it drew fast target-directed eye movements during saccadic flight, made target directed saccades generally slower and was more likely to capture the eyes to its location (Hickey & van Zoest, 2012).

Other studies with human participants have focused on manual responses rather than saccadic. Anderson, Laurent and Yantis (2011a) conducted experiments where the colour of the targets (red/green) signified high and low reward: high-reward targets were followed by high-reward on 80% of the trials and low reward on 20%, with the percentages reversed for low reward targets (Anderson et al., 2011a). They found that non-salient, task-irrelevant coloured stimuli previously associated with reward capture attention involuntarily as a consequence of reward learning (Anderson et al., 2011a). Slowing of response times during visual search is prolonged when a target appears in a location occupied by a high value distracter on the previous trial (Anderson et al., 2011a). This finding highlights the spatial component of the reward effect, and suggests that the subsequent act of disengagement leaves an inhibitory trace at the given spatial location (Anderson et al., 2011a). Further studies have extended these findings to show that the higher the magnitude of reward previously associated with a task-irrelevant distracter, the slower the visual search to the target (Anderson et al., 2011b). Additionally, there was a trend in the training phase towards faster responses to higher rewarded stimuli (Anderson et al., 2011b). Together these studies in human participants have focused mainly on attentional processes, and suggest a stronger effect of reward on oculomotor capture and attention rather than saccadic or manual response times. Recent work by Dunne, Ellison and Smith (2015) however, suggests a significant facilitation of saccadic reaction times for eye-movements directed to a rewarded location in human participants, and a persistence of this effect for a short period of time after removal of rewards. They demonstrated that this

modulation of the oculomotor system does not extend to untrained tasks (exogenous attention and IOR), suggesting that it is possible to modulate the oculomotor system without affecting covert attention (Dunne et al., 2015).

1.2.2 Attention and salience

Many studies investigating the effect of reward on behaviour have addressed the effect of reward on the salience of objects and on attentional capture (Anderson et al., 2011a, 2011b; Dunne et al., 2015; Hickey & van Zoest, 2012; Theeuwes & Belopolsky, 2012). Generally these experiments have explored the modality of eye movements, as there is a tight coupling between saccadic eye movements and shifts of spatial attention (Theeuwes & Belopolsky, 2012). Attentional mechanisms within the brain influence visual selection by prioritising one location in the visual field for perceptual enhancement or saccade planning (Markowitz, Shewcraft, Wong & Pesaran, 2011). Giving attentional priority to visual targets during selection is important as the visual field is constantly changing (Markowitz et al, 2011). Two processes drive visual selection in the oculomotor system: the first is sensory driven exogenous ("bottom-up") attention which can be automatic and can result in the capture of attention by salient distracters (Markowitz et al., 2011). The second is goal-driven endogenous ("top-down") attention which is voluntary and supports the monitoring of peripheral targets or locations and can be based on previous experience (Markowitz et al., 2011). The interaction of these two processes was studied by Markowitz and colleagues (2011) in rhesus macaque monkeys (*Macaca mulatta*) by manipulating both the relative luminance and reward values of two targets. The monkeys performed eye movements for liquid rewards in a two alternative forced choice paradigm (Markowitz et al., 2011). They found that exogenous and endogenous attention changed linearly as a function of time after stimulus onset, whereby fast reaction times lead to stronger sensory-driven bias, and slow reaction times lead to stronger goal-driven

attentional bias (Markowitz et al., 2011). This may be because for monkeys to make a choice in each trial they have to integrate information about the luminance and reward values, perhaps by converting these into a "common currency" (Markowitz et al., 2011). Early on in a trial, subjective value of choosing the bright target is highly driven by exogenous attention, and over time endogenous attention increases weighting on the high reward magnitude target (Markowitz et al., 2011).

Furthermore, other studies on the effect of reward on exogenous and endogenous attentional processes have suggested that associating reward with a stimulus can actually alter the salience of a stimulus (above and beyond its physical salience) in such a way that it can capture the eyes and disrupt ongoing goal-directed behaviour (Theeuwes & Belopolsky, 2012). They found that this effect was even sensitive to a modulation in the magnitude of the reward previously associated with the target (Theeuwes & Belopolsky, 2012). This is supported by the work of Anderson and colleagues (2011a, 2011b) using manual reaction times where they show similar effects of reward on attentional capture. Their results showed that participants took longer to find the target in a visual search task when a distracter previously associated with high reward was present relative to a distracter associated with low reward (Anderson et al., 2011a, 2011b; Theeuwes & Belopolsky, 2012).

It could be conjectured that the learned value of the stimulus may not have actually adjusted the attentional capture but may purely have increased to the time it takes to disengage attention from distracter stimulus after attention has been captured ('attentional dwell time') (Anderson et al., 2011b; Theeuwes & Belopolsky, 2012). However, Theeuwes and Belopolsky's (2012) findings in eye movements suggest that as there were no differences of learned value on fixation durations following oculomotor capture, the time it takes to disengage the eyes does not have a significant role in the effects of reward. Together these results show that stimuli associated with reward capture the eyes, slow manual responses and thus disrupt

goal-directed behaviour; this suggests the effect of reward is automatic and not driven by strategic, top-down control (Theeuwes & Belopolsky, 2012).

A theme across these studies in the idea that different signals from different sources (reward, perceptual salience etc.) converge in a common map to shape behaviour. Such a common *Priority map* (Fecteau & Munoz, 2006) provides a key mechanism by which signals about the importance of stimuli, such as reward value, can be coded in a common currency and lead to coordinated behaviour.

1.2.3 Primary and Secondary rewards

In the reward literature there are different definitions and opinions of what constitutes a sufficiently motivating reward. Generally monetary rewards are delivered in experiments with human participants, and appetitive rewards (i.e. juice) are given to non-human primates. Monetary rewards are defined as secondary rewards, whereas juice/water is a primary reward as it is a physiological requirement (Lamy, 2007). The assumption is that reward systems for physiological needs (primary rewards) may have adapted to process more abstract rewards such as money (secondary rewards) (McClure, Ericson, Laibson, Loewenstein & Cohen, 2007; cited in Lamy, 2007). The neurological and behavioural differences between receiving primary and secondary rewards have been studied partly to address whether parallels can be drawn between reward experiments on monkeys and humans. Some studies have actually directly compared primary and secondary rewards in human participants, with experiments using both monetary rewards and juice/water (McClure et al., 2007). These experiments often utilise paradigms involving delay discounting, which is the common finding that the value of a given reward declines with increasing delay in receiving the reward (Johnson & Bickel, 2002). In the framework of delay discounting, it has been found that primary rewards are less susceptible to

contextual framing than secondary rewards, meaning therefore that they have more rapid, stable temporal characteristics (McClure et al., 2007; cited in Lamy, 2007). This suggests that one main difference between primary reward and secondary rewards is that discounting is less susceptible to contextual factors and more related to internal states (satiety and temperature) (McClure et al., 2007; cited in Lamy, 2007). However, similar activation of brain regions in the delay discounting task using fMRI was found for both primary and secondary rewards (McClure et al., 2007).

Other methods of engaging the reward system in behavioural experiments have been explored, with some researchers focusing on abstract positive feedback as a proxy for primary or secondary rewards; it has been shown that this can activate the same brain structures as primary rewards (Ullsperger & Von Cramon, 2003). There is support for the use of hypothetical rewards in delay discounting research, where no systematic difference was found in discount rate between real and hypothetical monetary rewards (Johnson & Bickel, 2002). However, this may be specific to the delay discounting research, and not generalisable across other reward based paradigms.

1.2.4 Reward and punishment

It could be argued that if addressing the effect of reward associated with stimuli, the most interesting contrast to investigate might be between a highly rewarded stimulus and a stimulus associated with loss of reward/punishment. However, it has been postulated that rewards and punishments represent opponent processes and are unlikely to be governed by a common substrate (Schultz, Dayan, & Montague, 1997). In the decision-making literature the theory of negativity bias (Taylor, 1991; cited in Wächter, Lungu, Liu, Willingham & Ashe, 2009) suggests that motivation would be stronger when people are punished rather than rewarded, but behavioural experiments suggest this is not the case. A study by Wächter et al. (2009)

investigating the effect of reward and punishment on procedural learning in a serial reaction time task (SRT) found support for this theory behaviourally. They looked specifically at procedural learning as it is the foundation of many motor skills and arguably other forms of learning (Squire, 2004; cited in Wächter et al., 2009); procedural learning is also thought to be dependent on the basal ganglia which mediates the effect of reward and punishment (Wächter et al., 2009). Individual reaction time criteria were established for each participant after a test block: one group of participants were rewarded for fast responses, one group punished for responses slower than the criterion, and a final control group were not rewarded or punished for desired/undesired behaviour (Wächter et al., 2009). Reward and punishment were categorised as monetary gain and loss respectively. Learning the sequence of stimuli in the task enabled the participants to reduce their reaction time, therefore the procedural learning was linked to the reward/punishment delivered (Wächter et al., 2009). They found that only the reward group showed enhanced implicit learning of the motor sequence; the punishment group did not learn any better than the control participants (Wächter et al., 2009). This suggests that reward and punishment may be governed by different motivational systems.

1.2.5 Probability, Magnitude and Expected value of Reward

The reward value associated with a stimulus can differ in several ways. For example, the probability, magnitude or the expected value of reward received can be manipulated. The expected value of future rewards is the sum of possible reward magnitudes where each is weighted by its probability (Tobler, Fiorillo & Schultz, 2005). Milstein and Dorris (2011) found reward magnitude to have a stronger effect on choice and saccadic reaction times in non-human primates than reward probability, and that expressing reward as expected value had a greater effect than either measure separately. They observed that reward probability only had

an effect on saccadic reaction times when the magnitude of reward was similar across stimuli (Milstein & Dorris, 2011). It is logical that expected value would have the strongest effect on behaviour, as making decisions based on expected value maximises reward intake over time (Milstein & Dorris, 2007). However, the difference observed between the effect of reward magnitude and probability could be very specific to studying non-human primates, due to the fact that monkeys were given reward immediately after each trial rather than later in the experiment as in human economic experiments (Milstein & Dorris, 2011). Additionally, the nature of a probability manipulation in these paradigms means that the distribution has to be experienced and updated over the course of the experiment; in comparison, gaining information about the reward magnitude is more instantaneous even in human studies (Milstein & Dorris, 2011).

1.2.6 Reward Context

Understanding the effect of reward on saccadic and manual reaction times requires exploring whether it is the absolute or relative value of each reward stimulus that elicits the effect. In the economic literature, prospect theory posits that value (or utility) of an action is relative to the other available options (Kahneman & Tversky, 1979). Neurological experiments in nonhuman primates have shown absolute value of reward to influence decision-making by increasing global motivation: the more reward available overall, the more motivation to respond (Roesch & Olson, 2004; cited in Milstein and Dorris 2011). However, it is important to note that this research deployed primary rewards (juice) rather than the secondary rewards used in the economic literature. In an experiment with rhesus monkeys, Milstein and Dorris (2011) found that motivation, defined as the average reward per trial, had no effect on saccadic reaction times: when the reward magnitudes were 1x, 1.5x and 2x their initial amount, the SRTs were unchanged. The relative expected subjective value of a stimulus compared to other stimuli

had a large effect (Milstein & Dorris, 2011). This is supported by their work in humans demonstrating that saccade preparation is spatially allocated based on the relative value of potential targets (Milstein & Dorris, 2007, 2011). Allocating time and resources towards more profitable options relative to others may be more adaptive than being globally motivated by the prospect of reward.

1.2.7 Time course of reward effect

An additional parameter of the reward effect is the time course of its persistence. Learning about the rewarding characteristics of the environment could have an evolutionary advantage when revisiting a specific area, and this may persist even after the properties of the environment have changed. Theeuwes and Belopolsky (2012) found that more saccades were made to a task-irrelevant stimulus that was associated with high monetary reward than to the low reward distracters. Crucially, they found that the high rewarded distracters continued to increase exogenous capture of the eyes even after the stimulus no longer predicted reward (Theeuwes & Belopolsky, 2012). This suggests a long-term global mechanism governing attentional processes related to reward, indicating a need for relative consistency of reward values within behavioural experiments investigating this phenomena. Other studies have supported this finding in different response modalities, for example Stankevich and Geng (2015) found that a stimulus feature (colour) paired with reward produced an attentional bias towards the rewarded colour, indexed by manual reaction time (Dunne et al., 2015). The magnitude of the effect was reduced but not extinguished when rewards were removed from the task; this result suggests that rewards have a long-term effect on exogenous capture (Stankevich & Geng, 2015). There has been some investigation into whether the persistence of the effect of reward on learning in the oculomotor system transfers to other cognitive tasks (Dunne et al., 2015). This is an interesting area for discussion as there is a possibility that

rewards can be used to help patients with brain injuries to compensate for neuropsychological problems (Dunne et al., 2015). There is evidence for patients with spatial neglect that asymmetric reward distribution in space can bias visual exploration and target selection towards the neglected hemisphere (Lucas et al., 2013). However, although it has been found that facilitation of saccadic reaction times towards rewarded locations persist for some time after the removal of rewards, this does not transfer to untrained tasks that engage the oculomotor system (exogenous attentional orienting and IOR) (Dunne et al., 2015).

1.3 Probability and reward

1.3.1 Modelling reward and probability effects

In order to understand the effect of reward and probability on response times and how they might interact, it is important to examine the neurological and computational processes governing these effects. A dominant framework for modelling response time variability alongside error rates are accumulator models (Brown & Heathcote, 2008; Carpenter & Williams, 1995; Ratcliff, 1978). Within these models evidence for a given response rises over time from some baseline level until it reaches a threshold after which the response is generated. In many of these models, such as the diffusion model, the threshold is a relative one as it corresponds to a certain amount of net evidence in favour of one particular alternative relative to another (Ludwig, 2011). Carpenter and Williams (1995) developed the LATER (linear approach to threshold with ergodic rate) model specifically for saccadic responses. Within LATER the presence of a target causes a signal in a decision unit to rise linearly at rate r from an initial value (s_0) to a threshold whereby a saccade is made (Carpenter & Williams, 1995). The rate of accumulation is assumed to vary randomly between subsequent saccades, according to a Gaussian distribution. These types of models can be thought of as simplified decision-field

models; in these models the relevant parameters of movements towards the various response alternatives are coded in a continuous and dynamic activation field (Ludwig, 2011). At a physiological level, each accumulator can be thought of as representing the mean activity of neural populations encoding each alternative (Wong & Wang, 2006). The alternative targets in many experimental paradigms are well separated, so modelling choice and latency variability using accumulator models instead of a full decision-field is sufficient (Ludwig, 2011). Using the LATER model, it was shown that the effect of prior probability on reaction time is best accounted for by a change in the difference between the starting point of the accumulator and the threshold (Carpenter & Williams, 1995). The lower the probability of an alternative, the greater the distance between the starting point and the threshold and thus the longer the time taken to respond. Marshall, Bogacz and Gilchrist (2012) have argued from a computational perspective that this change is best implemented in a change in the baseline rather than the threshold. This suggestion is supported by neurophysiological evidence (Forstmann et al., 2008).

The effect of reward on saccadic latency can also be accounted for in terms of accumulator models of saccade production (Dunne et al., 2015). Neurological research in primates suggests that oculomotor neurons representing the location of an expected reward show heightened activity (Dunne et al, 2015; Platt & Glimcher, 1999; Dorris & Glimcher, 2004). As with probability, in principle this activity increase could be reflected in a shift in the baseline activity level, shortening the distance between baseline and execution threshold and resulting in faster saccadic latencies (Dunne et al, 2015). This is supported by the behavioural data in Dunne and colleagues (2015), where it was found that rewards modulated saccade latency in a stimulus-driven task but did not affect exogenous orienting or IOR. However, other human behavioural data do not support this interpretation. Liston and Stone (2008) found manipulating reward frequency (and in fact prior probability) in a saccadic task affected the

internal perceptual response which is more consistent with an effect on the rate of accumulation in the decision-making model framework (Ludwig, 2011).

1.3.2 Dopaminergic system

The neural substrate of reward has long been associated with dopamine. Dopaminergic neurons (which appear to carry an essential signal for reward based learning) are an important part of the basal ganglia system and project most heavily within the basal ganglia (Shultz, 1998; Hikosaka, 2007). The majority of midbrain dopamine neurons (75-80%) show phasic activations with latencies of <100ms and durations of <200ms following temporally unpredicted food and liquid rewards in primates (Schultz, 2010). As reward can be quantified by probability distributions of value, predictions of rewards involve the expected value and variance of the distribution (Schultz, 2010). The physiological data supports the previously discussed effects of reward probability and reward magnitude; in experiments with primates, dopamine responses do not differ between reward probability and magnitude as long as the expected value is identical (Schultz, 2010). It is postulated that dopamine neurons encode reward prediction error, the difference between the predicted reward and the actual reward received (Hikosaka, 2007). This means that a larger obtained reward than expected results in an increased response and a smaller reward than expected results in response suppression (Ludwig, 2011). It could be concluded from this that the prediction error enables learning of the rewards available over time in an unstable environment (Ludwig, 2011; Shultz, 1998).

Several of the studies focusing on how reward affects responses times have investigated the neural substrates of reward, particularly in non-human primates. Bendiksby and Platt (2006) found that increasing rewards reduced saccadic reaction times in macaques, and for many neurons in lateral parietal area (LIP) (suggested to be homologous to areas of human

parietal cortex) visual responses were modulated by expected reward size. Interestingly, neuronal responses were positively correlated with reaction times independent of reward size, which is consistent with re-orienting of attention to the target; this suggests that motivation (reward) and attention independently contribute to the responses (Bendiksby & Platt, 2006). This result is somewhat conflicting to previously discussed studies showing that reward affects attentional capture (Theeuwes & Belopolsky, 2012), highlighting the importance of understanding the neural processes underlying behaviour. Additionally, it calls into question how we can really disentangle the effects of attention and motivation, and what these processes really are.

The neurophysiological data from the reward system also supports the difference between processing of reward and punishment, as previously discussed. The majority of dopamine neurons are either depressed in their activity in response to aversive stimuli (in primate studies), or not even activated (Schultz, 2010). Furthermore, if a dopamine activation is shown in response to punishment, it is temporally slower in comparison to the reward activation (Schultz, 2007). Although aversive stimuli in primate studies (electric shocks/puffs of air) are quite different to a monetary loss in human behavioural experiments, the neurological currency could be as similar as it is with juice/monetary rewards.

The research on the reward system in humans and non-human primates corroborates the majority of behavioural data suggesting that the relative reward value rather than absolute value has a clear effect on responses. In study on macaques, nearly half of the striatal neurons measured shifted the processing for one reward relative to the other reward values available in a block (Cromwell, Hassani, & Schultz, 2005). Supporting this, Elliott, Agnew and Deakin (2008) used functional magnetic resonance imaging (fMRI) in humans to investigate the role of the medial orbitofrontal cortex in reward processing, and found the response to the same perceptual stimulus was greater when it predicted the more valuable of two rewards. This

suggests sensitivity within the reward processing structures in the brain to the relative value of rewards, which could be manifested in saccadic and manual response times.

1.3.3 Neurological basis and computational model of prior probability

The neural basis of the effect of prior probability on motor preparation has been studied in primates (Basso & Wurtz, 1997; Dorris & Munoz, 1998). Neural activity in the superior colliculus (SC) preceding target selection was found to increase as the probability increased (Basso & Wurtz, 1997; Dorris & Munoz, 1998; Liu et al., 2011). This may be produced by descending cortical influences, as suggested by Liu (2011) and colleagues who found that, in humans, transcranial magnetic stimulation (TMS) disrupted the effect of location probability when TMS was applied over frontal eye fields (FEF). This is supported by research in monkeys where populations of LIP neurons were found to represent the log of the prior probability of a specific target in their initial firing rate (Platt & Glimcher, 1999; Yang & Shadlen, 2007); the neurons of FEF have receptive fields encoding visual and saccadic locations in a similar way to LIP. This research suggests that FEF plays a crucial role in modulating the effects of target location probability on saccade execution (Liu et al., 2011).

A computational model of the encoding of prior probability in the brain corroborates these experimental findings. As discussed previously, the LATER model of saccadic response updates the starting point of the accumulator based on the probabilistic evidence for a particular alternative (Carpenter & Williams, 1995). This is formalised in Bayes rule, which combines current evidence with the prior probability of some event (Ludwig, 2011). In this proposed model of the cortico-basal ganglia circuit Bayes theorem is hardwired (Bogacz, 2009; Bogacz & Larson, 2011). Cortical integrators (populations of LIP neurons) selective for a particular alternative represent log of prior probability in their initial firing rate, developed from the

evidence of neurological recordings in probabilistic behavioural tasks with monkeys (Bogacz, 2009; Platt & Glimcher, 1999; Yang & Shadlen, 2007). The log of prior probability is updated according to the new sensory evidence, and the basal ganglia re-normalises the cortical activity such that all probabilities of alternatives sum to 1 (Bogacz, 2009). This depends critically on the subthalamic nucleus (STN) which inhibits the neurons selective for less likely responses (through indirect but prominent projections via the output nuclei and thalamus). Within the model, the log transform is necessary because of a biological constraint imposed by the neurons: multiplication and division cannot be computed between integrators, but summation and subtraction can (Bogacz, 2009). Carpenter and Williams (1995) study supports this model, as median saccadic reaction time is shown to be proportional to the log of the prior probability. As the saccadic reaction time is also proportional to the threshold minus the starting point, and the starting point is the decision variable that is assumed to vary as probability of an alternative changes, it follows that the starting point (represented by initial firing rate of neurons) should be proportional to the negative log of the probability (Carpenter & Williams, 1995). This model will be discussed in relation to the effect of deep brain stimulation in the STN of Parkinson's patients in the final section of the introduction, but first I will address the interaction between reward and probability effects.

1.3.4 The relationship between reward and probability

From the existing literature, prior knowledge about the reward of an event seems to have a similar effect to prior knowledge about the likelihood of the event occurring. These processes could therefore be interlinked and it could be suggested that experiencing a stimulus more frequently than another could be intrinsically rewarding. Comparing effects of reward and probability cues have been studied using a random dot motion paradigm, where a perceptual decision is required (Mulder, Wagenmakers, Ratcliff, Boekel & Forstmann, 2012). In these types of tasks, participants are required to maintain fixation on a central cross before a cue is presented, and then decide the direction of motion of a cloud of randomly moving white dots on a black background (Mulder et al., 2012). An increased number of decisions were made to the side cued more probable or rewarding, and the reaction times were faster (Mulder et al., 2012). This was quantified by fitting the drift diffusion model (an accumulator model) which assumes that for two-alternative forced choice decisions, sensory evidence in favour of one of the alternatives begins to accumulate from a starting point *z;* when the accumulation process (at drift rate *v*) reaches a threshold value (*a*), a response is initiated (Mulder et al., 2012). They found that the response bias for reward and probability was best accounted for by a change in the starting point of the accumulator (Mulder et al., 2012). Using 3T functional MRI, they showed the frontoparietal network to be involved in changing the starting points in both manipulations of probability and reward (Mulder et al., 2012). Supporting these neurological similarities between probability and reward processing, Nakahara, Nakamura and Hikosaka (2006) state that prior knowledge about the reward associated with an alternative leads to a bias in the excitability of SC neurons, which might be reflected in the elevated starting point in the LATER model for saccadic responses. As previously discussed, neural activity in the superior colliculus (SC) preceding target selection has also been found to increase as the probability increased (Basso & Wurtz, 1997; Dorris & Munoz, 1998; Liu et al., 2011). In addition, a study

investigating both prior knowledge of reward value or probability shapes perception and action in parallel, and suggests that a shared sensory weight amplifies perceptual experience while biasing motor action driven by attention and expected value (Liston & Stone, 2008). These results suggest that the effects of reward and probability on decision-making processes across different response modalities may be governed by the same system or overlap in some way.

Several studies that have been discussed on the effects of reward have linked the influence of associating reward with a target to increasing attentional capture (e.g. Theeuwes & Belopolsky, 2012). Additionally, prior probability of a stimulus is often classified as expectation, which can guide attention towards a likely location of a relevant item (Summerfield & Egner, 2009). However, the similarities between attention and expectation are not reflected in the neural activity in visual regions representing the stimulus, and some neurophysiological research has shown that reward (defined as 'motivation') and attention contribute independently to influence the responses (Bendiksby & Platt, 2006; Summerfield & Egner, 2009). One way in which reward and probability may contribute to attention (but not directly change it) is by increasing the salience of the target that is associated with high reward value or prior probability. Many studies in the reward literature have linked reward associations with increasing salience, which is defined as the physical, 'bottom-up' distinctiveness of an object relative to other objects in the environment (Fecteau & Munoz, 2006). Although there has not been a strong argument for the effect of prior probability on salience, studies have shown that in a Posner cueing style task, the cue acts as a salient event which enhances the behavioural benefit associated with capture of attention (Fecteau, Bell & Munoz, 2004). Additionally, it was found that these goal-driven changes in behaviour were associated with an increase in pre-target and target related activity, and weaker activity related to inhibition of return (Fecteau et al, 2004). Therefore it could be postulated that global knowledge of the prior

probability of the stimulus occurring in a particular location could act as an internal cue, given the effects seen on behaviour, and increase the salience of the target itself.

1.3.5 Parkinson's disease

If the STN is crucial to this integration of probabilities, then how will the decision process be affected if the STN is disrupted in some way? The STN is the main area affected during deep brain stimulation (DBS) for Parkinson's disease patients, where an electrode is surgically implanted into the basal ganglia. Generally, it has been found that DBS can cause severe behavioural side effects such as impulsivity and difficult decisions being made quickly and inaccurately (Frank, Samanta, Moustafa, & Sherman, 2007). If the STN is critical (as in the model) for inhibition of neurons for less likely alternatives, then the response times for these alternatives may be affected by DBS. We would predict response times for highly likely alternatives to be unaffected by stimulation of the STN. This is supported by research suggesting that patients with DBS are specifically unable to slow down responses in high conflict decisions (Frank et al, 2007). Intuitively this is most likely to be manifested in responses to less probable or less rewarding stimuli, for which the response latencies are usually longer in the general population.

In general, Parkinson's patients have trouble suppressing automatic prosaccades to visual stimuli, and reaction times for antisaccades are significantly longer than age-matched controls (Munoz & Everling, 2004). However, in the same study prosaccades in patients were actually faster and they made more express saccades than controls (Munoz & Everling, 2004). This is thought to be caused by the dysfunction of the basal ganglia in Parkinson's disease, as the basal ganglia functions to select the appropriate response, by exerting and removing tonic inhibition (Hikosaka, Takikawa,& Kawagoe, 2000). Additionally, an adaptive mechanism may be involved, whereby baseline response inhibition is reduced in an effort to initiate movements

more rapidly, to compensate for slow motor movements in Parkinson's disease (Chan, Armstrong, Pari, Riopelle, & Munoz 2005).

A recent study showed Parkinson's disease patients (on dopaminergic medication) made increased errors and had longer response latencies relative to controls when switching between stimulus-saccade associations which were stochastically reinforced (Hodgson, Sumner, Molyva, Sheridan, & Kennard, 2013). The task involved a colour cued fixation target, and participants had to learn the associations between the colour and the direction of the saccade to be made. Positive feedback was given with a 0.8 probability, with 0.2 probability of receiving incorrect negative feedback on a correct trial. The result was interpreted as evidence for impairment in associative learning processes in PD, and a possible deficiency in processing of negative feedbacks dependent on dopaminergic state (Hodgson et al., 2013). The inability of Parkinson's patients on dopaminergic medication to learn from negative feedback has been documented before (Frank et al., 2007), and it follows that impulsive and reward-seeking behaviour are also seen in this population.

One of the long term goals of the work of this thesis is to develop an experimental paradigm to test both reward and probability in this patient group.

1.4 Plan of the Thesis

The effect of probability on saccadic and manual responses will be addressed in Chapter 2 where I report two experiments investigating these response modalities concurrently. Throughout all the experimental chapters I use a paradigm where in each trial one of two targets is presented either side of a central fixation. In Chapter 2 the prior probability of the presentation of these two targets is manipulated. I discuss the robustness of the probability

effect across modalities, observing whether there is a correlation between saccadic and manual responses. Within this chapter I report the development of a paradigm with which to study saccadic and manual responses to the same stimuli.

Although there have been studies that have investigated the effect of reward and probability on different parameters of saccades (e.g. peak velocities), the experiments I report in this thesis are focused on saccade latencies. Several studies in non-human primates look at peak velocities and amplitude (Kawagoe et al., 1998; Takikawa et al., 2002). However, these studies have mainly involved non-human primates and there is little evidence in the existing literature on humans to suggest that reward and probability modulate peak velocities or other parameters. Furthermore, given the intention to directly compare manual and saccadic responses across the experiments in the thesis, the latency of response is the only comparable parameter.

In Chapter 3 the effect of reward on saccadic and manual responses is investigated, and I report four studies I have carried out in this area. These studies address the way in which secondary rewards are delivered, and the affects of presenting rewards as probabilities or magnitudes. The absolute and relative value of rewards is manipulated in this chapter, in order to understand how these affect behaviour independently.

The experiments reported in Chapters 2 and 3 were carried our concurrently and so there is some parallel development of the paradigms across these chapters. However for simplicity and clarity they are reported separately.

The aim of the studies reported in Chapter 4 is to understand how the effects of reward and probability might interact. The first experiment addresses this explicitly, to see how reward and probability manipulations can affect behaviour concurrently. This involves manipulations of the expected value of targets. In the second experiment, these effects are studied purely in manual responses and separated in a matched paradigm to directly compare the two effects. I

report a study with healthy older adults in the final experiment of this chapter, with a view to begin to understanding how reward and probability effects change over the lifespan. This study provides a control experiment for future work investigating these effects in Parkinson's patients with deep brain stimulators.

CHAPTER 2

2.1 Introduction

In this chapter I report two experiments that investigate the effect of probability on saccadic and manual response times. In designing these experiments concurrently with the experiments investigating reward in Chapter 3, I aimed to develop a paradigm to study both factors that was as closely matched as possible. Doing this enabled the studies reported in Chapter 4 to be carried out in which the two factors are combined. Although the probability effect is well established in the existing literature, it is often studied within just one response modality - primarily saccadic (Basso & Wurtz, 1997; Carpenter & Williams, 1995; Dorris & Munoz, 1998; Koval et al., 2004; Liu et al., 2010, 2011; Noorani & Carpenter, 2013). Additionally, not all studies of this effect have replicated the result that responses are faster to targets appearing with higher spatial probability. Specifically, these effects appear often to be more robust in more complex paradigms involving an element of visual search (Jóhannesson et al., 2013). By studying saccadic and manual responses concurrently, the experiments reported in this chapter attempt to understand the sensitivity of the probability effect and the extent to which they are present across response types.

As discussed in Chapter 1, the majority of previous human and primate studies on the effect of stimuli probability on performance have focused on one type of response: primarily either saccadic or manual (button presses) responses. Studies of the neural basis of such response generation provide one source of evidence of whether the probability effect is governed by a similar process in these two response modalities. One suggestion is that

probability affects arise by changes in baseline firing rate in cells in the SC (Basso & Wurtz 1997; Dorris & Munoz 1998; Liu et al, 2011). The SC is associated with the generation of saccades and does not play a central role in the generation of other types of movement (arm, hand etc.). This suggests that probability effects may differ across response modalities.

However, as discussed in the Chapter 1, the premotor theory of attention states that processes involved in the control of spatial attention, and required for selecting motor responses, share a common neural substrate (Eimer et al, 2006; Rizzolatti et al, 1994). The theory claims that response-induced attentional shifts are not restricted to the oculomotor system, and would be triggered when hand movements are being prepared (Eimer et al., 2006; Rizzolatti et al, 1994). Eimer and colleagues (2006) found that ERP (event related potential) components sensitive to the direction of a cued response were similar for both saccadic and manual tasks, and suggested that both manual and saccade preparation result in spatially specific modulations of visual processing. This suggests that there may be a global system governing the influence of and probabilistic information on responses, and that we might see similar reaction time effects from recording saccadic and manual responses concurrently.

The experiments reported in this chapter were preceded by a number of pilot studies that are not reported here. These pilot studies established a long-term global mechanism for the probability effect on saccades, whereby reaction times were reduced over several testing sessions (at least 500 trials in each condition) on probability manipulations from 0.05 to 0.95, supporting the research of Druker and Anderson (2010) showing that the probability effect can be produced by statistical learning about the probabilities of stimuli in the environment. However, manual drift correction was used in this experiment, to ensure the participants returned to fixation before the onset of each trial. This produced a highly variable and uncontrolled ISI meaning that the results were not reliable. Additionally, the paradigm involved

the participants being asked to fixate on a cross in the centre of the screen and then look at one of a possible two targets presented on either side. These targets were small round circles and no additional task was involved; over long testing sessions, participants would become fatigued and their gaze would frequently drift from fixation and the landing point of saccades would not be close enough to the targets. In all the studies I report in these three experimental chapters, the paradigms involve a simple perceptual task after a saccade is made to a target (and sometimes fixation) to ensure that participants stay motivated to complete the task and that saccades are directed close enough to the target. This is particularly important given the intention to study the effects investigated in the thesis in Parkinson's patients with deep-brain stimulators; these participants specifically would struggle with an experiment where the instruction was purely to 'look' towards a target from a fixation point. Additionally, the use of a perceptual task with a manual response ensures that there are multiple response modalities in each paradigm in case one has more feasibility with the patient group than the other.

2.2 Experiment 1

2.2.1 Methods

Participants

Twelve participants (6 female) were recruited from the student population of the University of Bristol (approximate age range 18-25). All the participants had normal or corrected-to-normal vision. Participants were reimbursed £7 for their time and the study was approved by The Faculty of Science Human Research Ethics Committee at the University of Bristol.

Procedure

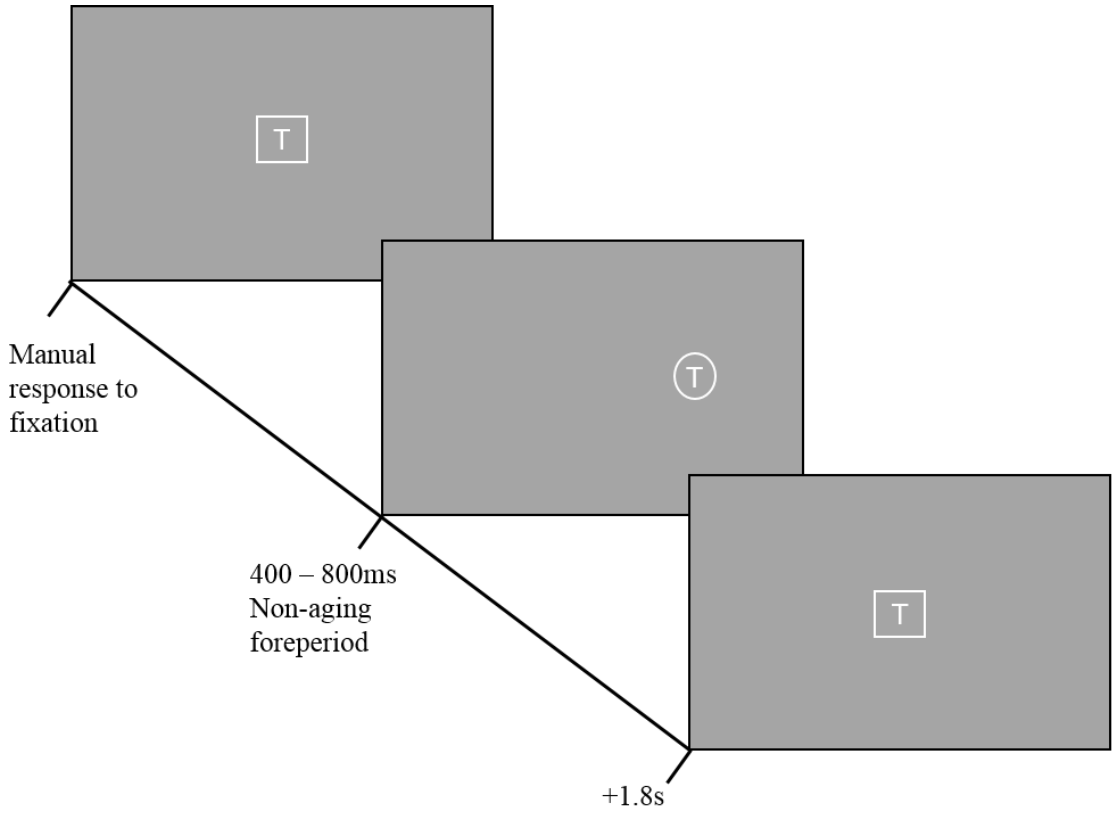

Figure 2.1; Diagram of the experimental procedure. The figure depicts an example trial, initiated by a manual response to the orientation of the letter T in the central fixation square. The trial shown is one in which the target appears on the right-hand side.

The sequence of a single example trial is shown in Figure 2.1. The participants were required to make a manual response to a capital letter "T" stimuli inside a square fixation point. The task was to indicate the orientation of the letter with a manual button press (one of two buttons). A circular target was then presented on the left or the right side of fixation, where the task was to make another manual response to the orientation of the letter T. The experiment consisted of a practice phase (10 trials) and then 12 blocks (4 blocks each of 3 conditions; 48 trials per block). Each block was preceded by a 9 point calibration procedure to allow accurate eye tracking.

Stimuli

All the stimuli were white (16.4 cd/m^2) and displayed on a grey background (10.4 cd/m^2). At the start of a trial a fixation square was presented centrally (1^o x 1^o; 0.18^o). Inside the fixation square was a letter T or inverted T in the centre. The letter T subtended 0.3^o, which is a size that Körner and Gilchrist (2007) have shown is small enough not to be recognised reliably above chance when fixation was 3^o away from the letter. Once a manual response was made to the T in fixation (the up arrow for letter T, the down arrow key for the inverted T) a variable non-aging foreperiod was initiated of between 400 – 800ms. This accounts for differences in expectancy over time by ensuring equal probability of the target onset at any point across the foreperiod (Weinbach & Henik, 2012). The fixation square and T remained on the screen for the duration of the foreperiod, but were removed from the screen as soon as the target was presented. The inclusion of a manual task at fixation ensured that participants had to always return to fixating at the centre of the screen prior to each trial.

The target presented in each trial was circular with a T or inverted T in the centre. The circle had a diameter of 0.9^o and a line thickness of 0.18^o. The presence of the T ensured that participants had to make an accurate target directed saccadic eye movement towards the target to complete the task. The target was presented at 6^o eccentricity from the centre on the left or the right-hand side.

The target was presented for a fixed amount of time (1.5 seconds), regardless of when the manual response was made to the orientation of the T in the target. If a manual response was made, the target was on screen for a further 300ms. If no manual response was made within 1.5s, then a message reading 'Please respond quicker' was displayed centrally (5^o above fixation and white) for 900ms.

The testing phase consisted of three probability conditions, where participants were exposed to each condition for four blocks. In the first condition, the target was equally likely to be presented on the left or right side of fixation. In the second condition, the target was presented on the left with probability 0.75 and the right with probability 0.25. In the third condition these probabilities were reversed. The proportions were fixed within the blocks rather than the probabilities, due to short block lengths, such that at the beginning of each block the number of targets appearing on a particular side were fixed at 50%, 75% or 25% of the total number of trials in the block. The order of trials were randomised for each block, giving a random permutation of trials in every block for each participant.

Apparatus

The experiment was created using the Psychophysics Toolbox (Brainard, 1997) running within Matlab 2013b running on Windows 7. The display was 17" running at 75Hz and with a resolution of 1600 x 1200 pixels, and the viewing distance was 57cm.

Movements of the right eye were recorded at a sampling rate of 1000Hz by the Eyelink II (SR Research, Canada) which has a typical operating spatial resolution of 0.5º. A chin and forehead rest was used to minimise head movements. A keyboard was used to record manual responses, the up arrow and down arrow for judgements on the orientation of the letter T.

Design

Probability condition (50/50, 75/25, 25/75) was the within participant repeated measure binary factor. Data combined from the left and right-hand side lead to three conditions: 50% probability, 75% probability, 25% probability.

The order of conditions were counterbalanced using a latin square design. The three conditions gave 6 unique orders, which were then repeated for the further 6 participants. The dependent measures were the manual response time to the target and saccadic latency.

2.2.2 Results

Manual Responses

A total of 6912 trials were recorded in the experiment (576 x 12 participants). In the manual data 34 of these trials were discarded (0.49% of total) due to response times of 10ms or less (including negative values); these were likely due to recording errors or responses that were initiated before/during the target onset or after the error message had been displayed. A total of 422 manual errors (6.12% of total trials; incorrect response to letter T in the target) were recorded. The distribution of errors across probability conditions is given in Table 2.1. This left a total of 6456 correct trials (93.4%) to be analysed.

	Probability		
	0.25	**0.5**	**0.75**
Response Error	7.29 (3.13 – 13.4)	5.73 (1.56 – 14.58)	5.96 (1.74 - 12.5)

Table 2.1; Distribution of errors across the three probability conditions. The values give the mean percentage of errors across the medians of participants, out of the total number of possible trials in each condition. The range across participants is given in brackets.

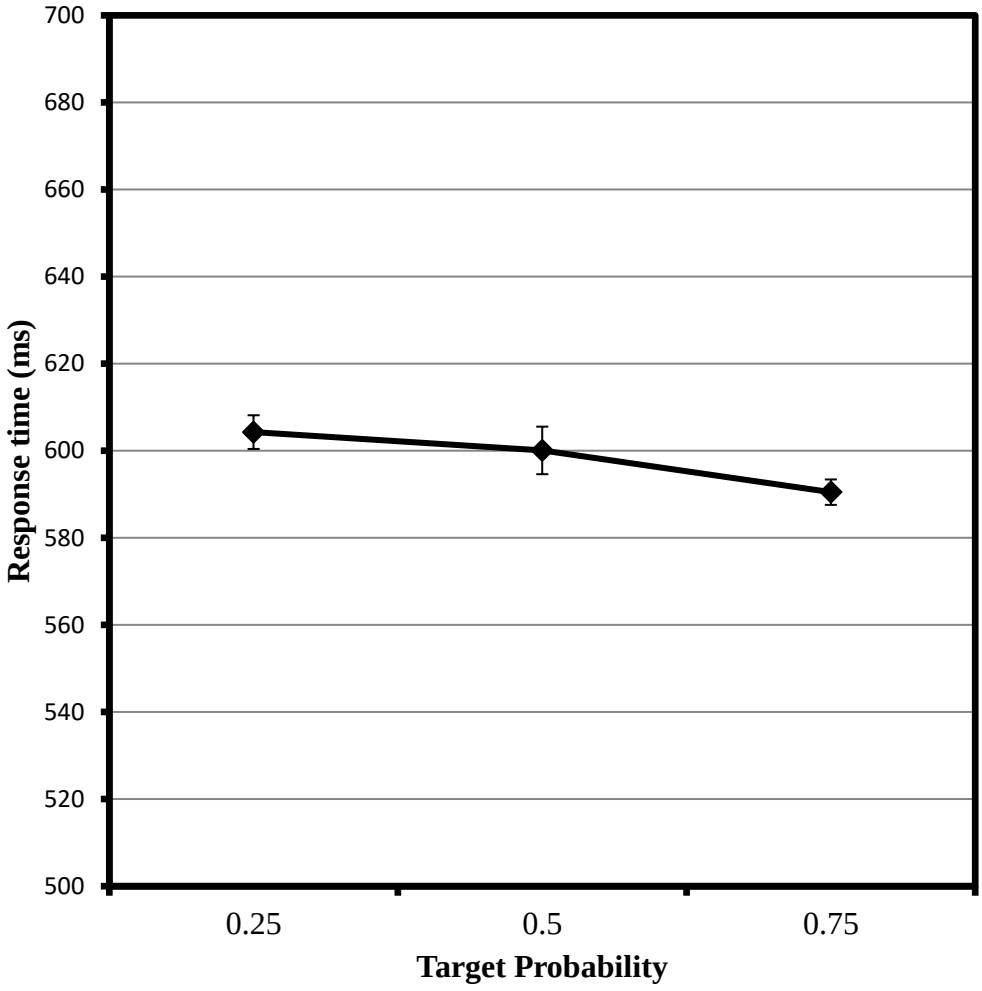

Figure 2.2; Graph of mean manual response times across the medians of 12 participants. The x-axis denotes the target probability, with the data having been pooled from targets presented in the left and right hemispheres. The error bars are calculated within subjects and are the standard error of the mean.

There was a significant effect of probability on the distribution of errors: more errors were made when responding to the 0.25 probability target than to the 0.5 or 0.75 probability targets (Repeated Measures ANOVA: [$F(2,11) = 4.57$, $p = 0.02$]; Effect size (partial ETA squared) = 0.29). There was no significant effect of the target probability on the manual response times (Figure 2.2), although there is a linear trend for response times to decrease as the probability increases.

Saccadic Responses

The initial analysis of the saccadic response data involved examining whether there was an offset in initial fixation towards either side. The median amount of drift away from central fixation at the starting point of the first saccade after target onset was calculated for each participant, in the equal and biased probability conditions. Of the 6912 trials recorded, 6907 trials were included in this analysis due to five trials having an error in the recording of the first saccade (due to a blink during target onset or recording failure). The mean offset across the twelve participants was 0.15°towards the high probability target in the 0.75/0.25 probability conditions (CI 95%: 0.03 – 0.28). The mean offset in the 0.5/0.5 condition was 0.08 degrees towards the right-hand side target (CI 95%: -0.21 – 0.37). The variance and overlap between the confidence intervals suggests no reliable effect of target probability on the starting point of the first saccade.

Therefore a general exclusion criteria was applied to the starting point of the first saccade, excluding trials where the starting position of the saccades was greater than 3 degrees either side of the centre of the fixation. No exclusion criteria was applied to the landing point of the first saccades, but if the saccade was generated in the wrong direction they were classed as error trials. After the application of these criteria, 190 trials were excluded from further analysis (Table 2.2). The remaining trials had a mean first saccade amplitude of 5.78°(range across participants: 5.14 – 6.21). This indicates that participants made a large hypo-metric saccade for their first saccade after target onset.

Reason for Exclusion	Number of saccades (trials) excluded and percentage of initial total	Total no of saccades **(Initial 6912)**
Initial fixation greater than 3 degrees from centre/starting point at 0	195 (2.82%; 0.9 – 5.9%)	6717 (97.18%)
Saccades in the incorrect direction (96.13% anticipatory)	181 (2.62%; 1.6 – 5.03%)	6536 (94.56%)
Anticipatory saccades (correct direction)	238 (3.44%; 2.08 – 5.21%)	6298 (91.12%)

Table 2.2; Pre-processing of the saccadic data. The data removed at each stage of pre-processing is quantified, with the percentage of the initial number of data points given in brackets, followed by the range across participants.

Of the saccades initiated in the incorrect direction, 96% had a response time of 75ms or less and these saccades were assumed to be anticipatory. All saccades initiated in the correct direction with response times of 75ms or less were therefore also classed as anticipatory and were excluded. Within the analysis of the anticipatory saccades, three of the trials were removed because of either a blink or recording error at target onset. After the pre-processing of the data, the remaining number of saccades to be analysed was 6298 (91.1%).

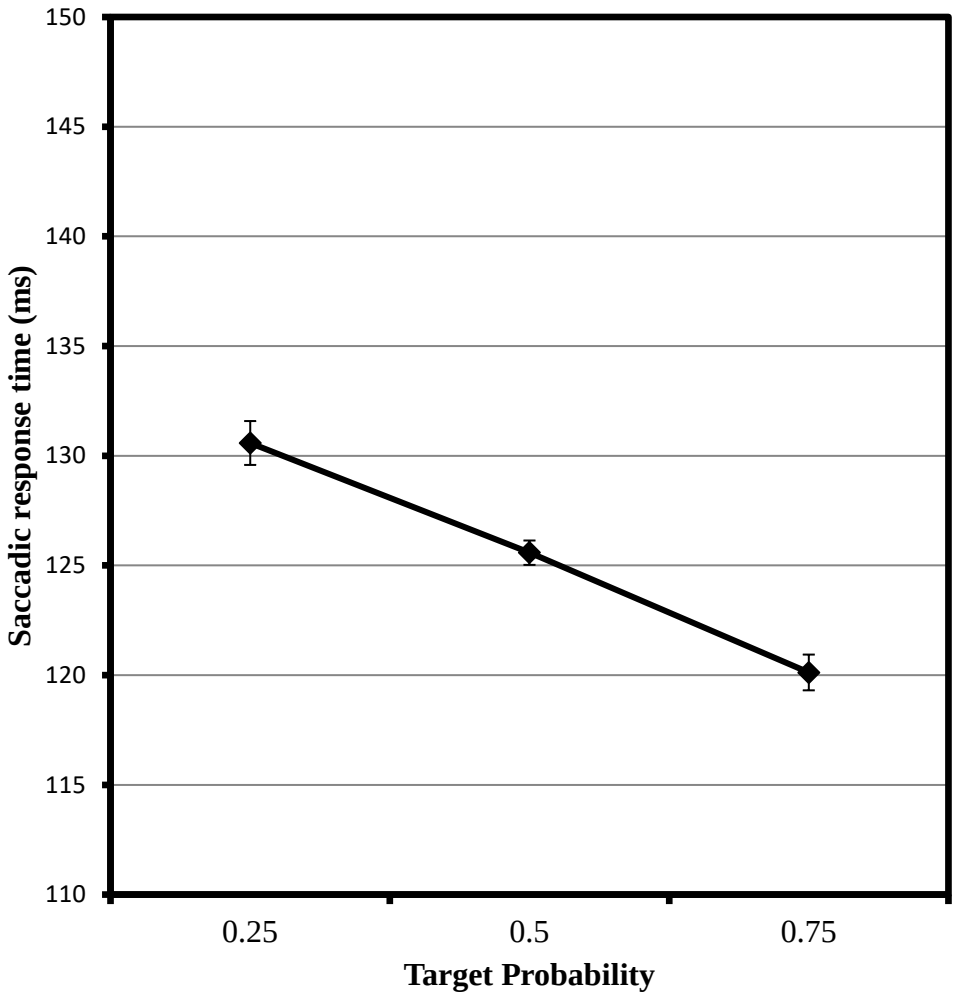

Figure 2.3; Graph of mean saccadic response times across medians of all 12 participants. The points on the x-axis denote the probability associated with the target, with the data pooled from responses to both hemispheres. The within-subject error bars are the standard error of the mean.

There was a significant effect of target probability on the saccadic response times, showing a linear decrease in response time as the probability increased (Figure 2.3) (Repeated Measures ANOVA: [$F(1,11) = 27.73$, $p < 0.001$]; Effect size (partial ETA) = 0.72). Additionally there was a significant effect of target probability on the frequency of correct anticipatory saccades, where more anticipatory saccades were made towards the target as the

target probability increases (Repeated Measures ANOVA: [$F(1,11) = 6.85$, $p = 0.005$]; Effect size (partial ETA) = 0.38). It follows that the reverse effect was seen in the frequency of incorrect anticipatory responses; the frequency of anticipatory saccades to the incorrect target increased as the probability of the correct target decreased (Repeated Measures ANOVA: [$F(1,11) = 20.93$, $p < 0.001$]; Effect size (partial ETA) = 0.66).

2.2.3 Discussion

There was a significant effect of target probability on saccadic response times, whereas there was no effect of probability on the manual response times. More anticipatory saccades were made towards higher probability targets, and more errors were made in response to the lower probability target compared to the equal and high probability targets. These findings are consistent with studies using prosaccade and antisaccade paradigms to show that higher probability locations demand more attention and result in an increased level of motor preparation (Koval et al., 2004; Liu et al., 2010).

One possible explanation for the lack of an effect of probability on manual responses could be the similarity of the manual response required following fixation between trials and of the response required to the actual targets. The same perceptual task (response to orientation of a letter T) is required both at fixation and at one of two targets on each trial. Given that the response to fixation is required on every trial, this means the probability of having to make this response is always higher than the probability of making a response to either of the targets. This between-trial response could have dominated and so reduced the potency of the probability manipulation for the manual responses.

Another explanation for the absence of the effect of probability on manual responses is that saccadic responses are directly linked to the spatial position of the targets and thus may be

more sensitive to the frequency of occurrence of the target at that specific spatial location. This could mean that they are more sensitive to the manipulations of probability, compared to the manual responses which are related to a binary decision that is identical for both targets location. Additionally, although the motivation for the saccadic response is to acquire information to make a perceptual response, once the target is fixated there is relatively little motivation/time pressure to make a manual response quickly to the target.

In order to address some of these possible explanations for the differences between the effect of probability on saccadic and manual responses I carried out a further study. In this study I focused on increasing the motivation for the participant to generate a fast manual response. To do this I introduced a pre-screening block in which I measured each participants manual response times in the experiment and used this to set a personalised time-out time for the main experiment. In this way each participant was under pressure to response quickly but this pressure was titrated to their particular speed of responding. In addition I removed the perceptual task at fixation between trials so that manual responses were only made to the targets.

2.3 Experiment 2

2.3.1 Methods

Participants

Eighteen participants (8 male) were recruited from the student population of the University of Bristol (approximate age range 18-25). All had normal or corrected-to-normal vision. Participants were reimbursed £7 for their time and given no other additional reward incentive.

The study was approved by The Faculty of Science Human Research Ethics Committee at the University of Bristol.

Procedure

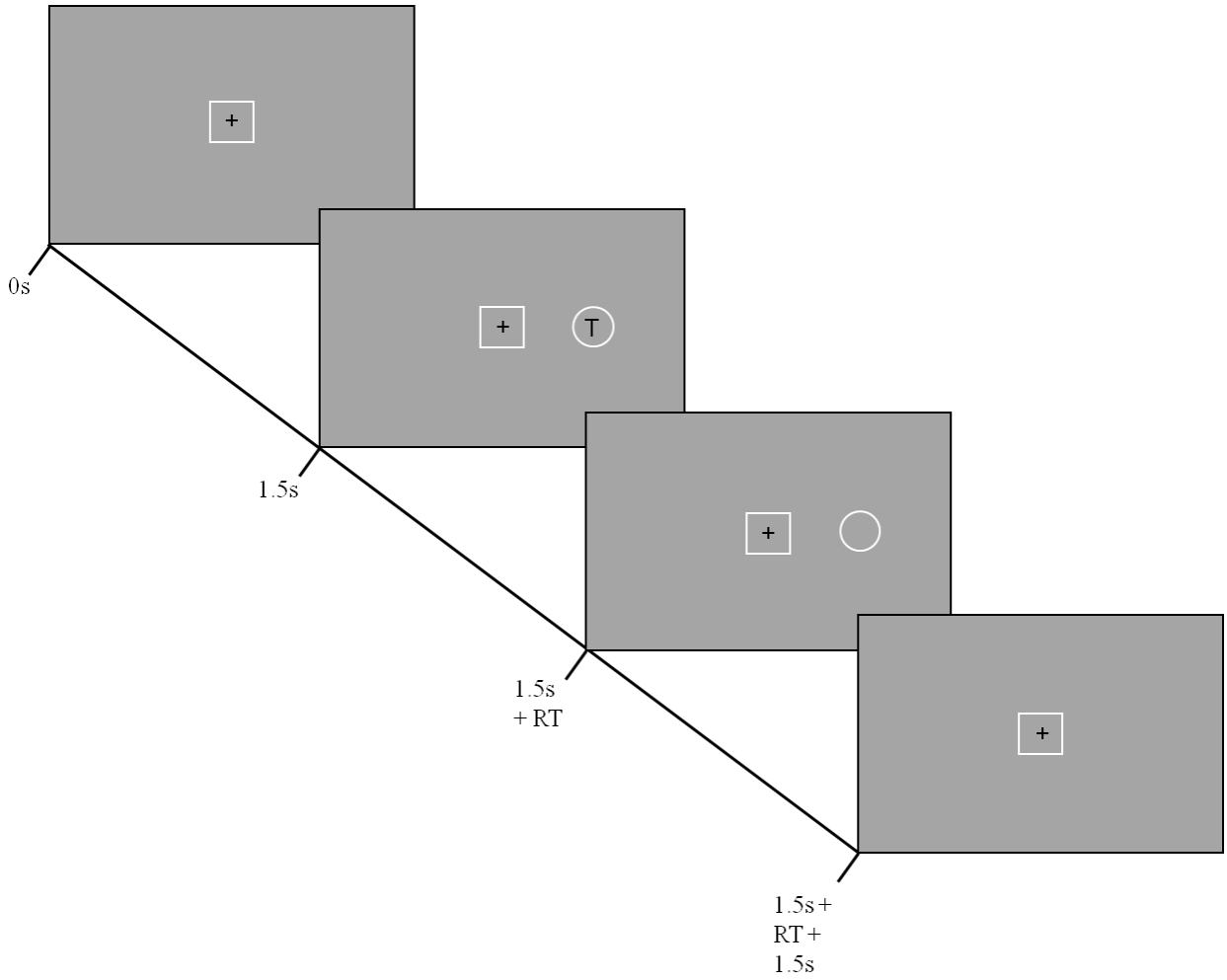

Figure 2.4; Diagram of the experimental procedure in the testing phase. The figure depicts an example trial where the target appears on the right-hand side.

The sequence of event in a single example trial are illustrated in Figure 2.4. The task for the participants was to respond to the "T" stimuli that appeared to the left or right of a central fixation point. The response required was to indicate the orientation of a letter with a manual button press. If the letter was on the left-hand side of the display the response was made with

the left hand and if the letter was on the right-hand side the response was made with the right hand. The experiment consisted of a practice phase (10 trials), a pre-test phase (48 trials), and then 6 blocks (48 trials each) of the testing phase. Each block was proceeded by a 9 point calibration procedure to allow accurate eye tracking.

Stimuli

All stimuli and the fixation square were white (16.4 cd/m^2) and displayed on a grey background (10.4 cd/m^2). A trial commenced with a centrally presented fixation square (1.65^o x 1.65^o; 0.18^o thick) which was presented for 1.5s. The fixation square contained a plus sign as a fixation point, which was presented in red (15.8 cd/m^2; font size 17).

This was immediately followed by the circle target with a T or inverted T in the centre. The circle had a diameter of 1.85^o and a line thickness of 0.18^o. The letter T subtended 0.3^o, which is a size that Körner and Gilchrist (2007) have shown is small enough not to be recognised reliably above chance when fixation was 3^o away from the stimuli. This ensured that participants had to make an accurate target directed saccadic eye movements towards the target to complete the task. The target was presented on the left or right in a varying number of trials across all phases of the experiment at 6^o eccentricity.

The testing phase consisted of three probability blocks. In one block the target was equally likely to be on the right or the left-hand side. In the second block, the target was presented on one side with probability 0.75 and the other side with probability 0.25. These probabilities were then flipped for the final block. The three probability block types were split into two separate consecutive blocks of 48 trials. The probabilities were not exact due to short block lengths, such that at the beginning of each block the number of targets appearing on a particular side were fixed at 50%, 75% or 25% of the total number of trials in the block. The

order of these fixed trials were then randomised for the length of the block, ensuring a random permutation of trials in every block across the whole experiment.

If the participant was too slow, or made an incorrect response, a message appeared in the centre of the screen reading 'Wrong!' or 'Too slow! (2.5^{o} above fixation and white). After the response to the letter T, the empty target (or error message) stayed on the screen for 1.5 seconds.

The pre-test block was included in the experiment to set an individual criteria for the time-out for the testing phase. In the practice and pre-test phases the fixation square contained an X in red (15.8 cd/m^2; font size 17). After a successful response to the letter T, an X was presented in the target in a golden yellow colour (19.8 cd/m^2). The distribution of manual response times from the pre-test block of the experiment were used to calculate a 70^{th} percentile of each participant's reaction time (ms) distribution. Without informing the participants, their individual 70^{th} percentile values were used as the length of time the target and letter T would be visible for in testing phase trials after which they would receive the time-out notice. This ensured motivation to respond quickly as participants inevitably were too slow on some trials.

Apparatus

The experiment was controlled by Psychophysics Toolbox (Brainard, 1997) running within Matlab 2013b running on Windows 7. The display was 17" running at 75Hz and with a resolution of 1600 x 1200 pixels, and the viewing distance was 57cm.

Movements of the right eye were recorded at a sampling rate of 1000Hz by the Eyelink II (SR Research, Canada) which has a typical operating spatial resolution of 0.5^{o}. The participants were provided with a chin and forehead rest to minimise head movements. Manual response were recorded via the keyboard (numeric right-hand section) – key 4 and 1 for the left hand and key 6 and 3 for the right hand responses.

Design

There was one within participant repeated measure binary factor: probability block type (75/25, 50/50, 25/75). Combining data from the right and left sides lead to three conditions: 75% probability, 50% probability and 25% probability.

The order of conditions were counterbalanced using a latin square design. Given the three block types, this gave 9 unique orders, which were then repeated for the further 9 participants. The dependent measures were the manual response time and saccade latency.

2.3.2 Results

Manual Responses

A total of 5184 trials were recorded (288 x 18 participants). The total number of errors in manual responses (time-out/response errors) made was 550, leaving 4634 trials to be analysed. The distribution of errors is shown in Table 2.3. The range of the total percentage of time-out/response errors of each participant's responses was 4.17% to 21.9%.

Target probability					
0.75		0.5		0.25	
Time-Out	Response Errors	Time-Out	Response Errors	Time-Out	Response Errors
5.52 (2.78-9.03)	4.05 (0-9.72)	6.02 (1.04-14.58)	4.57 (0-16.67)	8.33 (0-22.92)	5.44 (0-16.67)

Table 2.3; the mean percentage of errors (of the total number of possible trials in each condition), for both types; time-outs and response errors. The range across 18 participants is given in brackets.

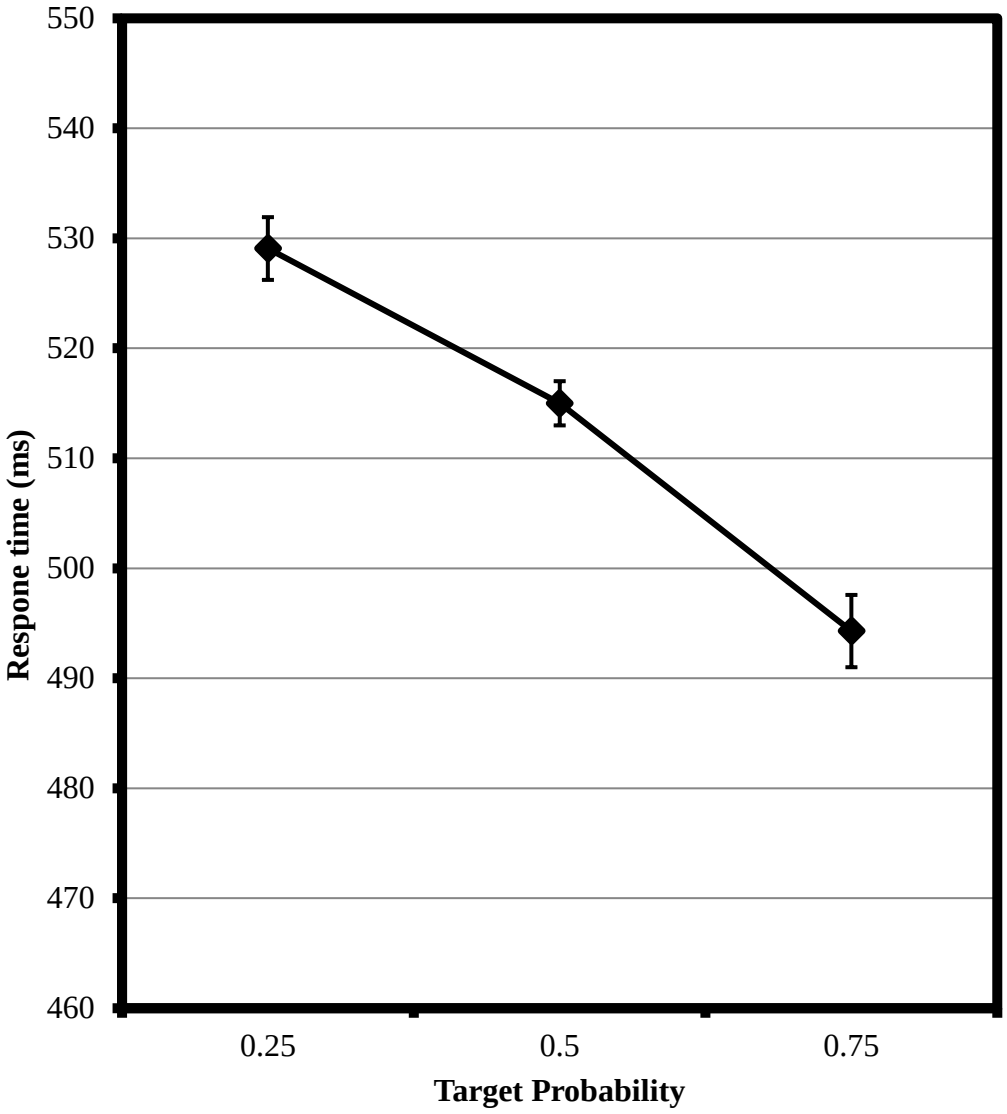

Figure 2.5; Graph of mean manual response times across medians of all 18 participants. The three x-axis points denote the different probabilities associated with targets, with the data having been pooled from targets presented in the left and right hemispheres. The error bars are calculated within subjects and are the standard error of the mean.

A significant effect of target probability on manual response times was seen, with a 14 ms (95% CI: 6.31 – 21.8ms) increase in response time from 0.5 and 0.25 target probability, and

a 21ms (95% CI: 10.9 – 30.5ms) decrease in response times between 0.5 and 0.75 probability (Repeated Measures ANOVA: [$F(2,17) = 26.65$, $p < 0.01$]; Effect size (partial ETA squared) = 0.61). Additionally, there was evidence that this effect had a significantly linear trend, as predicted from the literature discussed in Chapter 1 [$F(1,17) = 35.76$, $p < 0.001$]. There was a significant effect of error type (time-out/response errors) (Repeated Measures ANOVA: [$F(1,17) = 8.2$, $p = 0.01$]; Effect size (partial ETA squared) = 0.33) and target probability the distribution of errors across the experiment (Repeated Measures ANOVA: [$F(2,17) = 4.55$, $p = 0.02$]; Effect size (partial ETA squared) = 0.21). There were slightly more time-out errors than response errors recorded, and the frequency of errors increased a small amount as the probability decreased (Table 2.3).

Saccadic Responses

Initially the saccadic response data was assessed by looking at whether there was a spatial offset in initial fixation towards the high probability side. This was done by calculating the amount of drift away from the central fixation in the starting point of the first saccade after target onset. 5179 trials were included in this calculation, five having been discarded due to an error in the recording of the first saccade (due to blinks or otherwise). The mean offset across participants was 0.92 degrees towards the higher probability side in the 0.75/0.25 probability conditions (CI 95%: 0.56 – 1.3). In the 0.5 condition, the mean offset was 0.21 degrees towards the left-hand side of fixation. This suggests that spatial probability modulates the starting point of the first saccade, such that the saccades generally start closer to the higher probability target. This would not have reduced the latency of the saccades to the higher target in itself: Kalesnyka and Hallett (1994) found that saccade latency was not modulated by target eccentricity apart from for very small eccentricities (<1 degree).

Given these results a general exclusion criteria was applied to initial fixation starting point: excluding trials where the initial fixation was greater than 3 degrees either side of the centre of the fixation box. This was a liberal criteria as there was no specific fixation instruction to participants in the experiment. An additional criteria was applied so that all saccades initiated after the participant's 'time-out' were discarded. Two participants data had over 40% of trials excluded at this point, and were therefore removed from the rest of the saccadic analysis. There was no spatial exclusion criteria on the landing point of the first saccade, but saccades in the wrong direction were discarded as errors. The remaining trials had a mean first saccade amplitude of 6.0 degrees (range across participants: 5.5 – 6.4 degrees). This shows that generally all participants were making a large hypo-metric orienting saccade for their first saccade.

Reason for Exclusion	Number of saccades (trials) excluded and percentage of initial total	Total no of saccades **(Initial 4608)** **(excluding 2 participants)**
Initial fixation greater than 3 degrees from centre/initiated after 'time-out'	983 (21.33%; 3.13 – 36.1%)	3625 (78.7%)
Saccades in the incorrect direction (91.5% anticipatory)	142 (3.1%; 0 – 7.29%)	3483 (75.6%)
Anticipatory saccades (correct direction)	223 (4.84%; 0.69 – 12.15%)	3260 (70.75%)

Table 2.4; Pre-processing of saccadic analysis. Details of the data removed from further analysis, and the reasons for removing them. Percentage of initial number of saccades is included in brackets, followed by the range across participants. Two participants were discarded completely from analysis at the first stage, and are therefore not included in the table.

Of the saccades directed to the incorrect side, 91.5 % had a latency of less than 90ms and these are assumed to be anticipatory (Table 2.4). In addition to reflect this anticipatory criteria all saccades with reaction times less than 90ms in the correct direction were excluded. Some saccades within the incorrect saccades and anticipatory saccades categories had negative response times, due to the saccade being ongoing during the target onset. These saccades were

included in the anticipatory analysis as they still reflect an anticipation of the target appearing on a particular side. After removing the invalid, anticipatory and error saccades, the total number of analysed saccades was 3260 (70.8%).

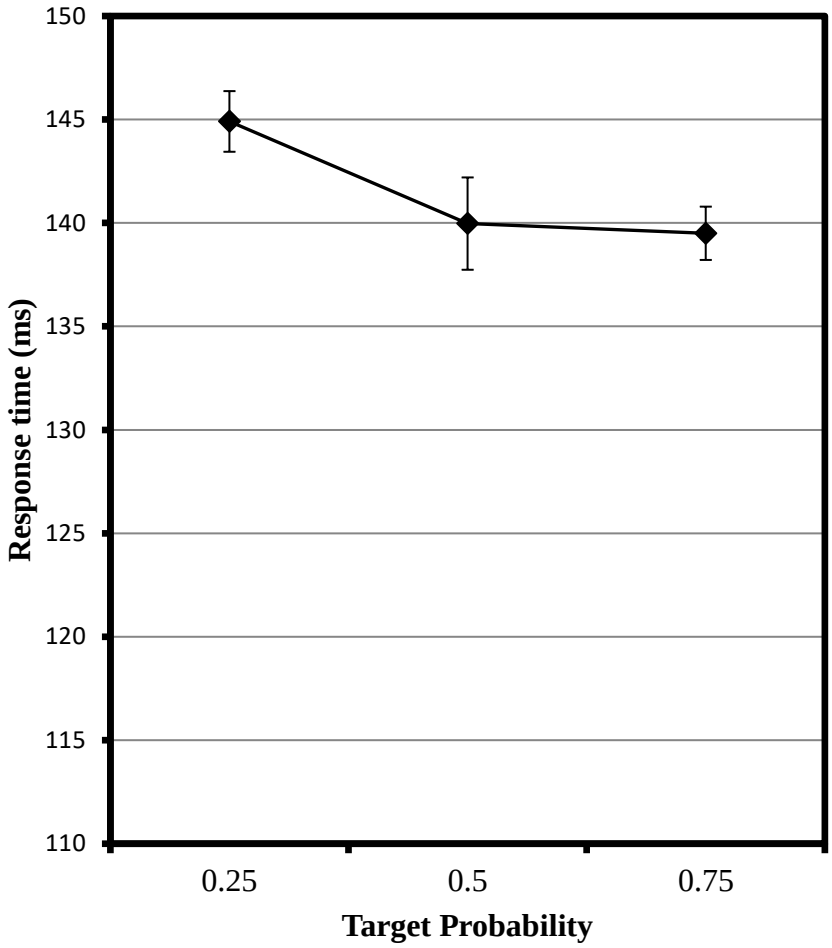

Figure 2.6; Graph of mean saccadic response times across medians of all 16 participants. The x-axis shows the target probabilities, which include data pooled from responses to targets in both left and right hemispheres. The within-subject error bars are the standard error of the mean.

In the saccadic data there was a significant linear trend between the mean response times across the three spatial probabilities (Repeated Measures ANOVA within-subjects contrast: [$F(1, 15) = 9.84$, $p = 0.007$]; Effect size (Partial ETA squared) = 0.4) (Figure 2.6). A significant

difference was found between the percentages of saccades that were anticipatory across the spatial probabilities. This was not present in the anticipatory saccades in the incorrect direction, but was very clearly present in the correct direction anticipatory saccades, where the percentage of anticipatory saccades increased as the probability of the target increased (Repeated Measures ANOVA: [$F = 20.79$, $p < 0.001$]; Effect size (Partial ETA squared) = 0.58). [Six of the anticipatory saccades were removed before analysing the frequencies, due to either errors in the eye tracker, or saccades disrupted by blinks.]

The relationship between the manual and saccadic responses within participants was investigated by calculating the size of the probability effect between 0.75 and 0.25 probability for each participant. The two participants excluded from the saccadic analysis were excluded from these calculations. There was no significant correlation between the two response modalities (correlation coefficient = 0.11, N.S. $p = 0.65$).

2.4 Discussion

I found a significant effect of probability on the manual response times, and a significant linear trend between the three probability levels. In the saccadic data, there was also a significant linear trend. There was no correlation between response modalities across the participants.

Our results support the existing literature showing that response times are increased as the probability is decreased, and conversely decreased as the probability is increased (Carpenter & Williams, 1995). However, in Experiment 1 the probability effect was found in the saccadic response but not in the manual responses; in Experiment 2, the probability effect is clearest in the manual responses, compared to only a significant linear trend in the saccadic responses.

This supports the finding that within the saccadic system this effect is not always present and is not robust (Jóhannesson et al., 2013). Some researchers have struggled to replicate the probability effect on saccadic responses shown by Carpenter & Williams (1995), as discussed in the Introduction, and have found the effect is only present in more complex tasks where decisions based on visual search have had to be made (Jóhannesson et al., 2013). Given that the results reported here show alternate effects on saccadic and manual responses in two different but simple paradigms, there are several factors that could give an explanation for the instability of this effect.

One reason there might be a clearer effect of probability on saccadic responses in Experiment 1 than in Experiment 2 is the differences in inter-stimulus interval (ISI; time from onset of fixation until onset of the target) across the experiments. In the first experiment the ISI was between 400 and 800ms, whereas in Experiment 2 it was substantially longer at a constant of 1.5 seconds. If we compare these ISI durations with the existing literature, Antonaides and colleagues (2014) replicated Carpenter and Williams' (1995) probability effect in healthy older adults using the same method with an ISI of between 0.5 and 1 second. In contrast, in a similar paradigm Jóhannesson and colleagues (2013) as discussed found no effect of probability (0.75/0.5/0.25) on saccadic response times: the ISI they used was 0.6 to 1.6 seconds. It could be hypothesised that manipulations of target probability can only modulate saccadic response times when the ISI is short (no longer than 1 second). It may be that with a longer ISI, Inhibition of Return (IOR: e.g. Klein, 2004) begins to affect response generation and so the more likely target location becomes inhibited and this effect counteracts the facilitation that results from the increased probability. There is research to suggest that IOR develops more quickly for saccadic than manual responses and at some range of cue-target stimulus onset asynchronies the spatiomotor map coding for eye movements is inhibited but the spatiomotor map coding for manual responses is facilitated (Briand, Larrison & Sereno,

2000). This is somewhat supported by the hypothesis discussed in Chapter 1 that saccadic responses can take better advantage of fast signals when they are available (Bompas & Sumner, 2008). The rapid speed at which saccades are initiated, compared to manual responses, could be related to the different effect of probability on the modalities. However, as addressed in the discussion of Experiment 1 there are other factors that could have affected the absence of a manual effect in this study.

The difference in the effect of probability on manual responses in these two experiments is elucidated by the motivation to make the manual response. Contrary to Experiment 1, in Experiment 2 the manual response is very specific to the presentation of the target (as opposed to the fixation) and the spatial location of the target. This ensured a direct link between the probability associated with the target and the manual response required. Additionally, there was a clear motivation to respond to the perceptual task at the target quickly and accurately: a participant-specific time constraint was applied and negative feedback was given in response to an incorrect/slow response. This meant that the manual response was the response on which the greatest motivation and importance would have been assigned by the participant. As discussed in the previous paragraph, the longer ISI in Experiment 2 could also have contributed to the significant effect of probability on manual response times; the longer latencies associated with manual compared to saccadic responses could require a longer period in between trials for the probability effect to manifest in behaviour. This could explain why there was an observed stronger effect of probability on manual reaction times than saccadic reaction times in Experiment 2.

Interestingly, the offset from fixation of the starting point of saccades was modulated by probability in Experiment 2 but not in Experiment 1. As discussed, this would not have reduced the latency to the higher probability target itself (Kalesnyka & Hallett, 1994). Additionally, there was no significant reduction in saccadic latency to the high probability target in

Experiment 2. It could be that the longer ISI in this experiment gave rise to the systematic offset towards the higher probability side. The small drift movements shown by the eye in fixations may reflect intentions to make a saccade (Kowler & Steinman, 1979; Liversedge & Findlay, 2000); expectation is likely to increase over longer ISIs as it allows top-down temporal preparation to develop consequently manifesting in a drift towards the higher probability target (Weinbach & Henik, 2012).

As these results have shown interesting differences in the effect of probability across saccadic and manual responses, in Chapter 3 I will investigate the effect of reward on these response modalities. This involves an exploration of the ways in which we can study reward associations in a similar way to probability to allow comparison of the two. This exploration aims to address the similarities and differences of the effect of probability and reward, and how these might interact.

CHAPTER 3

3.1 Introduction

In Chapter 2, I reported a series of studies investigating the effect of probability on saccadic and manual response times. In the current chapter I report four studies investigating the effect of reward on saccadic and manual response times. These experiments into the effects of probability and reward were carried out concurrently, such that both Chapter 2 and the current chapter culminate in experiments using a similar paradigm that has the potential to reliably show both a robust probability and reward effect.

As in the previous chapter investigating probability, in all of the reported reward experiments participants were required to make a manual response to a target which can be in one of two locations (left or right of the centre of a computer screen). I have manipulated the spatial distribution of reward in the experiments by setting a differential in the amount of reward associated with one side as opposed to the other. There are a number of different ways to present reward information experimentally and these experiments are an attempt to look at the various methods that have been used in the literature in order to search for a method that delivers reliable reward effects in the context of this paradigm.

Many studies in non-human primates have shown that saccadic responses have shorter latencies to targets that are associated with reward than to those that are not (Takikawa et al., 2002, Kawagoe et al., 1998). Additionally, Milstein and Dorris (2011) have shown that it is the relative value of a stimulus that affects choice and saccadic reaction times, rather than the global magnitude of reward available in a trial. They also found that the probability of receiving a reward after presentation of a target had a weaker effect on choice and reaction times than the relative magnitude of reward (Milstein & Dorris, 2011).

As discussed in Chapter 1, research investigating the effect of reward on human behaviour has generally focussed on how associating reward with targets (Theeuwes & Belopolsky, 2012), stimulus features (Stankevich & Geng, 2015) or hemifield (Lucas et al., 2013) influences salience and thus attentional capture. Some of these paradigms have recorded saccadic responses (Theeuwes & Belopolsky, 2012) and others have recorded manual responses (Anderson et al., 2011a, 2011b; Stankevich & Geng, 2015), rather than concurrently measuring the two. The paradigms in these studies have tended to focus on visual search and the affect of distracters associated with reward, rather than direct responses to a rewarded stimulus. Anderson and colleagues (2011a, 2011b) found that participants were slower in a search task when a distractor associated with high reward was present. Several studies have shown that these reward effects persist even after reward is no longer associated with these stimuli (Dunne et al., 2015; Stankevich & Geng, 2015; Theeuwes & Belopolsky, 2012).

Very few studies have investigated in humans how reward associated with a specific spatially located target affects reaction times, and these have tended to focus on rewarded targets relative to targets associated with no reward (Dunne et al., 2015). Thus although these reward associations are spatially specific, it means that only one hemifield is ever rewarded and does not tell us anything about whether reward values are processed relative to the other rewards in the environment.

Crucially, the majority of previous human and primate studies on stimuli associated with reward and probability have focused on one type of response: primarily either saccadic and manual (button presses) responses. In primate studies it has been shown that dopamine neurons show activation proceeding visual, auditory and somatosensory stimuli associated with reward (Schultz, 2010). Moreover, the activation occurs irrespectively of the response modalities (arm, mouth, eye movements) (Schultz, 2010). Reward processes then appear to have an influence across response systems.

As discussed in Chapter 1, the premotor theory of attention proposes that the processes involved in the control of spatial attention, and required for selecting motor responses, share a common neural substrate (Eimer et al., 2006; Rizzolatti et al., 1994). The theory claims that response-induced attentional shifts are not restricted to the oculomotor system, and would be triggered when hand movements are being prepared (Eimer et al., 2006; Rizzolatti et al., 1994).

This Chapter reports a set of four experiments that investigate the effect of reward on behaviour and does this across two response modalities – saccades and manual responses. One of the strengths of these experiments is the concurrent recording of saccade and manual responses, as in Chapter 2. In the paradigm participants are required to make a manual response but in order to make that manual judgement have to make a saccadic response to the target. In Experiment 3, I investigate how the relative probability of receiving a reward affects saccadic and manual response times. In Experiment 4, I investigate whether the relative magnitude of reward affects saccadic and manual response times. In Experiment 5, I concurrently investigate the relative and absolute value of reward. Finally, in Experiment 6 I examine how greater magnitudes of reward and increased time pressure affect saccadic and manual responses.

3.2 Experiment 3: Probability of Reward

3.2.1 Methods

Participants

Twelve participants (9 female) were recruited from the student population of the University of Bristol (approximate age range 18-25). All the participants had normal or corrected-to-normal vision. Participants were reimbursed £4 for their time and were told they would win up to £6 during the experiment. The study was approved by The Faculty of Science Human Research Ethics Committee at the University of Bristol.

Procedure

The sequence of a single example trial is shown in Figure 3.1. The participants were required to make a manual response to a capital letter "T" stimuli inside a square fixation point. As in Chapter 2, the task was to indicate the orientation of the letter with a manual button press (one of two buttons). A circular target was then presented on the left or the right side of fixation, where the task was to make another manual response to the orientation of the letter T. The experiment consisted of a practice phase (10 trials) and then 12 blocks (4 blocks each of 3 conditions; 48 trials per block). Each block was preceded by a 9 point calibration procedure to allow accurate eye tracking.

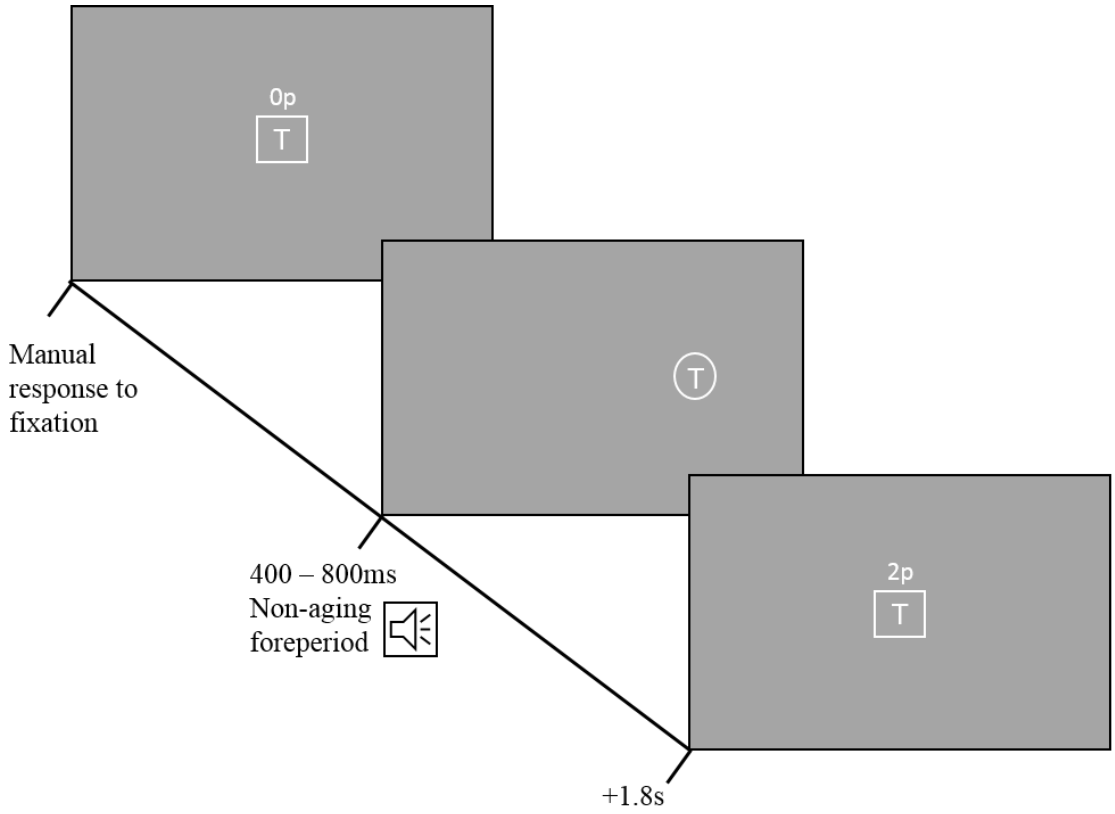

Figure 3.1; Diagram of the experimental procedure. The figure depicts an example trial, initiated by a manual response to the orientation of the letter T in the central fixation square. The trial shown is one in which the target appears on the right-hand side, and the presentation of the target is accompanied by a reward, indicated to the participant by the sound of a cash register.

Stimuli

All the stimuli were white (16.4 cd/m^2) and displayed on a grey background (10.4 cd/m^2). At the start of a trial a fixation square was presented centrally (1^o x 1^o; 0.18^o). Inside the fixation square was a letter T or inverted T in the centre. The letter T subtended 0.3^o, which is a size that Körner and Gilchrist (2007) have shown is small enough not to be recognised reliably

above chance when fixation was 3º away from the letter. Once a manual response was made to the T in fixation (the up arrow for letter T, the down arrow key for the inverted T) a variable non-aging foreperiod was initiated of between 400 – 800ms. The fixation square and T remained on the screen for the duration of the foreperiod, but were removed from the screen as soon as the target was presented. The inclusion of a manual task at fixation ensured that participants had to always return to fixating at the centre of the screen.

The target presented in each trial was circular with a T or inverted T in the centre, with a diameter of 0.9º and a line thickness of 0.18º. This ensured that participants had to make an accurate target directed saccadic eye movement towards the target to complete the task. The target was presented at 6º eccentricity from the centre on the left or the right-hand side.

The target was presented for a fixed amount of time (1.5 seconds), regardless of when the manual response was made to the orientation of the T in the target. If a manual response was made, the target was on screen for a further 300ms. If no manual response was made within 1.5s, then a message reading 'Please respond quicker' was displayed centrally (5º above fixation and white) for 900ms. If the trial was one in which a reward was received, the sound of a cash register was played through headphones to the participant at the same time as the target onset. Each time a reward was received, the running total reward in pence for the block was updated above the fixation at the start of the next trial. This was presented centrally 0.9º above the fixation square followed by 'p' with font size 11.

The testing phase consisted of three probability conditions and the participants were exposed to each condition for four blocks. In all three conditions, the left and right targets were presented with equal probability (fixed at exactly 50% of trials). In the first condition, the left and right targets were equally likely to be accompanied by a reward. A reward was given on exactly half of the trials in which the left target was presented, and half of the trials in which

the left target was presented. These proportions were fixed due to short block lengths; the order of trials were randomised for each block, giving a random permutation of trials in every block for each participant. In the second condition, the probability of receiving a reward on left target trials was 0.75 and on the right target trials was probability 0.25. In the third condition these probabilities were reversed.

Apparatus

The experiment was created using the Psychophysics Toolbox (Brainard, 1997) running within Matlab 2013b running on Windows 7. The display was 17" running at 75Hz and with a resolution of 1600 x 1200 pixels, and the viewing distance was 57cm.

Movements of the right eye were recorded at a sampling rate of 1000Hz by the Eyelink II (SR Research, Canada) which has a typical operating spatial resolution of 0.5º. A chin and forehead rest was used to minimise head movements. A keyboard was used to record manual responses, the up arrow and down arrow for judgements on the orientation of the letter T.

Design

The within participant repeated measure binary factor was the reward probability condition (50/50, 75/25, 25/75). Data combined from the left and right-hand side lead to three conditions: 50% probability, 75% probability, 25% probability.

The order of conditions were counterbalanced using a latin square design. The three conditions gave 6 unique orders, which were then repeated for the further 6 participants. The dependent measures were the manual response time to the target and saccadic latency.

3.2.2 Results

Manual Responses

The total number of trials recorded was 6912 (576 x 12 participants). Manual responses were excluded when there was an error in the recording: there were 89 trials excluded (1.43% of total), and a further 459 trials (6.64%) were separated from the rest of the analysis as they were trials in which the participant made an error (incorrect response to the letter T in the target). The distribution of errors across probability conditions is given in Table 3.1. After pre-processing of the manual data, 6364 (92.1%) trials remained to be analysed.

	Reward probability		
	0.25	**0.5**	**0.75**
Response Error	7.34 (1.56 – 14.06)	6.16 (2.08 –12.5)	5.96 (2.6 – 13.54)

Table 3.1; Distribution of manual errors across the three reward probability conditions of the experiment. The values are the mean percentage of error trials out of the total possible trials in each condition, and the range across participants is given in brackets.

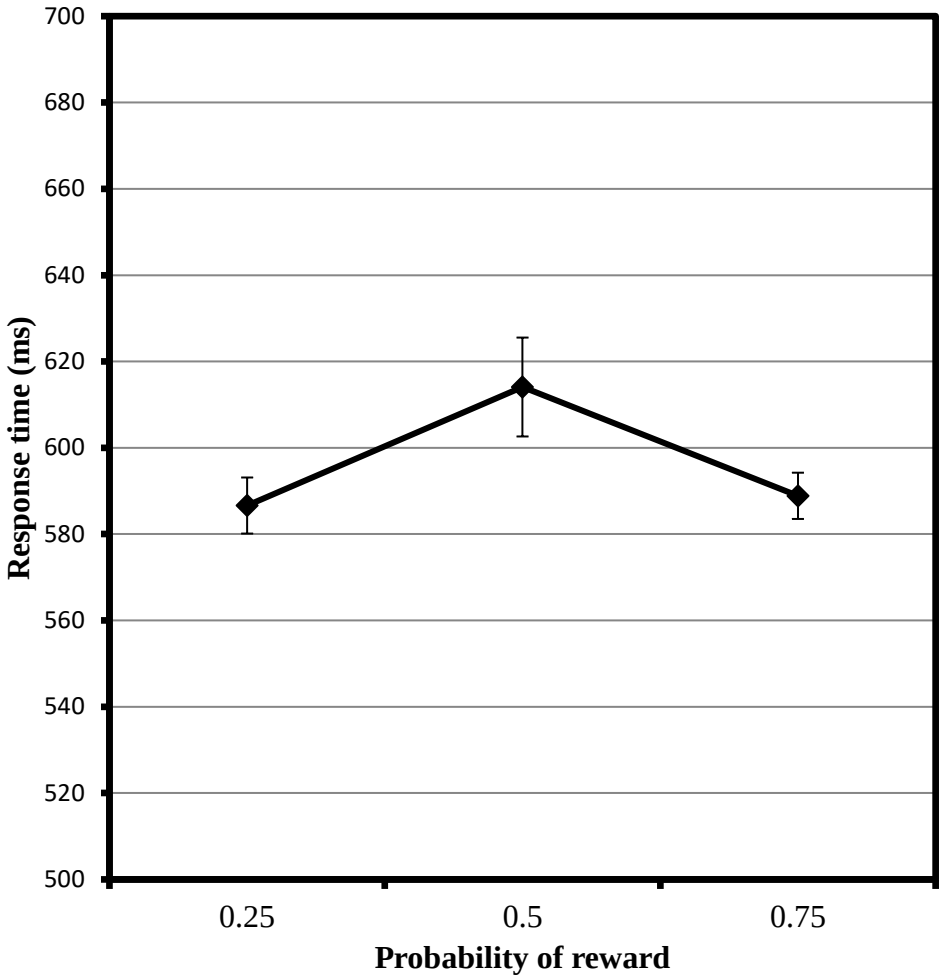

Figure 3.2; Graph of the mean manual response time across medians of participants, for each reward probability condition. The within participant error bars give the standard error of the mean.

There was no significant effect of reward probability on the distribution of manual errors and additionally no significant effect of the reward probability on the manual response times (Repeated Measures ANOVA: [$F(2,11) = 2.3$, $p = 0.12$]; Effect size (partial ETA) = 0.17) (Figure 3.2). Despite the presence of an auditory stimulus during the initiation of the response to the rewarded trials, there was no significant difference between the response times to the rewarded and unrewarded trials.

Saccadic Responses

We analysed the saccadic response data first by examining whether there was an offset in initial fixation towards either side. This was done by calculating the median amount of drift away from central fixation at the starting point of the first saccade after target onset for each participant, in the equal and biased probability conditions. Of the 6912 trials recorded, 6871 trials were included in this analysis. Forty one trials were excluded either because a blink occurred during target onset or there was a recording error around that time. The mean offset of the medians of all participants was 0.015 degrees towards the high reward probability target in the 0.75/0.25 conditions (CI 95%: -0.15 – 0.18). The mean offset from fixation in the 0.5/0.5 condition was 0.06 degrees towards the right-hand side target (CI 95%: -0.18 – 0.3). These results suggest that there is no effect of target reward probability on the starting point of the first saccade.

Given the outcome of the drift analysis, a general criteria was applied to the starting point of the first saccade in each trial: any saccades initiated more than 3 degrees (Euclidean distance) either side of fixation were excluded. Trials with a saccadic response time of less than 1000ms were also excluded, to ensure the first saccade was a direct response to the target presentation. As in the previous experiment, no exclusion criterion was applied to the landing point of the first saccades, but saccades generated in the wrong direction were classed as error trials. After the application of these criteria, and including the trials excluded from the first stage, 130 trials were excluded from further analysis (Table 3.2). The remaining trials had a mean first saccade amplitude of 5.81 degrees (range across participants: 5.39 – 6.21), indicative of large hypo-metric saccades.

Reason for Exclusion	Number of saccades (trials) excluded and percentage of initial total	Total no of saccades **(Initial 6912)**
Initial fixation greater than 3 degrees from centre/starting point at 0	130 (1.88%; 0.17 – 7.8%)	6782 (98.12%)
Saccades in the incorrect direction (97.6% anticipatory)	164 (2.37%; 1.22 – 3.47%)	6618 (95.75%)
Anticipatory saccades (correct direction)	192 (2.78%; 0.87 – 5.73%)	6426 (92.97%)

Table 3.2; Pre-processing of saccadic data. The number of trials excluded/separated at each stage and the number of remaining trials is given. The percentage of total trials at each stage is stated in brackets, followed by the range across participants.

The majority of trials in which a participant initiated a saccade in the wrong direction had a response time of 80ms or less. After examining the distribution of correct and incorrect response times, these trials were classed as anticipatory in addition to all correct trials with a saccadic response time of 80ms or less. Three of the anticipatory trials were removed due to the first saccade having a recorded response time of 0 (likely because of blinks/recording errors). After the pre-processing of the data, the remaining number of saccades to be analysed was 6426 (92.97%).

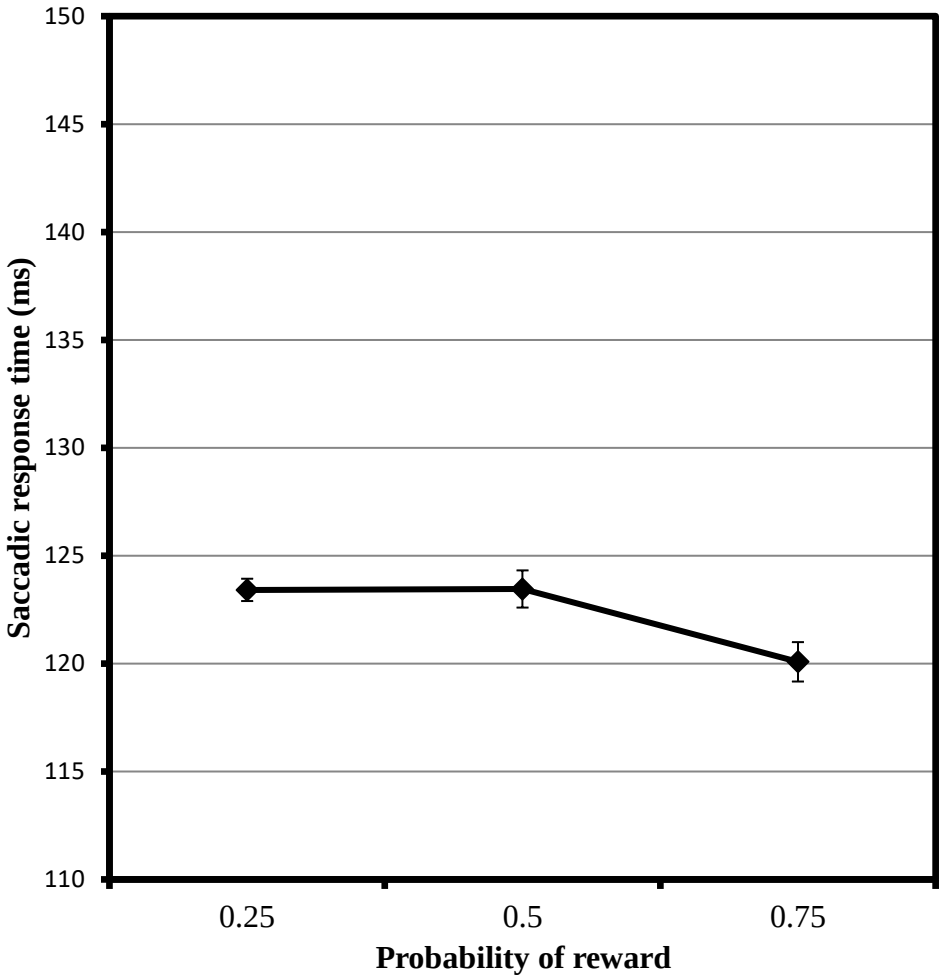

Figure 3.3; Graph of mean saccadic response times across medians of all 12 participants. The points on the x-axis denote the reward probability associated with the target, with the data pooled from responses to both hemispheres. The within-subject error bars are the standard error of the mean.

There was a marginally significant effect of target reward probability on the saccadic response times (Repeated Measures ANOVA: [$F(2,11) = 4.07$, $p = 0.03$]; Effect size (partial ETA) = 0.27) (Figure 3.3). The probability of receiving reward did not have an effect on the frequency of correct anticipatory saccades or the incorrect anticipatory saccades. No effect was found between the response times for rewarded vs non-rewarded trials.

3.2.3 Discussion

There was no effect of reward across manual responses in the experiment, and a marginal effect in saccadic responses but only between the low/equal and high conditions. One explanation for the absence/weak effect of reward is that the presence of an auditory stimulus coinciding with the visual stimulus to signify a rewarded trial could have had an aversive effect. Although if this was the case, we might expect to see a difference between the manual response times of the unrewarded and rewarded trials, as the manual response is initiated after the onset of the auditory stimulus. This difference is not apparent, which is supported by previous findings that visual stimuli dominate auditory stimuli in spatial tasks due to the superior acuity of vision (Recanzone, 2003).

An alternative explanation for the absence of reward effect is that the auditory stimuli were not salient enough. The auditory stimuli was not explicitly linked to reward value, and the information provided by the total reward above fixation was not explicitly linked to the presentation of spatial locations of stimuli either. This could mean that the probability of receiving reward does not become associated with a specific target. Additionally, the representation of the monetary value may change over time, due to the context of the running total reward presented in the centre. It could be that an increment of 2p at current total of 8p manifests as more rewarding than at 30p. The reward received on a trial could be perceived as a fraction of the total, rather than as a constant value associated with presentation of a target.

A further explanation for why we do not see a clear reward effect could be related to the strength of the reward probability manipulation compared to a manipulation of reward magnitude. As discussed in Chapter 1, Milstein and Dorris (2011) found reward magnitude to have a stronger effect on choice and saccadic reaction times in non-human primates than

reward probability. This was the motivation for the next experiment I report which focuses on reward magnitude rather than probability of reward.

3.3 Experiment 4: Magnitude of Reward

3.3.1 Methods

Participants

Twelve participants (5 female) were recruited from the student population of the University of Bristol, and all the participants had normal or corrected-to-normal vision. Participants were told they could win up to £12 during the experiment, accumulated in small increments. Each participant received £12 (rounded up from £11.52) and the reward was not dependent on performance. The study was approved by The Faculty of Science Human Research Ethics Committee at the University of Bristol.

Procedure

The sequence of a single example trial is shown in Figure 3.4. As in the previous experiments, the participants were required to make a manual response to a capital letter "T" stimuli inside a square fixation point; this initiated the start of the trial. The task was to indicate the orientation of the letter with a manual button press (one of two buttons). A circular target was then presented on the left or the right side of fixation, and the participants were then required to make another manual response to the orientation of the letter T. The experiment consisted of a practice phase (10 trials) and then 12 blocks (4 blocks each of 3 conditions; 48 trials per block). Each block was preceded by a 9 point calibration procedure to allow accurate eye tracking.

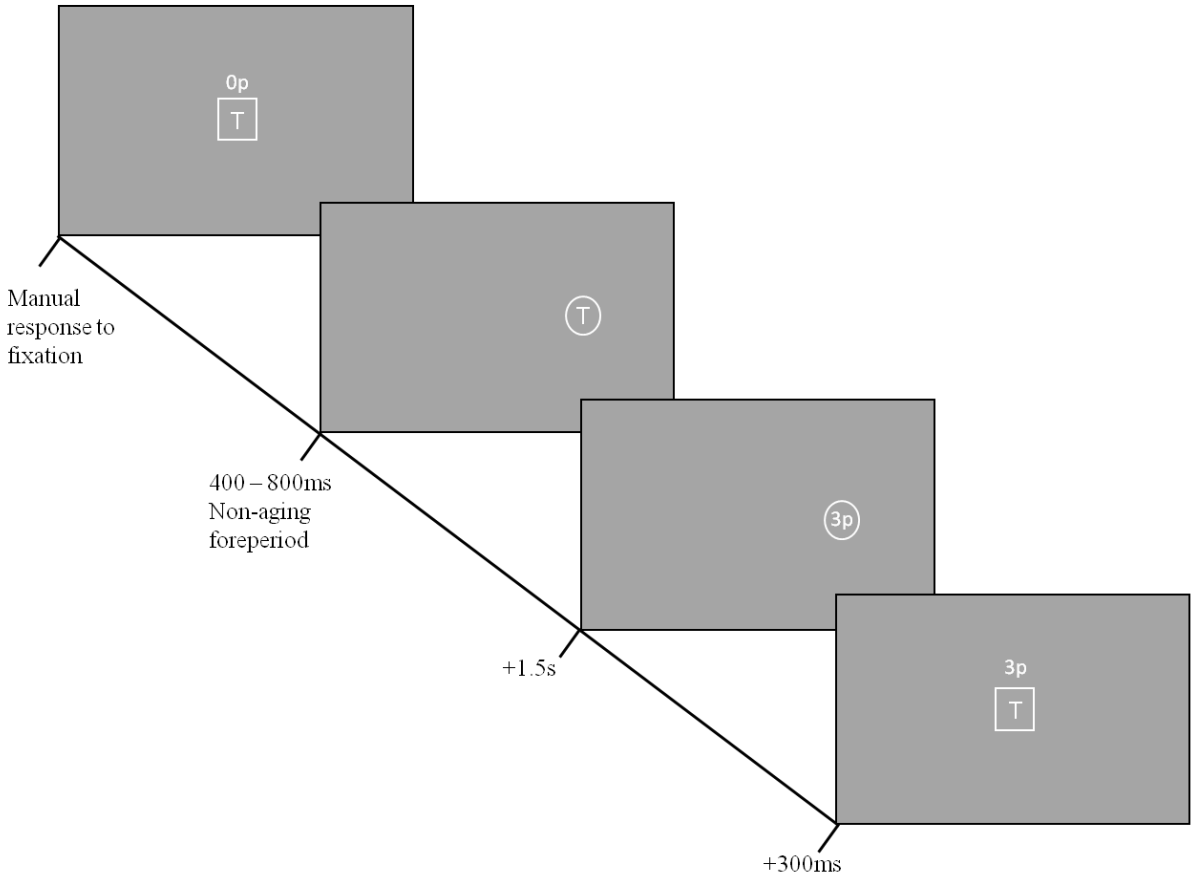

Figure 3.4; Diagram of the experimental procedure. The figure depicts an example trial, initiated by a manual response to the orientation of the letter T in the central fixation square. The trial shown is one in which the target appears on the right-hand side, in the condition where the reward magnitude is 3 pence and the left side reward magnitude is 1 pence.

Stimuli

All the stimuli were white (16.4 cd/m^2) and displayed on a grey background (10.4 cd/m^2). At the start of a trial a fixation square was presented centrally (1^o x 1^o; 0.18^o). Inside the fixation square was a letter T or inverted T in the centre. A manual response to the letter T in fixation (the up arrow for letter T, the down arrow key for the inverted T) initiated the trial. A variable non-aging foreperiod followed for 400 – 800ms. The fixation square and letter T remained on

the screen for the duration of the fore-period, but were removed from the screen as soon as the target was presented.

The target presented in each trial was circular with another T or inverted T in the centre. The target had diameter of 0.9º and a line thickness of 0.18º. The target was presented at 6º eccentricity from the centre on the left or the right-hand side. The target was presented for a fixed amount of time (1.5 seconds), regardless of when the manual response was made to the orientation of the T in the target. If a manual response was made, the target was on screen for a further 300ms and the reward value was displayed in the centre of the target followed by 'p' in font size 11. If no manual response was made within 1.5s, then a message reading 'Please respond quicker' was displayed centrally (5º above fixation and white) for 900ms. The running total reward in pence for the block was updated above the fixation at the start of the next trial, presented centrally 0.9º above the fixation square followed by 'p' in font size 11. This value was reset to 0 at the start of each block.

There were three reward magnitude conditions in the testing phase and the participants were exposed to each condition for four blocks of 48 trials each. In all three conditions, the left and right targets were presented with equal probability (fixed at exactly 50% of trials). In the first condition, the left and right targets were associated with equal reward (2 pence for each trial). In the second condition, the magnitude of reward on left target trials was 3 pence and on the right target trials was 1 pence. In the third condition these probabilities were reversed.

Apparatus

The experiment was created using the Psychophysics Toolbox (Brainard, 1997) running within Matlab 2013b running on Windows 7. The display was 17" running at 75Hz and with a resolution of 1600 x 1200 pixels, and the viewing distance was 57cm.

Movements of the right eye were recorded at a sampling rate of 1000Hz by the Eyelink II (SR Research, Canada) which has a typical operating spatial resolution of 0.5^{o}. A chin and forehead rest was used to minimise head movements. A keyboard was used to record manual responses, the up arrow and down arrow for judgements on the orientation of the letter T.

Design

The reward magnitude condition was the within participant repeated measure binary factor (2p/2p, 3p/1p, 1p/3p). Data pooled from the left and right-hand side lead to three conditions: equal reward, high reward, low reward.

The order of conditions were counterbalanced using a latin square design. The three conditions gave 6 permutations, which were then repeated for the further 6 participants. The dependent measures in the experiment were the manual response time to the letter T in the target and the saccadic latency.

3.3.2 Results

Manual Responses

The total number of trials recorded was 6912 (576 x 12 participants). Manual responses were excluded for the trials when there was an error in the recording giving a response time of 1ms or less. There were 22 trials excluded (0.32% of total), and 619 trials (8.96%) were separated from the rest of the analysis as they were trials in which the participant made an error (incorrect response to the letter T in the target). The distribution of errors across probability conditions is given in Table 3.3. After pre-processing of the manual data, 6271 (90.73%) trials remained to be analysed.

	Reward Magnitude		
	Low	**Equal**	**High**
Response Error	9.55 (5.21 – 28.13)	8.55 (3.65 – 19.79)	8.77 (2.6 – 10.94)

Table 3.3; Distribution of manual errors across the three reward probability conditions of the experiment. The values are the mean percentage of error trials out of the total possible trials in each condition, and the range across participants is given in brackets.

Reward magnitude had no effect on the frequency of manual errors across the twelve participants. Additionally, reward magnitude did not have an effect on the correct manual response times (Repeated Measures ANOVA: [$F(2,11) = 0.2$, $p = 0.82$]; Effect size (partial ETA) = 0.02) (Figure 3.5).

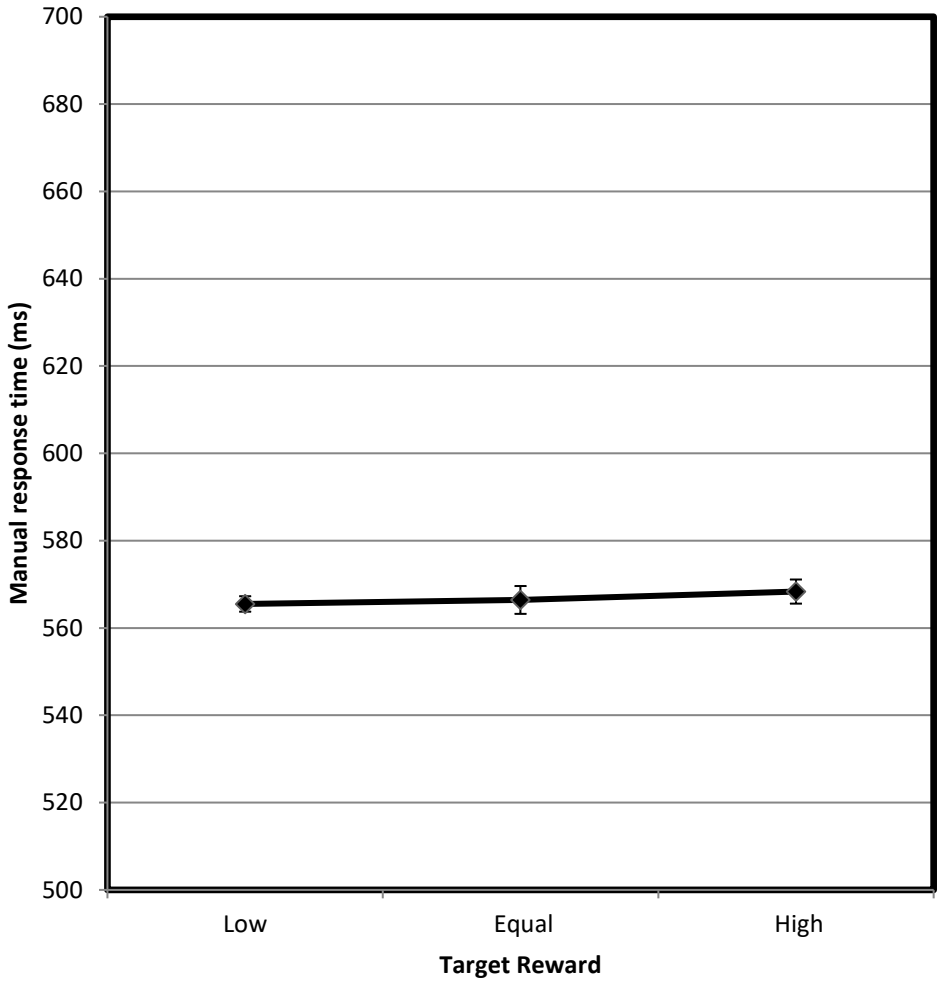

Figure 3.5; Graph of the mean manual response times across medians of each participant, for the three reward magnitude conditions. The within-subject error bars are the standard error of the mean.

Saccadic Responses

For the saccadic response data, I first examined whether there was an offset in initial fixation towards either side. This was done by calculating the median amount of drift away from central fixation at the starting point of the first saccade after target onset for each participant in each of the three conditions. 6912 trials were recorded and of these 53 trials were

excluded because there was an error in the recording of the first saccade either because of a blink or system error.

The mean offset of the medians of all participants was 0.04 degrees towards the high reward magnitude target in the biased reward conditions (CI 95%: -0.08 – 0.15). The mean offset in the equal reward magnitude condition was 0.05 degrees towards the right-hand side target (CI 95%: -0.1 – 0.21). These results suggest that there is no effect of target reward magnitude on the starting point of the first saccade.

Reason for Exclusion	Number of saccades (trials) excluded and percentage of initial total	Total no of saccades **(Initial 6912)**
Initial fixation greater than 3 degrees from centre/starting point at 0	253 (3.66%; 0.69 – 9.2%)	6659 (96.34%)
Saccades in the incorrect direction (98.1% anticipatory)	154 (2.23%; 0.34 – 3.82%)	6505 (94.1%)
Anticipatory saccades (correct direction)	174 (2.52%; 0.35 – 4.34%)	6331 (91.6%)

Table 3.4; Pre-processing of saccadic data. The number of trials excluded/separated at each stage and the number of remaining trials is given. The percentage of total trials at each stage is stated in brackets, followed by the range across participants.

Given the outcome of the drift analysis, a general criteria was applied to the starting point of the first saccade in each trial: any saccades initiated more than 3 degrees (Euclidean distance) either side of fixation were excluded. As in previous experiments, no exclusion criterion was applied to the landing point of the first saccades, but saccades generated in the wrong direction were classed as error trials. After the application of these criteria, a total of 253 trials were excluded from further analysis (Table 3.4). The remaining trials had a mean first saccade amplitude of 5.87 degrees (range across participants: 5.45 – 6.37), indicative of large hypo-metric saccades.

Most of the trials in which a participant initiated a saccade in the incorrect direction had a response time of 90ms or less (98.1% of incorrect saccades). The correct response times of less than 90ms were therefore classed as anticipatory, along with the incorrect trials within the same criteria. Three of the anticipatory trials were removed due to the first saccade having a reported response time of 0 (likely because of blinks/recording errors). After the pre-processing of the data, the remaining number of saccades to be analysed was 6331 (91.6%).

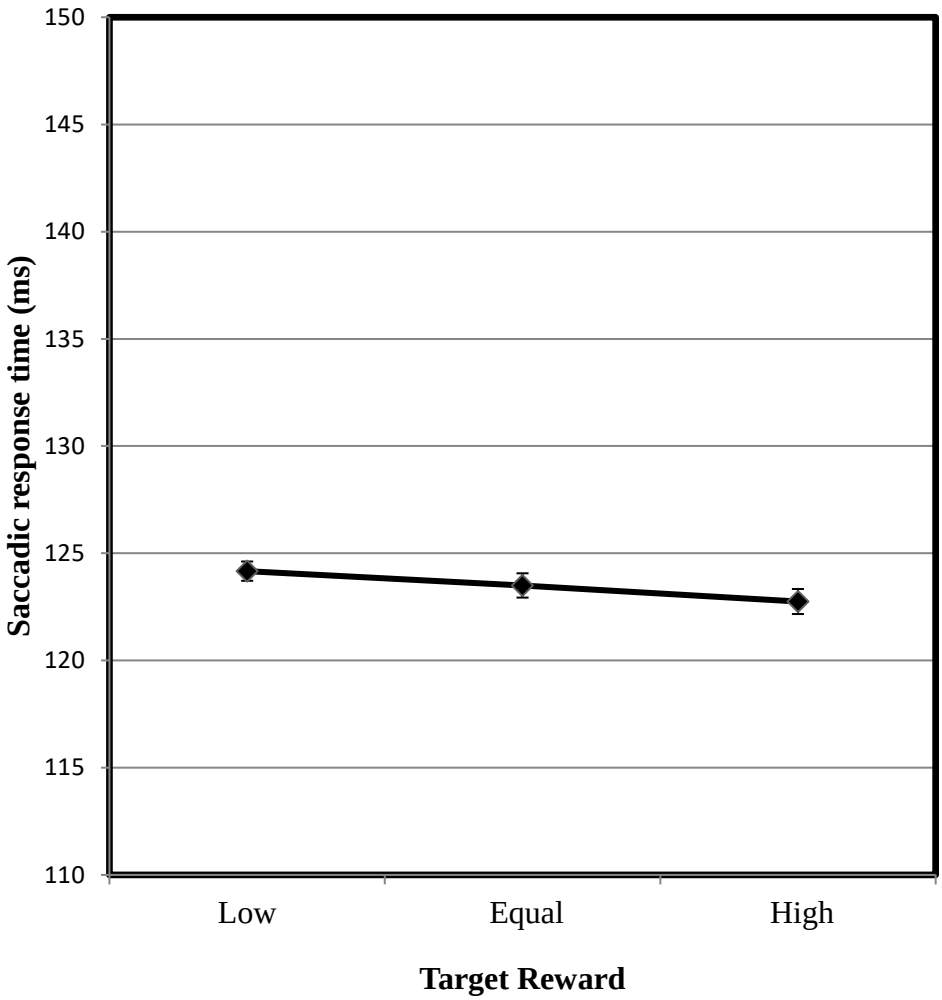

Figure 3.6; Graph of mean saccadic response times across medians of all 12 participants. The points on the x-axis denote the reward probability associated with the target, with the data pooled from responses to both hemispheres. The within-subject error bars are the standard error of the mean.

Reward magnitude had no significant effect on the saccadic response times (Repeated Measures ANOVA: [$F(2,11) = 1.16$, $p = 0.33$]; Effect size (partial ETA) = 0.1) (Figure 3.6). In addition, the reward magnitude did not have an effect on the frequency of correct anticipatory saccades or the incorrect anticipatory saccades.

3.3.3 Discussion

There was no effect of reward magnitude across the saccadic and manual responses. This could be explained by the small value of rewards associated with the targets. Although over several trials reward accumulates to a reasonable amount, on a trial-by-trial basis the magnitudes are very small and may not be enough to affect the salience of the target and decrease response times. This is a tricky issue as large numbers of trials are needed and there are ethical and financial implications associated with giving large amounts of money to participants per trial. However, it is possible that using larger values (points) that are do not directly correspond to the amount of money received would not engage the reward system. As discussed in Chapter 1, there is support for the use of hypothetical rewards in delay discounting research, where no systematic difference was found in discount rate between real and hypothetical monetary rewards (Johnson & Bickel, 2002). Although this might not generalise to other paradigms, it could be worth employing a points-based reward system that equates to a reasonable amount of reward to enable the use of larger values on a trial-by-trial basis.

In support of this theory, the relative reward value of the two targets may be indistinguishable if the reward magnitudes are very small. Although the relative proportion is the same, 1p and 3p could be too similar to produce a difference in activation of the reward system. In comparison, £10 and £30 could engage the reward system enough to produce a differentiation between response times. This is supported by research showing the relative value of objects affect saccadic response times (Milstein & Dorris, 2007, 2011) and prospect theory postulating that the value (utility) of an action is relative to the other available options (Kahneman & Tversky, 1979).

One possible reason we did not see a reward effect in manual responses in this experiment could be because of the absence of spatial mapping between the key press made in response to the target on a specific side of the screen. Regardless of whether the target was on the left or the right-hand side, the same binary judgement was made in response to the letter T. However, given that we do not see an effect of reward on saccadic responses either, this is likely to be less of an issue than the problems associated with the reward schedule.

Given the results of this study, in the next reported experiment I address the issues discussed by employing a points-based rewards distribution, mapping motor responses for the left/right targets to the left/right hands, and manipulating the absolute and relative value of rewards.

3.4 Experiment 5: Points based reward

3.4.1 Methods

Participants

Twenty four participants (16 female) were recruited from the student population of the University of Bristol with corrected-to-normal vision. Participants were told they could win £6 on average during the experiment, which was accumulated in small increments of one, ten and one hundred points. Each participant received £6 (8712 points) on completion of the task regardless of their performance during the experiment. The study was approved by The Faculty of Science Human Research Ethics Committee at the University of Bristol.

Procedure

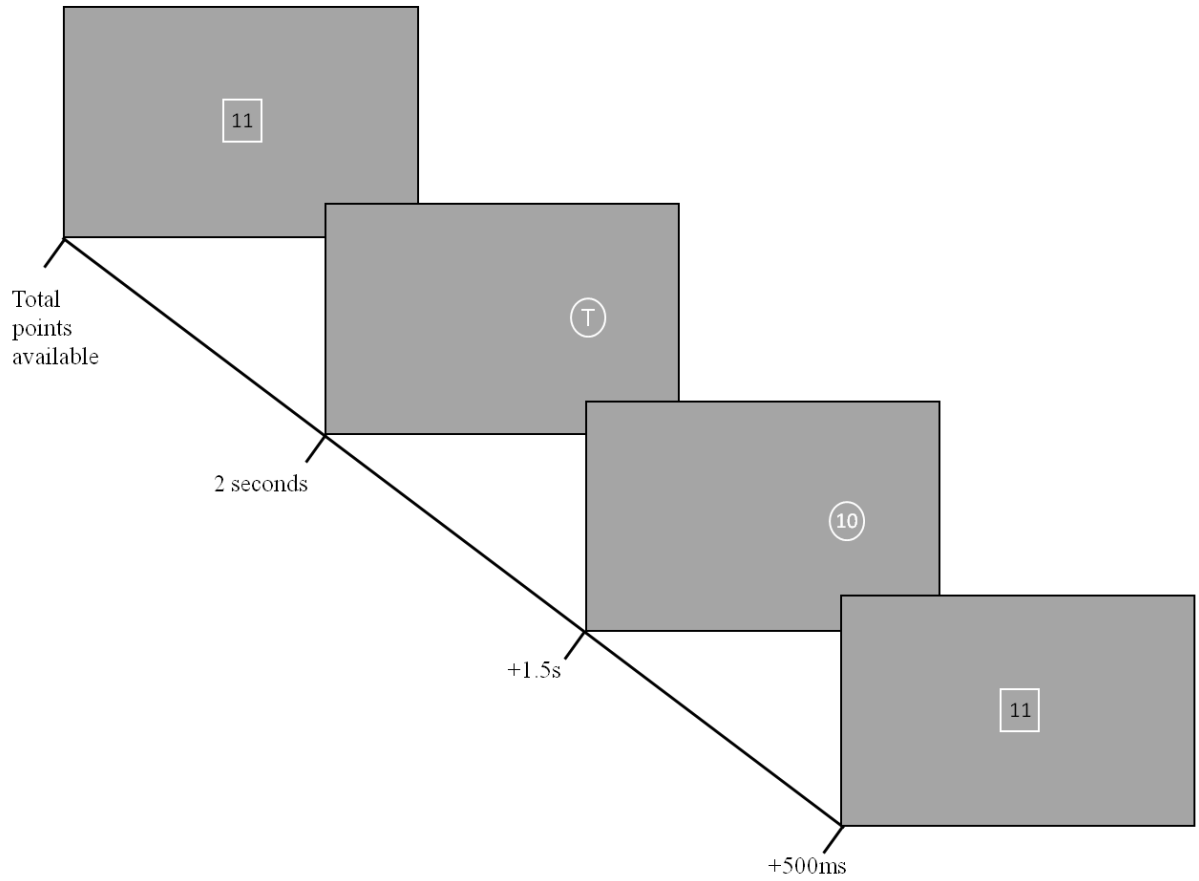

Figure 3.7; Diagram of the experimental procedure. The figure depicts an example trial, where the reward magnitude is low and the high reward side for the participant is the right-hand side. The trial shown is one in which the target appears on the right-hand side, so is associated with high reward (10 points). The total reward available (1 point left, 10 point right) was presented in the fixation square.

The sequence of a single example trial is shown in Figure 3.7. The participants were instructed to fixate on the square in the centre of the screen, but there was no manual task accompanying this. Information about the reward magnitude of the task was presented in the centre of the fixation square, as trials of different reward magnitude were interleaved within blocks. The total reward available (11 or 110) was presented in the fixation square so that it

was clear whether the trial was a high reward magnitude or low reward magnitude trial. Although it was not possible to receive 110 (100 vs 10) or 11 (10 vs 1) this method was employed to signal the type of trial and total reward available, and to distinguish the value from either value presented in the targets. A circular target was then presented on the left or the right side of fixation, and the participants were then required to make a manual response to the orientation of a letter T. The participants used the keyboard to make the response, and were asked to press one of four buttons which were spatially mapped to the side that the target was presented on. The experiment consisted of a practice phase (10 trials) and then 6 blocks (48 trials per block). Each block was preceded by a 9 point calibration procedure to allow accurate eye tracking.

Stimuli

All the stimuli (apart from reward values) were white (16.4 cd/m^2) and displayed on a grey background (10.4 cd/m^2). At the start of a trial a fixation square was presented centrally (1.1^o x 1.1^o; 0.18^o). Inside the fixation square was the number of points available in the trial (right target reward + left target reward), presented in red (15.8 cd/m^2). This was '110' for the high reward magnitude trials and '11' for the low reward magnitude trials. The trial started after an ISI of 2 seconds; this was of substantial length and kept constant to ensure processing of the reward magnitude of the current trial. The fixation square remained on the screen for the duration of the foreperiod until the target was presented.

The target presented in each trial was circular with another T or inverted T in the centre. The target had diameter of 1.25^o and a line thickness of 0.18^o and was presented at 6^o eccentricity from the centre on the left or the right-hand side. The target was presented for 1.5 seconds, regardless of when the manual response was made to the orientation of the T in the target. If a manual response was made, the target stayed on screen for 500ms and the reward

value of the trial in points was displayed in the centre of the target. The number of points were presented in a golden yellow colour (19.8 cd/m^2). If no manual response was made within 1.5s, then a message reading 'Please respond quicker' was displayed centrally (5^o above fixation and white) for 600ms.

There were two reward magnitude conditions (high and low) in the testing phase and trials of each magnitude condition were interleaved such that there was an equal number of each within blocks. In each block, the left and right targets were presented with equal probability (fixed at exactly 50% of trials). Half of the twenty four participants were assigned the right target as the high reward side, and for the other half the left target was associated with high reward. The high and low reward targets in the high reward magnitude condition were associated with 100 and 10 points respectively. In the low reward magnitude condition, the high and low reward targets were associated with 10 and 1 points.

Apparatus

The experiment was created using the Psychophysics Toolbox (Brainard, 1997) running within Matlab 2013b running on Windows 7. The display was 17" running at 75Hz and with a resolution of 1600 x 1200 pixels, and the viewing distance was 57cm.

Movements of the right eye were recorded at a sampling rate of 1000Hz by the Eyelink II (SR Research, Canada) which has a typical operating spatial resolution of 0.5^o. A chin and forehead rest were used to minimise head movements. A keyboard was used to record manual responses, in the numerical section on the right-hand side. For the left-hand side target, the number '4' key was pressed for a normal letter T orientation and the number '1' key for an inverted T. The number '6' key was required for the normal orientation in the right-hand side target, and the number '3' key for the inverted T. These keys were chosen as their proximal position was spatially mapped to the targets on the screen.

Design

There were two within participant repeated measures binary factors: reward magnitude and reward target side. These factors gave four conditions: high reward magnitude and high reward target side (100 points), high magnitude and low target (10 points), low magnitude and high target (10 points), low magnitude and low target (1 point). Half of the participants had high reward side fixed as left, and the other half as right. The dependent measures in the experiment were the manual response time to the letter T in the target and the saccadic latency.

3.4.2 Results

Manual Responses

The total number of trials recorded was 6912 (288 x 24 participants). Five trials were excluded from the analysis of manual responses, due to large negative response times likely caused by an error in the recording. There were 287 trials (4.2%) where participants made errors in their manual response (wrong key – side or letter orientation) and these were separated from the rest of the analysis. The distribution of errors across probability conditions is given in Table 3.5. After pre-processing of the manual data, 6620 (95.8%) trials remained to be analysed.

	Reward Magnitude	
	Low	**High**
Low Reward Target	3.2 (0 – 15.3)	4.2 (0 – 16.7)
High Reward Target	4.1(0 – 19.4)	5.1(0 – 29.2)

Table 3.5; Distribution of manual errors across the four conditions of the experiment. The values are the mean percentage of error trials out of the total possible trials in each condition, and the range across participants is given in brackets.

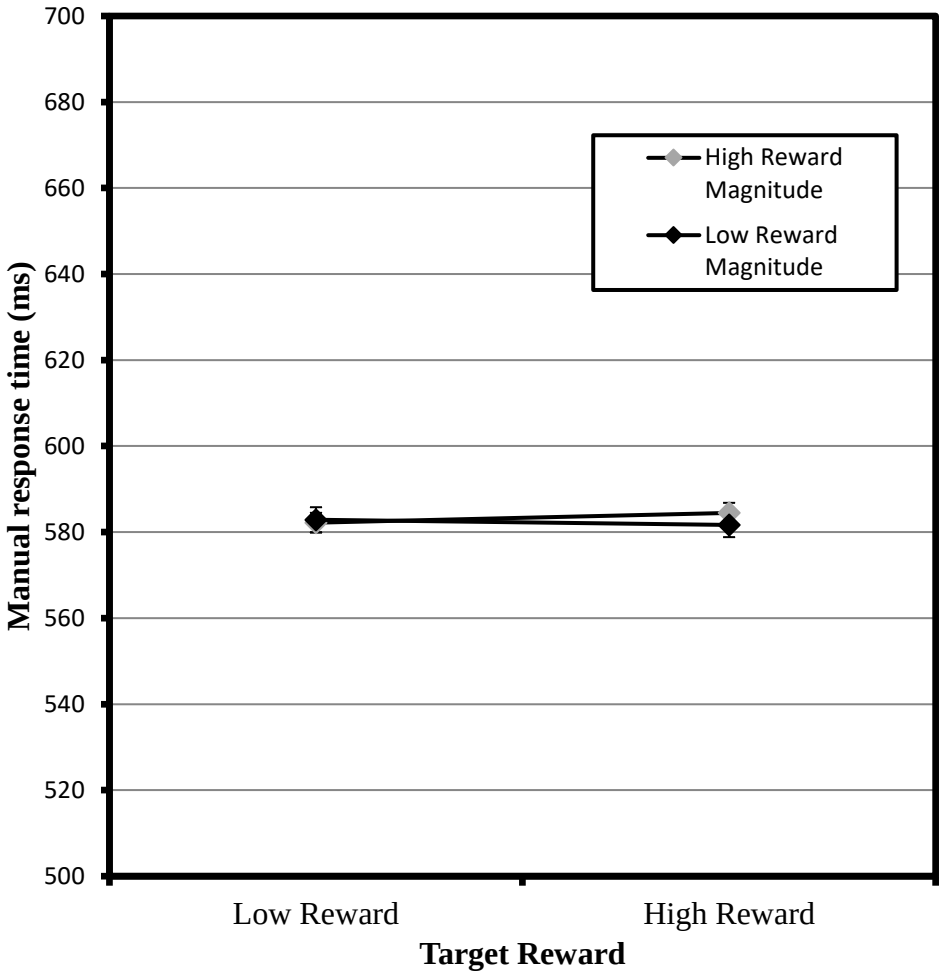

Figure 3.8; Graph of the mean manual response times across medians of each participant, for the three reward magnitude conditions. The within-subject error bars are the standard error of the mean.

The majority of errors (all but five) were errors in response to the orientation of the letter T, rather than a response to the incorrect target side. There was a marginally significant higher percentage of errors in the high magnitude condition than the low magnitude condition (Repeated Measures ANOVA: [$F(1,23) = 4.55$, $p = 0.04$]; Effect size (partial ETA) = 0.17). However, there was no effect of reward side on the distribution of errors. As is evident from Figure 3.8, there was no effect of reward magnitude or reward target side on the manual response times (Reward Magnitude: Repeated Measures ANOVA: [$F(1,23) = 1.44$, $p = 0.24$];

Effect size (partial ETA) = 0.06) (Reward Side: (Repeated Measures ANOVA: [$F(1,23) = 0.1$, $p = 0.75$]; Effect size (partial ETA) < 0.01).

Saccadic Responses

6912 trials were recorded and of these three trials were excluded from the first stage of saccadic analysis because there was an error in the recording of the first saccade. The median amount of drift away from central fixation at the starting point of the first saccade after target onset was calculated for each participant, separated in to participants with high reward right and high reward left. This was to investigate whether there was an offset in initial fixation towards either target side.

The mean offset of the medians across participants in the high magnitude trials was -0.001 degrees (towards low reward side) (CI 95%: -0.19 – 0.17) and in the low magnitude trials was -0.01 (towards low reward side) (CI 95%: -0.17 – 0.17). This indicates that there was no effect of reward magnitude condition on the starting point of the first saccade.

Reason for Exclusion	Number of saccades (trials) excluded and percentage of initial total	Total no of saccades **(Initial 6912)**
Initial fixation greater than 3 degrees from centre/starting point at 0	153 (2.21%; 0 – 5.9%)	6759 (97.79%)
Saccades in the incorrect direction (94.6% anticipatory)	242 (3.5%; 0 – 8.33%)	6517 (94.29%)
Anticipatory saccades (correct direction)	310 (4.48%; 0 – 10.76%)	6207 (89.8%)

Table 3.6; Pre-processing of saccadic data. The number of trials excluded/separated at each stage and the number of remaining trials is given. The percentage of total trials at each stage is stated in brackets, followed by the range across participants.

A general criteria was applied to the starting point of the first saccade in each trial after the analysis of starting point position, whereby saccades initiated more than 3 degrees (Euclidean distance) either side of fixation were excluded. No exclusion criteria were applied to the landing point of the first saccades. Saccades in the wrong direction were classed as error trials. A total of 153 trials were excluded from further analysis (Table 3.6), including the three trials excluded before the analysis of the offset at fixation. The remaining trials had a mean first saccade amplitude of 5.7 degrees (range across participants: 5 – 6.38 degrees) indicative of large hypo-metric saccades.

Most of the trials in which a participant initiated a saccade towards the incorrect target had a response time of 90ms or less. The correct response times of less than 90ms were additionally classed as anticipatory, along with the incorrect trials within the same criteria. Four anticipatory trials were removed due to a failure to record the first saccade mainly due to blinks. The remaining number of saccades to be analysed was 6207 (89.8%).

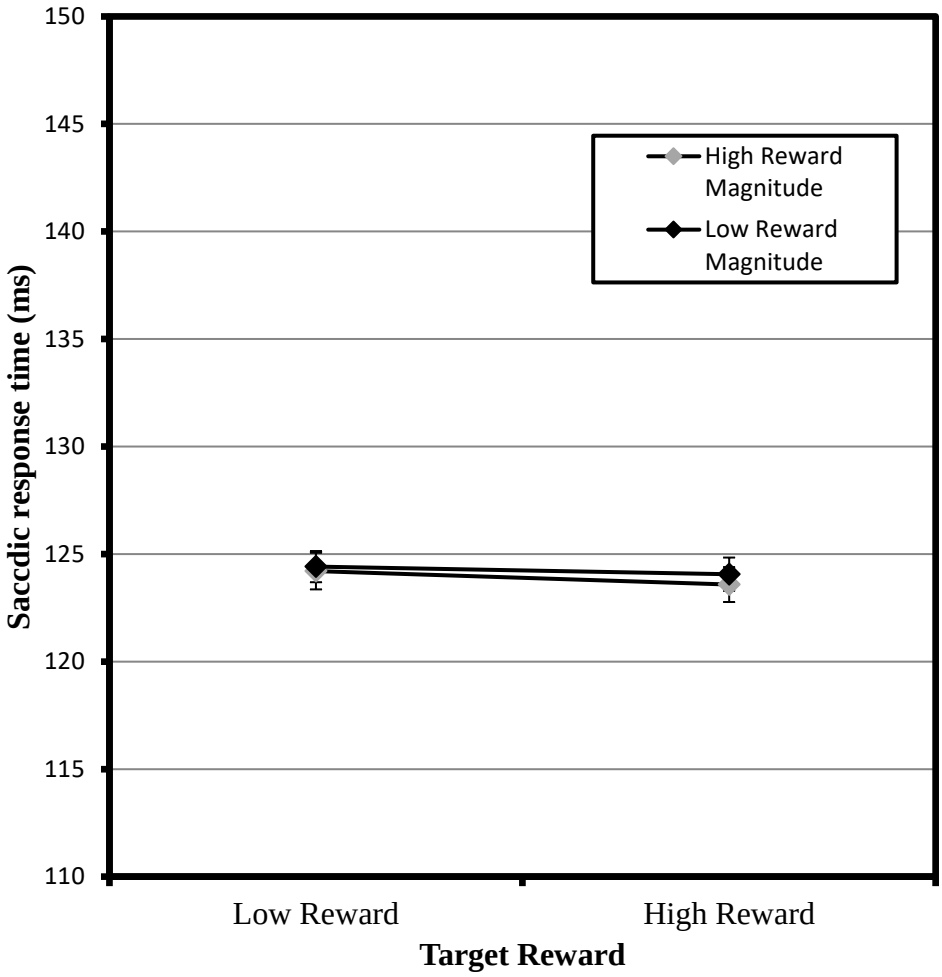

Figure 3.9; Graph of mean saccadic response times across medians of all 24 participants. The points on the x-axis denote the reward associated with the target. The within-subject error bars are the standard error of the mean.

Reward magnitude condition and reward target side had no significant effect on the saccadic response times (Figure 3.9) (Reward Magnitude: Repeated Measures ANOVA: [$F(1,23) = 0.21$, $p = 0.65$]; Effect size (partial ETA) = 0.01) (Reward Side: (Repeated Measures ANOVA: [$F(1,23) = 0.02$, $p = 0.89$]; Effect size (partial ETA) < 0.01). There was no effect of reward magnitude condition or reward side on the frequency of correct anticipatory saccades or the incorrect anticipatory saccades.

3.4.3 Discussion

There was no effect of reward across the saccadic and manual responses, aside from a marginal effect of reward on the frequency of errors in judgement of the orientation of the letter T. There are several factors that the absence of a reward effect could be attributed to. Although the existing literature suggests that rewards are processed relative to the other available rewards in the environment (Milstein & Dorris, 2007, 2011), the rapid change in reward magnitude from trial to trial could confound any possible effects of absolute reward value on behaviour. This theory is supported by previously discussed research into the persistence of an observed reward effect, showing that exogenous capture of the eyes is increased and saccadic responses are faster to targets previously associated with reward (Dunne et al., 2015; Theeuwes & Belopolsky, 2012). Even though relative reward association does not change - the more highly rewarded side is consistent across our experiment – the absolute values change between trials. These changes will frequently adjust the expected value of each target, not allowing sufficient time to cause a consistent adjustment in dopamine activity and thus a modulation in behaviour, particularly given the long-term time course of the previously established reward effect (Dunne et al., 2015; Theeuwes & Belopolsky, 2012).

The points-based reward schedule in this experiment might not have been salient enough to engage the reward system in the brain; it could be that the values were not explicitly linked enough to the monetary value. However, given that we have not seen a reward effect across the two previous studies, this is unlikely to be the only contributing factor. The accumulation of rewards having no link to the performance of participants may have contributed to the absence of reward effect across Experiments 3 to 5. This was initially decided to ensure that the paradigms investigating reward and probability were as similar as possible, to allow for close comparison of the processes. However, the nature of rewards in our environment is that they are often inextricably linked to performance; in many scenarios, if we respond correctly or do a good job in a task, we seek to be rewarded. This could be a key difference between primary and secondary rewards in these kinds of tasks. As discussed in the Introduction (Chapter 1), secondary rewards (in delay discounting) are more susceptible to contextual framing than primary rewards (McClure et al., 2007; cited in Lamy, 2007). Rewarding a nonhuman primate for completing a saccade by giving them an immediate juice reward is sufficient to engage the reward system, but rewarding human participants with an abstract value that is not immediate and not explicitly linked to how quickly or accurately they performed the task is unlikely to be sufficient. Additionally, when the paradigm of these experiments involves aspects that are similar to how a computer game might be played (responding to events on a screen), many participants may be used to receiving immediate reward or positive/negative feedback for successfully completing each step of the task. This issue also relates to the absence of time pressure in Experiments 3 to 5; reward-based games are often directly related to the speed-accuracy trade-off of responses, and this is relied on to increase the motivation to respond to keep the participant engaged.

Another aspect of the reward schedule that could have prevented a reward effect is the presentation of the total reward available in the fixation square. As this represented the total

reward available on each trial, rather than the expected value, it was always the largest value presented relative to the values associated with the targets. This value could have become associated with the fixation square, therefore making the fixation square more salient than the targets themselves. This is supported by the research previously discussed in this chapter and in Chapter 1, demonstrating that saccade preparation is spatially allocated based on the relative value of potential targets, and neurological studies suggesting that rewards are processed relative to other rewards available (Elliott et al., 2008; Milstein & Dorris, 2007, 2011). This confound would interfere with any possible reward effect on responses to the targets.

In the next reported experiment we addressed these in a paradigm where the motivation to respond quickly and accurately was increased by a fixed time window and partly performance-related rewards. We employed a random lottery incentive reward system in Experiment 6, which means that one trial is selected at random from the whole experiment and the participant receives the reward from that trial (Cubitt, Starmer & Sugden, 1998). The validity of this system in economic experiments has been tested and shown to have no significant difference on behaviour in comparison to a design where participants are rewarded on every trial (Cubitt et al., 1998). This addresses the problem of the salience of rewards, as large monetary reward values can be used without having to rely on a points-based rewards system that may not provide enough of an explicit link to monetary rewards.

3.5 Experiment 6: Lottery controlled reward

3.5.1 Methods

Participants

Eighteen participants (5 male) were recruited from the student population of the University of Bristol (approximate age range 18-25). All had normal or corrected-to-normal vision. Participants were reimbursed £7 for their time and received a variable performance related reward (£0, £0.1, £1 or £10) as outlined below. The study was approved by The Faculty of Science Human Research Ethics Committee at the University of Bristol.

Procedure

The sequence of event in a single example trial are illustrated in Figure 3.10. The task for the participants was to respond to the "T" stimuli that appeared to the left or right of a central fixation point. The response required was to indicate the orientation of a letter with a manual button press. If the letter was on the left-hand side of the display the response was made with the left hand and if the letter was on the right-hand side the response was made with the right hand. The experiment consisted of a practice phase (10 trials), a pre-test phase (48 trials), and then 4 blocks (72 trials each) of the testing phase. Each block was preceded by a 9 point calibration procedure to allow accurate eye tracking.

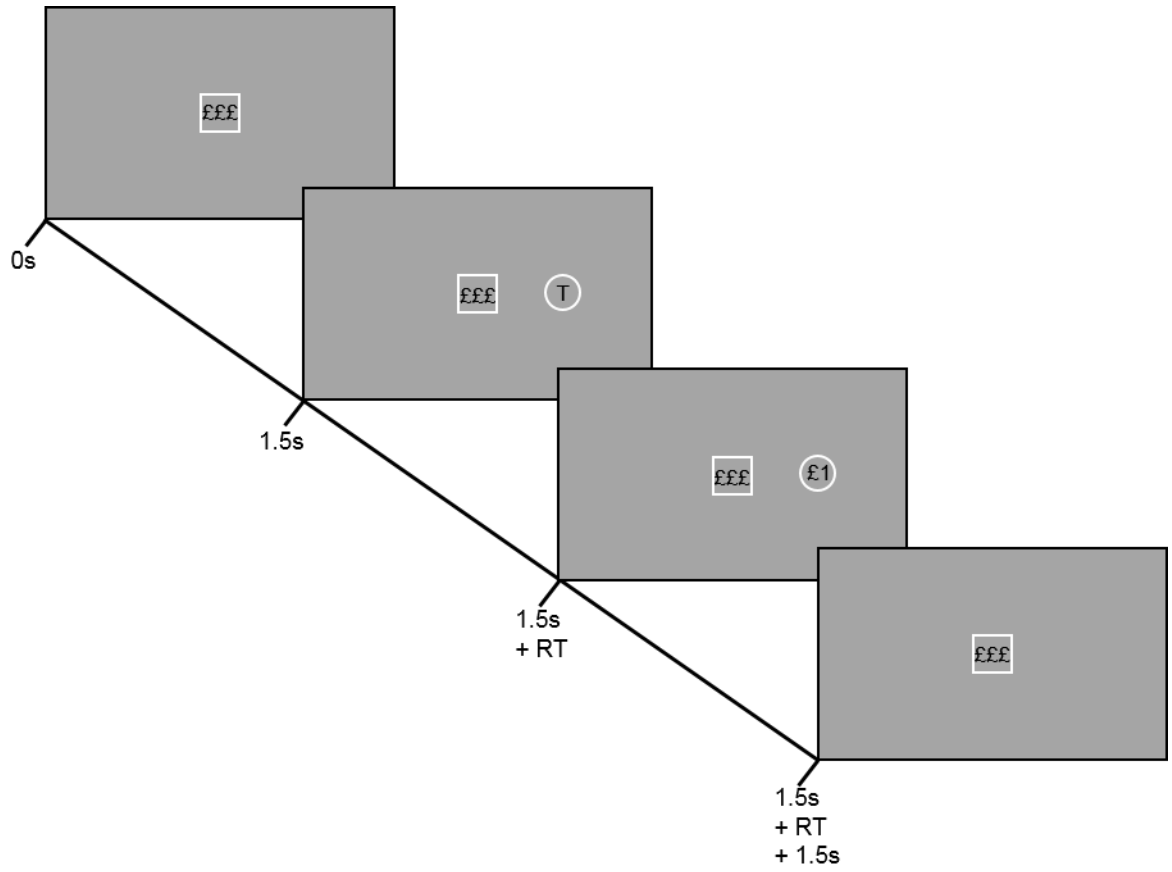

Figure 3.10; Diagram of the experimental procedure in the testing phase. The figure depicts an example trial from a high magnitude block with a target appearing on the right-hand side, where the high reward side for the participant is the left.

In the testing phase correct responses in each trial were associated with a reward. The reward value was displayed on each trial at the location of the target after the response was given. Participants were informed that a trial from the testing phase would be selected at random at the end of the experiment and that they would receive that reward. If the manual response was too slow or incorrect then a message was displayed after the trial. Participants were informed at the outset of the experiment that they were receive no reward if one of these error trials was selected at the end of the experiment. All participants were explicitly told the

reward values associated with the block they were about to perform and also the reward values associated with each side of the display.

Stimuli

All stimuli and the fixation point were white (16.4 cd/m^2) and displayed on a grey background (10.4 cd/m^2). A trial commenced with a centrally presented fixation square (1.65^o x 1.65^o; 0.18^o thick) which was presented for 1.5s. This was immediately followed by the circle target with a T or inverted T in the centre. The circle had a diameter of 1.85^o and a line thickness of 0.18^o. The letter T subtended 0.3^o, which is a size that Körner and Gilchrist (2007) have shown is small enough not to be recognised reliably above chance when fixation was 3^o away from the stimuli. This ensured that participants had to make an accurate target directed saccadic eye movements towards the target to complete the task. The target was presented on the left or right in an equal number of trials across all phases of the experiment at 6^o eccentricity.

In the testing phase there were two block types – low reward blocks and high reward blocks. The fixation square contained a single pound sign (£) in the low reward magnitude blocks and three pound signs (£££) in the high magnitude blocks. All pound signs were presented in red (15.8 cd/m^2).

Across the testing phase one side of the display (left or right hand targets) was also consistently associated with a higher reward than the other. In the high reward blocks, the reward associated with the high rewarded side was £10, and the lower reward side was £1. In the low reward blocks, the value for the highly rewarded side was £1, and the lower target side was £0.10. These reward values (including the pound sign) were presented inside the corresponding target after a successful manual response to the target in each trial. The rewards were presented in a golden yellow colour (19.8 cd/m^2). If the participant was too slow, or made

an incorrect response, no reward value was shown and a message appeared in the centre of the screen reading 'Wrong! No reward' or 'Too slow! No reward' (2.5^{o} above fixation and white). The reward value (or error message) stayed on the screen for 1.5 seconds.

The pre-test block was included in the experiment to set an individual criteria for the time-out for the testing phase. In the practice and pre-test phases the fixation square contained an X rather than a £ sign as no rewards were given on these trials. The distribution of manual response times from the pre-test block of the experiment were used to calculate a 70th percentile of each participant's reaction time (ms) distribution. Without informing the participants, their individual 70th percentile values were used as the length of time the target and letter T would be visible for in the testing phase trials after which they would receive the time-out notice and forfeit the chance of gaining the reward on that trial. This ensured motivation to respond quickly as participants inevitably were too slow on some trials.

Apparatus

The experiment was controlled by Psychophysics Toolbox (Brainard, 1997) running within Matlab 2013b running on Windows 7 The display was 17" running at 75Hz and with a resolution of 1600 x 1200 pixels, and the viewing distance was 57cm.

Movements of the right eye were recorded at a sampling rate of 1000Hz by the Eyelink II (SR Research, Canada) which has a typical operating spatial resolution of 0.5^{o}. The participants were provided with a chin and forehead rest to minimise head movements. Manual response were recorded via the keyboard (numeric right-hand section) – key 4 and 1 for the left hand and key 6 and 3 for the right hand responses.

Design

There were two within participant repeated measure binary factors: block (high or low reward) and side (high or low reward) leading to four conditions: high block, high side (£10 reward); high block, low side (£1); low block, high side (£1); low block, low side (£0.1).

The order of the blocks and the side with the high reward were counterbalanced across participants. The dependent measures were the manual response time and saccade latency.

3.5.2 Results

Manual Responses

A total of 5184 trials were recorded (288 x 18 participants). One participant was removed before further analysis because over 50% of their responses saccadic responses did not meet the fixation criteria applied. Given the magnitude of this percentage (68.4%), I decided to remove this participant from the manual analysis as well. I analysed the remaining manual reaction times excluding 839 time-out or response errors, leaving a total of 4131 data points. The distribution of errors is shown in Table 3.7. The range of the total percentage of time-out/response errors of each participant's responses was 3.1% - 36.1%.

Side	Block Type			
	High Block		Low Block	
	Time-Out	Response Errors	Time-Out	Response Errors
High Reward	6.62 (0-13.9)	7.19 (0-20.8)	7.92 (1.40-19.4)	6.78 (0-20.8)
Low Reward	9.89 (1.39-34.7)	8.25 (1.39-19.4)	9.72 (2.77-25.0)	6.54 (0-19.4)

Table 3.7; The mean percentage of errors (of the total number of possible trials in each condition), for both types; time-outs and response errors. The range across 17 participants is given in brackets

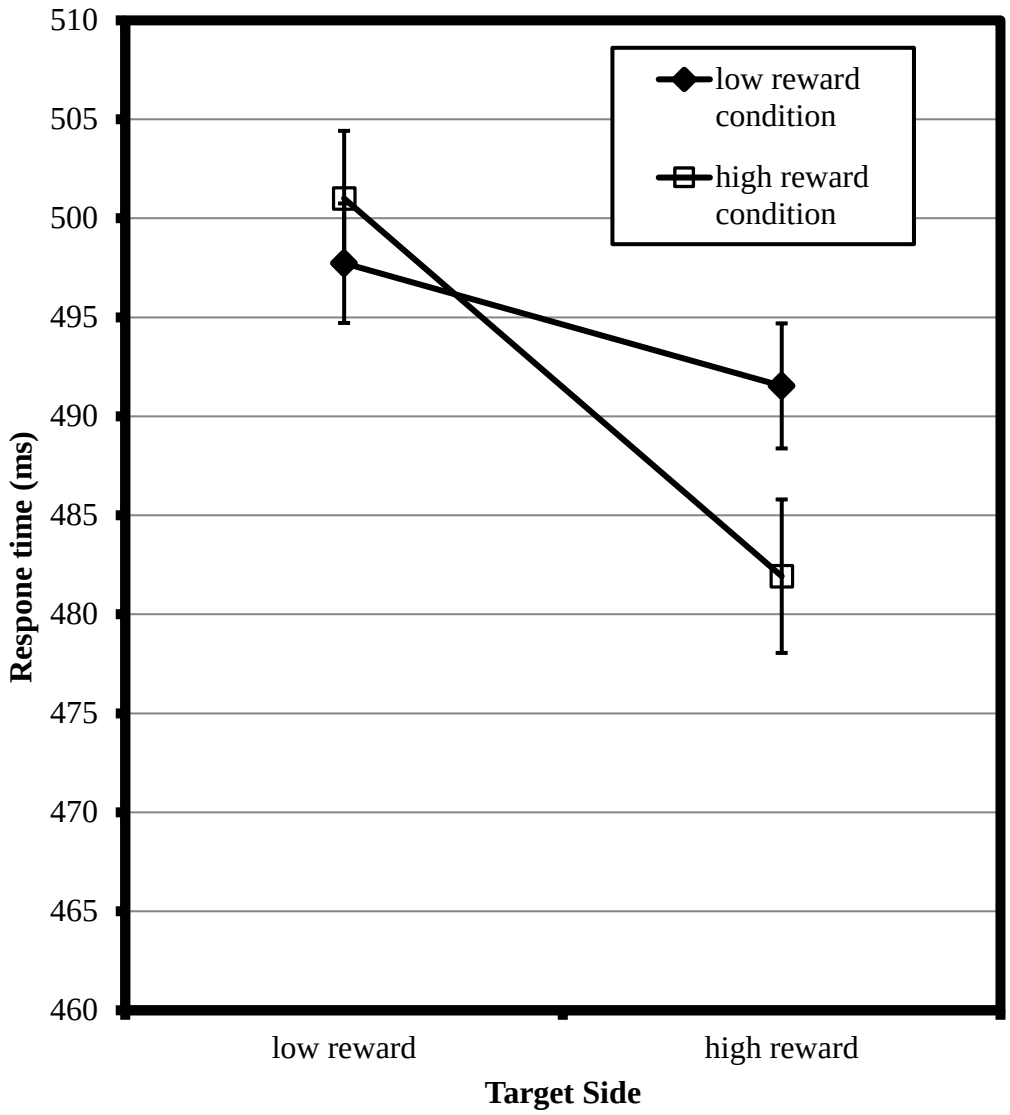

Figure 3.11; Graph of mean manual response times across medians of all 17 participants. The two lines show the two different conditions (high reward magnitude and low reward magnitude) and the two x-axis points denote the reward associated with the targets (high and low reward). The high and low reward sides include responses to targets in both hemispheres, as these were balanced across participants. The within-subject error bars are the standard error of the mean.

Reward associated with the target side had a significant effect on manual reaction times leading to a 19.1ms (95% CI: 6.44 – 31.73) decrease (high condition) and 6.2ms (95% CI: -2.5 – 14.9) decrease (low condition) in response times for the high reward side (Repeated Measures ANOVA: [$F(1,16) = 8.49$, $p = 0.01$]; Effect size (partial ETA squared = 0.33). The effect of block was not significant, but the interaction between the block and target side was significant [$F(1,16) = 7.87$, $p = 0.01$; Effect size (partial ETA squared = 0.32)]. There was no significant effect of target side/reward condition on the frequency of errors, or between the different types of errors (Table 3.7).

It was observed that reaction times to the £1 target in the high reward condition (low side) are on average slower by 9.47ms (95% CI: -2.27 – 21.22ms) than to the target associated with the same reward in the low reward condition (high side) (Figure 3.11), however this difference was not significant. This trend suggests that the effect of the reward values on reaction times may dependent on the context within which they are presented.

Saccadic Responses

As a first step in analysing the saccadic response data, we looked for evidence for a systematic offset in initial fixation towards the high reward side by analysing the amount of drift away from the central fixation in the starting point of the first saccade after target onset. The mean offset across participants was 0.062 degrees away from the more highly rewarded side (CI 95%: -0.290 – 0.165 degrees). There was no evidence of a modulation of this effect by block type (-0.058 vs -0.067; $F<1$).

Following this analysis we applied a general exclusion criteria to initial fixation starting point. As there were no explicit fixation instructions in the task we applied a liberal criteria and excluded trial where the initial fixation was great than 3 degrees either side of the fixation box. There was no spatial exclusion criteria on the landing point of the first saccade, but

saccades in the wrong direction were discarded as errors. The remaining trials had a mean first saccade amplitude of 6.19 degree (range across participants 5.43 – 6.74). Showing that all participants were, in general, making a large hypo-metric orienting saccade for their first saccade.

Reason for Exclusion	Number of saccades (trials) excluded and percentage of initial total	Total no of saccades **(Initial 4896)**
Initial fixation greater than 3 degrees from centre	584 (11.9%; 0 – 33%)	4312 (88.1%)
Saccades in the incorrect direction (95% anticipatory)	118 (2.41%; 0 – 7.29%)	4194 (85.7%)
Anticipatory saccades (correct direction)	276 (5.64%; 0 – 22.9%)	3918 (80.0%)

Table 3.8; Pre-processing of saccadic analysis. Details of the data removed from further analysis, and the reasons for removing them. Percentage of initial number of saccades is included in brackets, followed by the range across participants. One participant was discarded completely from analysis, and is not included in this pre-processing.

95% of the saccades directed in the wrong direction had a latency of less than 90ms and we assume that these are anticipatory and were excluded from further analysis (Table 3.8). In addition to reflect this anticipatory criteria we exclude all saccades with reaction times less than 90ms in the correct direction.

After removing the invalid, anticipatory and error saccades, the total number of analysed saccades was 3918 (80.0%).

There was no significant effect of reward condition (block) or reward side but there was a significant interaction (Repeated Measures ANOVA: [$F(1, 16) = 13.45$, $p = 0.002$]; Effect size (Partial ETA) = 0.46). Post-hoc testing on the high reward block in isolation shows a significant effect of reward side (Mean 125ms vs 132ms, Paired Samples t-test: [$t(16) = -2.769$, $p = 0.014$]). This could indicate that although reward affects saccadic reaction times relatively (high vs low within a block), the overall saliency of a highly rewarded condition has some influence. Further analysis showed no effect of reward condition or reward side on the frequency of anticipatory saccades.

In order to investigate if there was a relationship between individual performances across the two response modalities (saccadic and manual) we calculated the size of the reward effect for each of the 17 participants in the high and the low reward blocks separately. There was no strong correlation between the two response modalities: the Pearson's correlation r was 0.457 ($p = 0.065$) and 0.365 ($p = 0.149$) for the high and low reward conditions respectively.

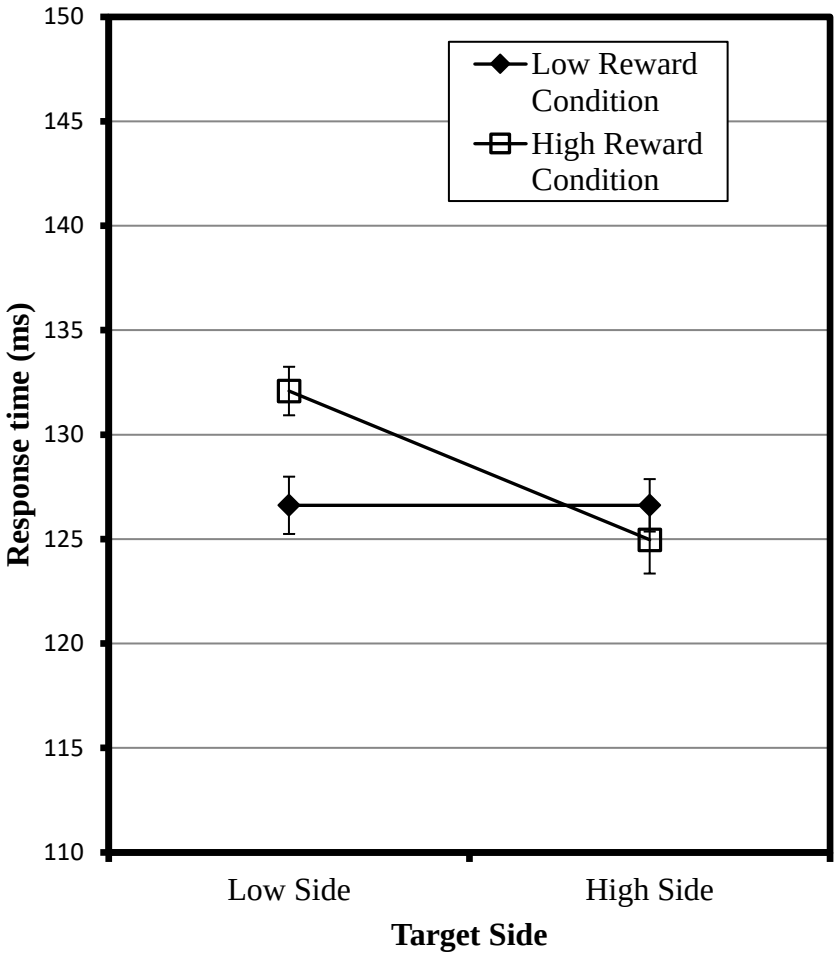

Figure 3.12; Graph of mean saccadic response times across medians of all 17 participants. As in Figure 2 the lines show the two different conditions (high reward magnitude and low reward magnitude) and the two x-axis points denote the reward associated with the targets. The within-subject error bars are the standard error of the mean.

3.6 Discussion

There is evidence that both saccadic and manual responses were faster to visual targets that were associated with higher rewards when compared to targets associated with lower rewards. Overall these effects were larger for the manual responses than for the saccadic responses. However, given the absence of any effect in Experiments 3 to 5 (besides a marginal affect on saccadic response in Experiment 3), the effect found is clearly relatively specific to the reward schedule and paradigm. Both types of response were modulated by the overall reward level in the block. For low as compared to high reward block, there was a reduction in the difference between high and low reward targets for manual responses and the absence of any evidence of an effect of reward for saccadic responses in the low reward blocks.

The higher reward targets in the low reward block carried the same level of monetary reward as the lower rewarded target in the high reward block (£1 in both cases). These conditions allowed an investigation to see if the reward effects were associated with the absolute value of the reward or the relative value of the reward in that context. There was a strong, but non-significant, trend for the context to have an effect on manual reaction times which resulted in faster responses when the reward was the higher rather than the lower of the two reward values.

This effect of reward on both the manual and saccadic component of the response is consistent with idea that reward processes mediated by dopamine neurons affect all response systems irrespective of response modality (Schultz, 2010). However the clearest test of this association would be a strong correlation between the size of the reward effects across modalities. In the current experiment I found no such strong correlations. In other words, participants who showed a particularly strong reward effect in their saccadic responses were

not necessarily the ones who showed a strong reward effect in their manual responses, or vice versa.

As discussed in the introduction, there is evidence to suggest a common system for reward processing that affects all motor systems to optimise the chance of getting the reward. Reward-related activity in the dopamine system initiates a series of events—one stage of which involves the anterior cingulate that eventually leads to changes in sensory representation (Hickey, Chelazzi, & Theeuwes, 2010a). Anterior cingulate and surrounding cortex is also known to be fundamentally involved in the control of attention and processing of attended stimuli (Hickey et al., 2010a; Mesulam, 1999; Hopfinger, Buonocore & Mangun, 2000) A study using TMS (transcranial magnetic stimulation) found that the ACC (anterior cingulate cortex) facilitates implementation of a selected action, and is activated across three different output modalities (verbal, manual, oculomotor) (Paus, 2001). However, the difference in the results reported here between the effect of reward on response times in manual and saccadic modalities might suggest otherwise. These differences could be explained by the effect that reward has on motor systems over time, if dopaminergic activation drives the reaction time effect. The dopamine reward signal is rapid and differs from the slower dopamine responses that have been associated with uncertainty, punishment and movement (Schultz, 2007). Activations in dopamine neurons to primary rewards, novel stimuli and reward-predicting stimuli have latencies of 60-100ms and endure for less than 200ms (Schultz, 2007). Given our results show very fast saccadic reaction times, it could be that the saccadic response is initiated too early to be strongly affected by the dopaminergic activation. This could be plausible if we assume that the dopamine activation occurs after the onset of the target given that the reward values are known. The manual responses however are much slower, and therefore could be affected more by the dopamine surge.

A number of studies have identified individual differences in sensitivity to reward. For example, Hickey, Chelazzi and Theeuwes (2010b) measured trait reward-seeking using a personality index, and found this correlated with the magnitude of reward priming in a visual search task. The term 'reward priming' was used to describe the bias towards selection of objects previously characterised as rewarding (Hickey et al., 2010b). They also found in a similar study that the ERP component known to be a sufficient index for reward processing in the anterior cingulate cortex is elicited during reward feedback processing, and that the magnitude of this predicts the effect of reward on each participant's behaviour during visual search (Hickey et al., 2010a). Linking reward to a personality trait and linking it to a single neural system would suggest that the magnitude of the reward effects across response types should be correlated across participants. If a participant is particularly reward sensitive this sensitivity should be expressed both in their saccadic and their manual responses. In the current study there is no evidence in favour of such a correlation, despite having quite large variability in reward sensitivity across participants and finding reliable reward effects overall in both response types. The absence of correlation could be due to the general absence of correlation between the two response modalities. However, given the results of Experiments 3 to 5, large variability in the reward effect is also likely to be attributable to the instability of the effect in general and it's sensitivity to the exact specifications of the paradigm.

The effect of a perceptual task at the saccadic target could explain why there was no correlation between response modalities. The inclusion of a perceptual task at the landing point of the saccade clearly constitutes a form of information worth gathering as a correct response leads to receiving reward. Supporting this Montagnini and Chelazzi (2005) found that a perceptual task at a saccadic target reduces reaction times by more than 15%, and Bray and Carpenter (2015) showed that saccades to locations expected to provide information about a subsequent target are faster. The saccade serves to gather information at the current target, and

the effect of reward may be to allocate more attentional resources to the highly rewarded target (Hickey et al., 2010a). Conversely, the manual response is more explicitly goal-oriented and directly linked to the correct/incorrect response and thus retrieval of the varying reward value. There is a clear difference between these two tasks which supports the more reliable reaction time modulation in manual compared to saccadic responses.

In Experiment 6 there was a reduction in the difference between high and low reward targets for manual responses and no evidence of an effect of reward for saccadic responses in the low reward blocks. The modulation in reaction times between high and low reward targets could be explained by the effect of reward on the salience of stimuli. The general salience of stimuli has a similar effect to reward value on attentional processes. Many dopamine neurons are activated by intense and physically salient stimuli, especially when these stimuli are novel (Schultz, 2010). In their study of reward modulation reducing spatial neglect, Malhotra, Soto, Li and Russell (2012) suggested that the relative salience of targets may be changed following varying incentive gain and performance feedback. Hickey, Chelazzi, and Theeuwes (2014) have supported this theory by showing that when targets have been previously associated with reward, participants are primed to return to the target location and biased away from a salient distractor location. Furthermore, Failing and Theeuwes (2014) showed that non-rewarding salient cues and rewarding non-salient cues similarly capture attention, indicated by a decrease in reaction times when the cues validly indicate target location. Given this evidence, in Experiment 6 the reward associated with the targets in the low reward condition may not increase salience sufficiently to bias attention towards the higher target. This is supported by the absence of reward effect in Experiments 3 and 4 where low reward values are deployed.

It is interesting to examine the similarities between the results of this chapter and Chapter 2 where we investigated manipulations of probability. The modulation of reaction times in response to varying reward values associated with target locations is similar to the effect of

varying prior probability of the target locations. Additionally, in a similar paradigm of the last experiment of Chapter 2 and Experiment 6 of this chapter, we saw a more significant effect of both manipulations on manual responses compared to saccadic responses. Probability is often discussed in the literature as a form of prior information; if we categorise reward in the same way, this could explain why similar effects from reward values assigned to targets on reaction times are found. However, it could be argued that as the purpose of saccades is to acquire information about the environment, a monetary reward value assigned to a target should not have a similar effect to modulating probabilities (Bray & Carpenter, 2015). This is particularly true given that the participants are explicitly informed of the reward schedule in our experiment. Moreover, the similarities between the effect of reward value and prior probability on saccadic responses could suggest a closer relationship; it has been suggested that a more appropriate way to describe them would be 'bias' rather than 'information' (Bray & Carpenter, 2015; Lauwereyns, 2010). This supports the adaptive argument for biasing attention to rewarding locations that are otherwise uninformative: environmental stimuli that have provided rewards (such as food) in the past are worth paying attention to in the future (Hickey et al., 2010a).

In order to understand the similarities between the effect of reward and probability on saccadic and manual responses, the next step is to combine these two forms of 'bias' within on paradigm to see if they interact in a simple manner. Studying this across two response modalities again will additionally help to corroborate and further understand the differences between these processes.

CHAPTER 4

4.1 Introduction

In Chapter 2 and 3, I reported a series of studies investigating the effect of reward and probability on saccadic and manual response times. In the final studies of those chapters I established a paradigm that has the potential to reliably show both a robust probability and reward effect. In the current chapter I report a systematic investigation of both of these effects (and how these effects change with age) and importantly investigate for the first time the interaction between these two determinants of performance.

To reiterate, in these experiments participants are required to make a manual response to a target which can be in one of two locations (left or right of the centre of a computer screen) The first manipulation changed the likelihood of a target occurring on the left or the right-hand side of the display – I have called this the probability manipulation. In the experiments reported in Chapter 2 this manipulation lead to faster manual responses to targets that were placed on the more frequently occurring side and a reduction in the latency of the initial saccade to the target. Again the experiments in Chapter 2 suggest that this effect is relatively sensitive to the exact experimental conditions. This is perhaps surprising given that for saccadic response that this is a well-established effect (Basso & Wurtz, 1997; Carpenter & Williams, 1995; Dorris & Munoz, 1998; Jóhannesson et al, 2013; Koval et al, 2004; Liu et al, 2010, 2011; Noorani & Carpenter, 2013).

The second manipulation is to set a differential in the amount of reward associated with correct responses on one side as opposed to the other. In the experiments in Chapter 3 I found that this differential reward lead to faster manual responses to targets on the more highly rewarded side and that the initial saccade to the target was also faster to that side. However this

effect appeared to be sensitive to the type of reward schedule as well as other specific features of the design. Having found a paradigm on which both effects appear to be present I can now study them concurrently and investigate how they interact.

As discussed in Chapter 1, one popular framework for modelling changes in response times are accumulator models (Brown & Heathcote., 2008; Carpenter & Williams, 1995; Ratcliff, 1978). Within such models a motor response results from activity in a decision unit rising over time towards a threshold. When activity reaches that threshold then the motor response is initiated. Two factors determine how quickly a response is made – the rate of rise of activity in the unit and the setting of the threshold. In these models the threshold level and the initial activity level are indistinguishable. Marshall et al. (2012) have argued from a computational perspective that this change is best implemented in a change in the baseline rather than the threshold; this suggestion is supported by neurophysiological evidence (Forstmann et al., 2008). One open question within this modelling framework is how different factors that affect latency are combined. As discussed in Chapter 1, the effects of reward and probability have been postulated in saccadic responses to affect the baseline of the accumulator rather than the rate of rise (Carpenter & Williams, 1995; Dunne et al., 2015). This is supported by the finding in Chapters 2 and 3 that manipulating reward and probability has a similar effect on responses, and both have a stronger effect on manual responses than saccadic in a similar paradigm. As discussed in the Discussion of Chapter 3, given these similarities reward and probability could be described collectively as 'bias' rather than prior 'information' (Bray & Carpenter, 2015; Lauwereyns, 2010); in the current series of experiments one suggestion would be that both reward and probability both act on a single accumulator to shape the resultant latency distribution. In Experiment 7 in this chapter, I test this theory explicitly by combining modulations of probability and reward. If increasing reward value and probability associated with a target has an additive effect on the latencies, this would suggest both factors affecting a

single accumulator framework. Additionally, it would follow that decreasing one factor while increasing the other factor (matching reward rates across two targets) would effectively cancel out the effects of probability/reward bias.

As mentioned, a stronger effect of reward and probability was observed on manual responses in comparison to saccadic in a similar paradigm (Experiment 2 and Experiment 6). In the reward manipulation this was postulated to be due to several factors: dopaminergic activation possibly being too slow to affect rapid saccadic responses, and the clear motivation on the goal-orientated manual response to the perceptual task in the paradigm used. In the probability manipulation, this finding was also linked to the time course of the two response modalities: longer ISIs were associated with a stronger manual response. Again the clear motivation of the goal-orientated manual response was likely to be a strong factor. Given this, in Experiment 8 and 9 in this chapter, only manual responses were recorded when investigating reward and probability effects in isolation in a matched paradigm. Additionally, in the final experiment of Chapter 3 it was found that very small reward values (such as £0.10) were unlikely to affect the saliency of the target enough to produce an effect relative to the other larger reward values (such as £1): therefore, in all experiments reported in this Chapter, the lowest reward value used was £2.

One of the aims of the research reported in this thesis is to establish a paradigm that can be used to study the cognitive side effects of deep-brain stimulation (DBS) in Parkinson's patients. Given that this disease is associated with patients who are typically older than the student participant group in the studies carried out so far, it is important to address the changes that occur in these effects over the lifetime and in particular the effects studied here. In an experiment using a four-alternative choice-reaction task, event-related potentials (ERPs) were recorded to analyse at what stage of processing (stimulus processing, response selection, and motor-response generation) age-related (average 58 years) response slowing occurred,

compared to younger controls (average 22 years) (Falkenstein, Yordanova & Kolev, 2006). They found that age-related delay occurred during the central stage of response generation, and the timing of stimulus processing and response selection mechanisms were virtually unaffected; this was found in both visual and auditory stimulus, suggesting a modality-independent deficit produces delayed responses in older adults (Falkenstein et al., 2006). Given the general response slowing in this population, it is important to have a control experiment for research with Parkinson's patients. Specifically, this research suggests that there would not be an issue with utilising the same paradigm for older adults, rather that there would need to be more allowance for the time frame that they were able to respond in.

This chapter reports a set of three experiments that investigate the interactions between the reward and probability effect. In Experiment 7, this is carried out across two response modalities, saccades and manual responses. Despite the lack of correlation in the results of the experiments in Chapters 2 & 3, I decided to continue to test both responses concurrently as some degree of effect was seen in both and could still be influenced by the interaction of reward and probability. In Experiment 8 and 9 only manual responses are recorded. In Experiment 7, I combine manipulations of reward and probability to see how the effects explored in Chapter 2 and 3 interact. This takes the form of a pair of experiments (1a and 1b) which combine both effects and investigate their interactions. In the first of these experiments (1a) I manipulate probability while keeping reward fixed and in the second (1b) I manipulate reward while keeping probability fixed. In both experiments this allows me to have conditions where the reward rate is constant across the two possible target sides, this is achieved by having one side with a high reward but a low probability matched with the other side which would have a low reward but high probability of occurring. In this way it was possible to set up the displays so that over a block of trials both sides would deliver the same average chance of reward. In Experiment 8, I investigate the effects of reward and probability separately in a

matched paradigm in the manual responses of participant's dominant hand. In Experiment 9, I compare the effects of reward and probability in the healthy older adult population.

4.2 Experiment 7: Combined reward and probability

4.2.1 Methods

Participants

Thirty six participants (9 male) were recruited from the student population of the University of Bristol (approximate age range 18-25). All had normal or corrected-to-normal vision. Participants were reimbursed £7 for their time and, if the manual response on that trial was correct and completed before the time-out, also won the reward value from a randomly chosen trial (£2, £6, or £10). The study was approved by The Faculty of Science Human Research Ethics Committee at the University of Bristol.

Procedure

The sequence of event in a single example trial are illustrated in Figure 4.1. The task for the participants was to respond to the "T" stimuli that appeared to the left or right of a central fixation point. The response required was to indicate the orientation of a letter with a manual button press. If the letter was on the left-hand side of the display the response was made with the left hand and if the letter was on the right-hand side the response was made with the right hand. The experiment consisted of a practice phase (10 trials), a pre-test phase (48 trials), and then 9 blocks (48 trials each) of the testing phase. Each block was proceeded by a 9 point calibration procedure to allow accurate eye tracking.

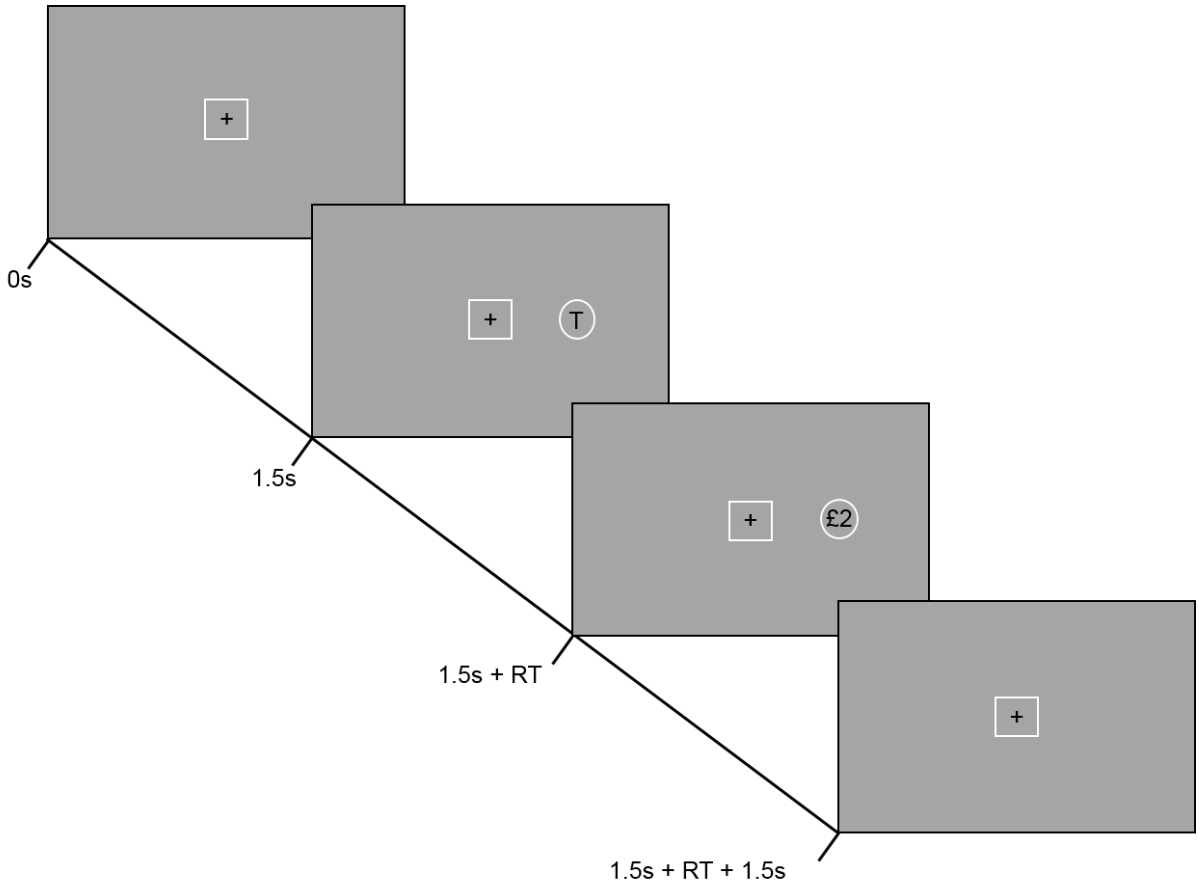

Figure 4.1; Diagram of the experimental procedure in the testing phase. The figure depicts an example trial where the target appears on the right-hand side and the high reward side for the participant is the left.

In the testing phase correct responses in each trial were associated with a reward. The reward value was displayed on each trial at the location of the target after the response was given. Participants were informed that a trial from the testing phase would be selected at random at the end of the experiment and that they would receive that reward. If the manual response was too slow or incorrect then a message was displayed after the trial. Participants were informed at the outset of the experiment that they were receive no reward if one of these error trials was selected at the end of the experiment. All participants were explicitly told the

reward values associated with the block they were about to perform and also the reward values associated with each side of the display.

Stimuli

All stimuli and the fixation square were white (16.4 cd/m^2) and displayed on a grey background (10.4 cd/m^2). A trial commenced with a centrally presented fixation square (1.65^o x 1.65^o; 0.18^o thick) which was presented for 1.5s. The fixation square in the testing phase contained three pound signs (£££) presented in red (15.8 cd/m^2). This was intended to increase salience and motivation across the rewarded phase of the experiment.

This was immediately followed by the circle target with a T or inverted T in the centre. The circle had a diameter of 1.85^o and a line thickness of 0.18^o. The letter T subtended 0.3^o, which is a size that Körner and Gilchrist (2007) have shown is small enough not to be recognised reliably above chance when fixation was 3^o away from the stimuli. This ensured that participants had to make an accurate target directed saccadic eye movements towards the target to complete the task. The target was presented on the left or right in a varying number of trials across all phases of the experiment at 6^o eccentricity.

Experiment 7a. Probability Manipulation

The testing phase consisted of nine probability blocks. Half of the participants were exposed to constant reward values in the testing phase, while the probability of targets being presented on either side was manipulated. Of these eighteen participants, half were shown higher reward (£10) on the right and low reward on the left (£2) and the other half were shown the opposite. There were three experimental conditions, each consisting of three consecutive blocks. In one condition, the target was equally likely to be on the right or the left-hand side. In the second condition, the target was presented on one side with probability 0.83 and the other side with probability 0.17. These probabilities were chosen as they are the closest match

to £10/£2 reward proportions. These probabilities were then flipped for the final condition. The probabilities were not exact due to short block lengths, such that at the beginning of each block the number of targets appearing on a particular side were fixed at 50%, 83% or 17% of the total number of trials in the block (to the nearest integer). The order of these fixed trials were then randomised for the length of the block, ensuring a random permutation of trials in every block across the whole experiment.

Experiment 7b. Reward Manipulation

The other eighteen participants were exposed to constant probabilities of the presentation of targets across the experiment, while the reward values associated with targets was manipulated. Nine participants were presented with targets appearing on the right-hand side with probability 0.83 and the left-hand side with probability 0.17, and the other nine were shown the opposite. Again there were three experimental conditions, each consisting of three consecutive blocks. In one condition, the target was associated with equal reward (£6) on the right and the left-hand side. In the second condition, the target presented on one side was associated with £10 reward and other side with £2. The reward values were then flipped for the final condition. As in the probability manipulation, the order of the fixed trials were randomised for each block, ensuring a random permutation of trials.

The reward values (including the pound sign) were presented inside the corresponding target after a successful manual response to the target in each trial. The rewards were a golden yellow colour (19.8 cd/m^2) to increase the saliency. If the participant was too slow, or made an incorrect response, a message appeared in the centre of the screen reading 'Wrong! No reward' or 'Too slow! No reward' (2.5^o above fixation and white). After the response to the letter T, the reward value (or error message) stayed on the screen for 1.5 seconds.

For both Experiment 7a and 7b, a pre-test block was included to set an individual criteria for the time-out for the testing phase. In the practice and pre-test phases the fixation square contained an X (red; 15.8 cd/m^2; font size 17) rather than a £ sign as no rewards were given on these trials. The distribution of manual response times from the pre-test block of the experiment were used to calculate a 70^{th} percentile of each participant's reaction time (ms) distribution. Without informing the participants, their individual 70^{th} percentile values were used as the length of time the target and letter T would be visible for in testing phase trials, after which they would receive the time-out notice and forfeit the chance of gaining the reward on that trial. This ensured motivation to respond quickly as participants inevitably were too slow on some trials; these time-out errors were often less than 30%, as participants responded faster in reaction to the time constraint.

Apparatus

The experiment was controlled by Psychophysics Toolbox (Brainard, 1997) running within Matlab 2013a running on Windows 7. The display was 17"running at 75Hz and with a resolution of 1600 x 1200 pixels, and the viewing distance was 57cm.

Movements of the right eye were recorded at a sampling rate of 1000Hz by the Eyelink II (SR Research, Canada) which has a typical operating spatial resolution of 0.5º. The participants were provided with a chin and forehead rest to minimise head movements. Manual response were recorded via the keyboard (numeric right-hand section) – key 4 and 1 for the left hand and key 6 and 3 for the right hand responses.

Design

There were two within-participant repeated-measure binary factors in both forms of the experiment: In the reward manipulation, one was block (£2/£10, £10/£2, £6/£6) and the other was side (0.83% probability and 0.17% probability). This led to 6 conditions: low probability,

low reward; low probability, high reward; high probability, high reward; high probability, low reward; high probability, equal reward; low probability, equal reward. In the probability manipulation, one factor was block (83%/17%, 17%/83%, 50%/50%) and the other was side (£2 and £10). This led to 6 conditions: high reward, high probability; high reward, low probability; low reward, high probability; low reward, low probability; high reward, equal probability; low reward, equal probability. Therefore there were only 2 conditions in each form of the experiment that differed from the other: each was an isolated manipulation of reward or probability.

The order of conditions were counterbalanced using a latin square design. Given the three block types in the probability and reward manipulations, this gave 9 unique orders, which were then repeated for the further 9 participants. The dependent measures were the manual response time and saccade latency.

4.2.2 Results

Experiment 7a: Probability manipulation

Manual Responses

There were a total of 7776 trials recorded in the probability manipulation experiment (432 x 18 participants) and of these 6872 manual responses were correct/before the time-out. The distribution of the remaining 904 time-out/response errors is shown in the table below. The range of the total percentage of time-out/response errors across all participants was 3.7% to 18.52%.

Side	Block Type					
	Equal Probability		Probability same direction as reward		Probability opposite direction to reward	
	Time-Out	Response Errors	Time-Out	Response Errors	Time-Out	Response Errors
High Reward	7.1 (2.78 - 23.6)	5.25 (0 - 9.7)	4.81 (0.83 - 13.3)	4.58 (0.83 - 7.5)	6.94 (0 - 29.17)	6.94 (0 - 16.67)
Low Reward	8.1 (0 - 20.83)	4.5 (0 - 22.2)	10.42 (0 - 25)	5.79 (0 - 16.67)	5.93 (0 - 14.17	3.98 (0 - 9.17)

Table 4.1: Mean percentage of errors (of the number of trials in each condition) across the three probability conditions and two reward sides. Errors are split into time-out errors, where participants did not make the manual response within the allocated time, and response errors where they made an incorrect button press. The range of error percentages across participants in each condition are given in brackets.

There was a marginally significant effect of error type, with generally more time-out errors than response errors being present across participants (Repeated Measures ANOVA: [$F(1, 17) = 4.28$, $p = 0.05$]; Effect size (partial ETA) = 0.2).

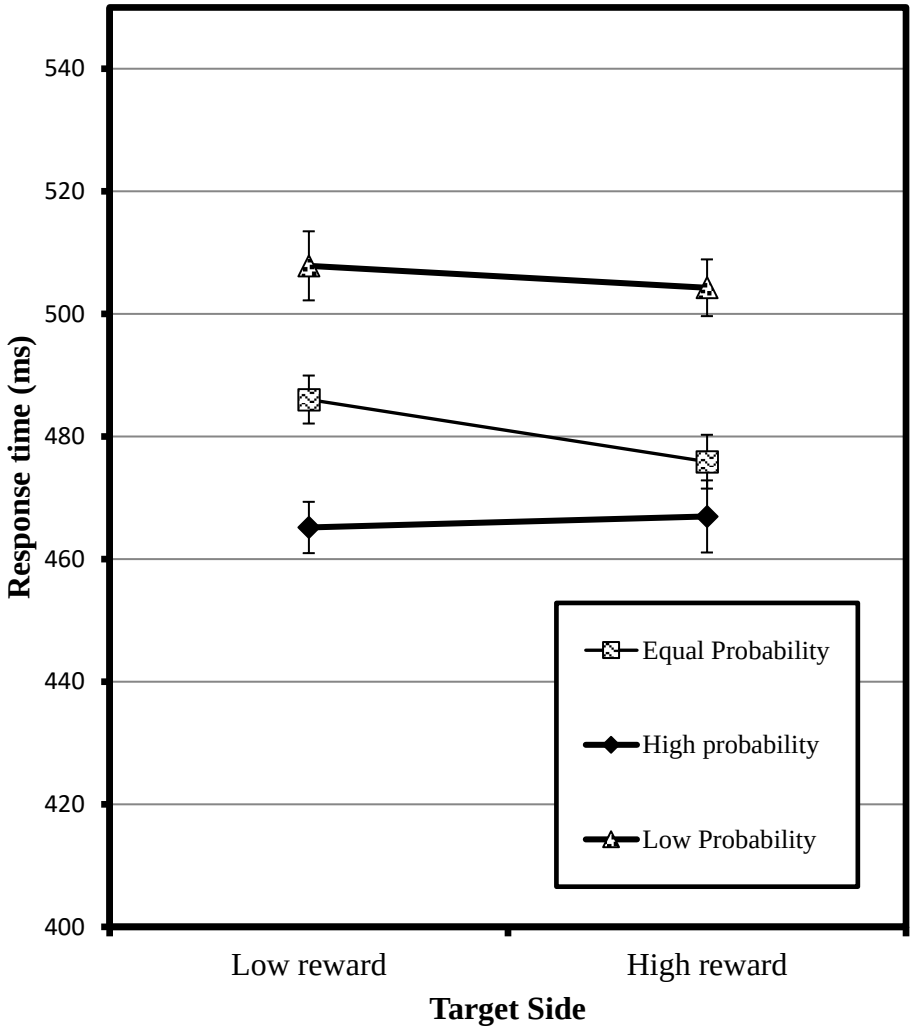

Figure 4.2: Graph of the mean of median manual reaction times across participants. Each line represents a different probability, with the data split within blocks according to the probability associated with a particular target. The two x-axis points show the reward associated with the target. The within-subject error bars are the standard error of the mean.

A significant effect of target probability was seen on the manual response times (Repeated measures ANOVA: [$F(2,17) = 26.6$, $p < 0.001$]; Effect size (partial ETA) = 0.61). This significant effect is not present between the equal and high probabilities, as shown by the large and overlapping confidence intervals (CI 95%: High = 443.6 – 488.5; Equal = 462.3 – 499.6), compared to a clear difference between these probabilities and the low probability (CI 95%: 484.3 – 527.8).

Although not significant, the data suggests a small effect of reward when the probability is equal across targets; this is clearly extinguished once the probabilities are unequal (Figure 4.2).

Saccadic Responses

Initially I assessed the saccadic response data by looking at whether there was an offset in initial fixation towards the high probability side. This was done by calculating the amount of drift away from the central fixation in the starting point of the first saccade after target onset. 7747 trials were included in this calculation, 29 having been discarded due to blinks or other failures to record eye position at the start of the trial.

The saccadic starting point data were binned into seven bins of 2 degrees; the central bin around fixation had a midpoint of the exact position of the fixation cross. The percentage of each participants' starting points in each bin was calculated, separated according to probability condition. The data was then collated across the 3 bins on either side of the fixation, giving a percentage of starting points towards the high reward side and likewise to the low reward side. There was a significant effect of probability condition on the proportional difference between percentages of starting points towards the low and high reward side (Repeated Measures Anova: $[F(2, 17) = 47.19, p < 0.001]$; Effect size (partial ETA squared) = 0.74). This supports our significant finding in the earlier probability experiment, as the data suggests a bias towards the higher probability side. Interestingly, when the probability was equal the mean percentage of saccades that were initiated nearer the high reward side was 24% (CI 95%: 11.45 – 36.77) compared to 9% (CI 95%: 3.89 – 13.78) on the low reward side, suggesting a small effect of reward on starting point bias when presented without a probability modulation. However, high levels of variance given by the confidence intervals suggests weak evidence for this finding.

Given these results the same general exclusion criteria as the previous experiments was applied to initial fixation starting point: excluding trials where the initial fixation was greater than 3 degrees either side of the centre of the fixation box. This was a liberal criteria as there was no specific fixation instruction to participants in the experiment, and to account for the fact that there was a spatial bias in the starting points of saccades. An additional criteria was applied so that all trials where the first saccade was initiated after the participant's 'time-out' were discarded. Two participants had over 40% of trials excluded when these criteria were applied, so they were removed from the rest of the saccadic analysis. There was no spatial exclusion criteria on the landing point of the first saccade, but saccades in the wrong direction were discarded as errors. The remaining trials had a mean first saccade amplitude of 5.6 degrees (range across participants: 5.0 – 6.3 degrees).

Of the saccades directed to the incorrect side, 93.4 % had a latency of 80ms or less and these are assumed to be anticipatory (Table 4.2). In addition to reflect this anticipatory criteria all saccades with reaction times 80ms or less in the correct direction were excluded. Some saccades within the incorrect saccades and anticipatory saccades categories had negative response times, due to the saccade being ongoing during the target onset. These saccades were included in the anticipatory analysis as they still reflect an anticipation of the target appearing on a particular side. After removing the invalid, anticipatory and error saccades, the total number of analysed saccades was 5379 (77.82%).

Reason for Exclusion	Number of saccades (trials) excluded and percentage of initial total	Total no of saccades **(Initial 6912)** **(2 Participants excluded)**
Initial fixation greater than 3 degrees from centre/initiated after 'time-out'	1127 (16.3%; 1.39 - 39.1%)	5785 (83.7%)
Saccades in the incorrect direction (92.7% anticipatory)	136 (1.97%; 0.46 - 3.94%)	5649 (81.73%)
Anticipatory saccades (correct direction)	270 (3.91%; 0.23 - 10.42%)	5379 (77.82%)

Table 4.2; Pre-processing of saccadic analysis. Details of the data removed from further analysis, and the reasons for removing them. Percentage of initial number of saccades is included in brackets, followed by the range across participants. Two participants were excluded from analysis so are not included in this table.

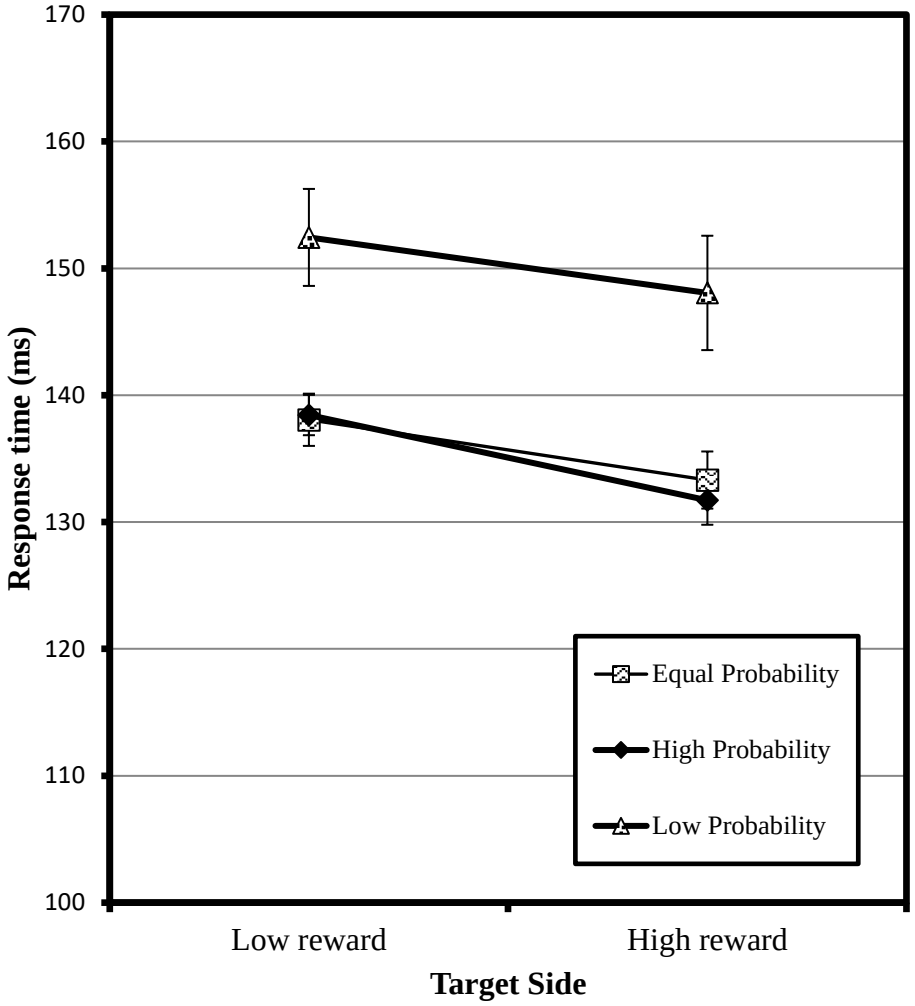

Figure 4.3: Graph of mean across participants' median saccadic reaction times, where the x-axis denotes the relative reward associated with the target. The three lines on the graph join the two data points associated with each probability condition, as shown in the figure legend. Conditions have been grouped as the target probabilities presented, rather than in the conditions within which they were recorded in the task. The within participant error bars show the standard error of the mean.

The target probability had a significant effect on saccadic response times (Repeated Measures ANOVA: [$F(2,15) = 25.39$, $p < 0.001$]; Effect size (partial ETA) = 0.63). Although the data shows a trend towards participants making faster saccades when the target is associated with high reward relative to low reward (Figure 4.3), this effect is not significant. The effect of

probability is only present between the low probability condition (CI 95%: 138 – 162.5) and the high/equal probability condition (CI 95%: High = 126.9 – 143.3; Equal = 127.8 – 143.6), as can be clearly seen in the graph (Figure 4.3). When the reward rates were matched across the two targets, (the 'high reward, low probability' and the 'low reward, high probability' points in Figure 4.3) there was a 9.63ms (CI 95%: -1.48 – 20.73) increase in response time between the high probability side and the low probability side. This result suggests that the processes underlying the reward and probability effect are not governed by reward rate (or expected value). If that had been the case, it would have been expected that there would be no effect across matched reward rates. However, it could be argued that the probability manipulation might dominate the responses rather than reward, as expected value is constant across the two targets.

The correct anticipatory saccade trials were analysed by frequency within probability condition and reward sides, and the percentages of the total possible trials were calculated for each participant, to account for higher numbers of trials in high probability conditions. Seventeen trials were removed from the anticipatory analysis, due to either blinks or by errors in the eye tracker recording. There was a significant interaction between the percentages of correct anticipatory saccades with reward side and probability condition across participants (Repeated measures ANOVA: [$F(2, 15) = 8.69$, $p = 0.001$]; Effect size (Partial ETA) = 0.37). There was no significant effect of reward side or probability condition on the percentage of correct anticipatory saccades. Additionally, there was no effect of either reward or probability on the percentage of anticipatory saccades in the incorrect direction.

Experiment 7b: Reward manipulation

Manual Responses

As in experiment 7a, the total number of trials recorded was 7776. Of these trials 719 manual responses were discarded due to an incorrect response or to the participant not responding in time. This left a total of 7057 trials in the manual data. The distribution of errors across conditions is given in the table below. The range across participants of the total percentage of response/time-out errors was 2.5% to 16.7%.

Side	**Block Type**					
	Equal Reward		Reward same direction as probability		Reward opposite direction to probability	
	Time-Out	Response Errors	Time-Out	Response Errors	Time-Out	Response Errors
High Probability	3.7 (0 – 8.3)	4.07 (0.83 - 10)	3.66 (0 – 9.17)	3.8 (0 - 10)	3.98 (0 – 9.17)	4.07 (0 – 12.5)
Low Probability	9.95 (0 – 16.7)	6.25 (0 - 25)	10.42 (0 – 29.17)	7.41 (0 – 20.83)	8.33 (0 – 20.83)	7.64 (0 – 29.17)

Table 4.3: Mean percentage of errors across the three reward conditions and high and low probability sides. Errors are split into time-out errors, where participants did not make the manual response within the allocated time, and response errors. The range across participants is given in brackets.

There was a significant effect of probability on both the frequency of time-out and response errors made, where more errors were made overall in the low probability direction (Time-out errors: Repeated measures ANOVA: [$F(1, 17) = 36.16$, $p < 0.001$]; Effect size (Partial ETA) = 0.68; Response errors: Repeated measures ANOVA: [$F(1, 17) = 7.8$, $p = 0.012$]; Effect size (Partial ETA) = 0.32).

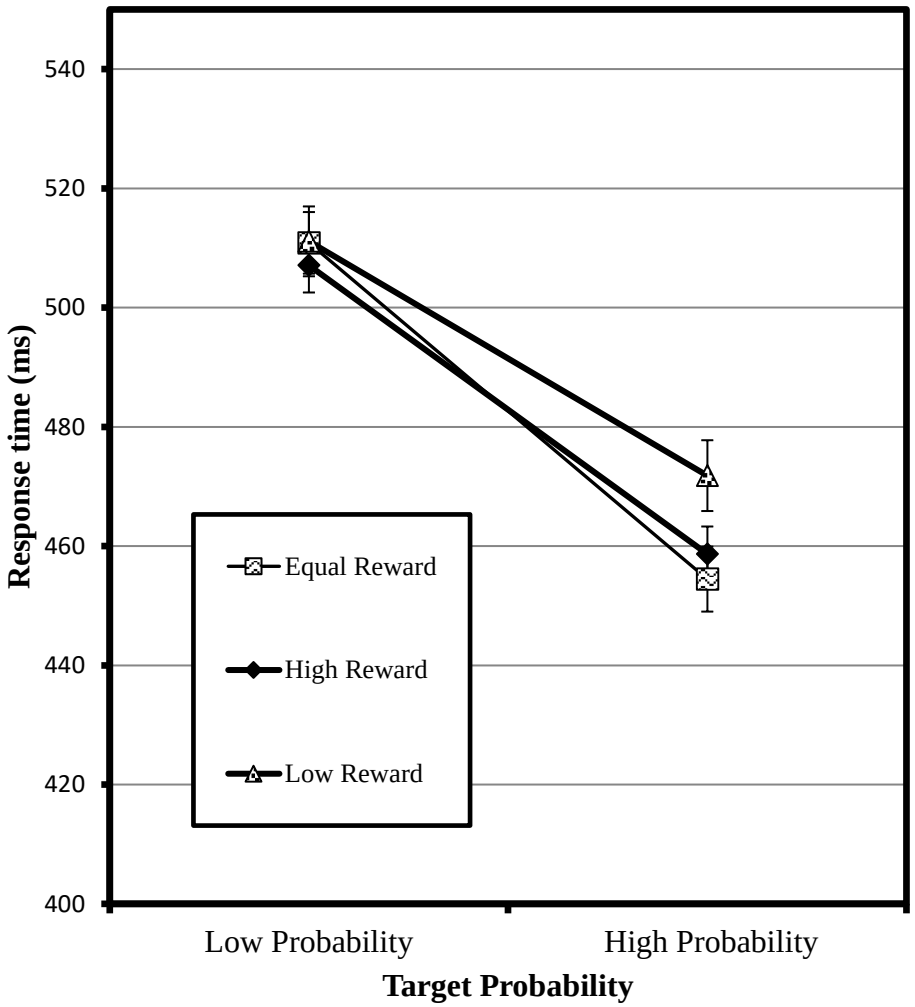

Figure 4.4: Graph of the mean manual response time across the medians of all participants. The three lines show the different reward conditions, which are grouped into low/high/equal reward rather than the conditions within the experiment. The x-axis gives the target probability. The within-subject error bars are the standard error of the mean.

Target probability had a significant effect on manual responses, as response times were shorter for the higher probability side (Repeated Measures ANOVA: [F = 39, p <0.001]; Effect size (partial ETA) = 0.7). The reward manipulation had no significant effect on the manual responses across participants.

Saccadic responses

As in experiment 7a, I looked at whether there was an offset in initial fixation towards the high probability side in the saccadic response data. I calculated the amount of drift away from the central fixation in the starting point of the first saccade after target onset. 7737 trials were included in this calculation as 39 were discarded due an error in recording the first saccade (due to blinks or otherwise).

The saccadic starting point data were binned into seven bins of 2 degrees; the central bin around fixation had a midpoint of the exact position of the fixation cross. The data was separated according to reward condition and the percentage of each participants' starting points in each bin was calculated. The data was then collated across the 3 bins on either side of the fixation, giving a percentage of starting points towards the high probability side and likewise to the low probability side. There was no effect of reward condition on the proportional difference between percentages of starting points towards the low and high reward side. However, there were a significantly higher percentage of saccades initiated on the high probability target side of fixation compared to the low probability target side, across all three conditions (Repeated Measures ANOVA: [F(1, 17) = 17.45, p = 0.001]; Effect size (partial ETA) = 0.51). Given these results the same general exclusion criteria as the previous experiments was applied to initial fixation starting point: excluding trials where the initial fixation was greater than 3 degrees either side of the centre of the fixation box. As in experiment 7a, this liberal criteria reflected the lack of specific fixation instruction to participants in the

experiment, and to account for the fact that there was a spatial bias in the starting points of saccades. All trials where the first saccade was initiated after the participant's 'time-out' were also excluded. Five participants had over 40% of trials excluded when these criteria was applied, so they were removed from the rest of the saccadic analysis. There was no spatial exclusion criteria on the landing point of the first saccade, but saccades in the wrong direction were discarded as errors. The remaining trials had a mean first saccade amplitude of 5.29 degrees (range across participants: 4.37 – 5.79 degrees).

Reason for Exclusion	Number of saccades (trials) excluded and percentage of initial total	Total no of saccades **(Initial 5616)** **(5 Participants excluded)**
Initial fixation greater than 3 degrees from centre/initiated after 'time-out'	818 (14.57%; 1.85 – 40.97%)	4798 (85.43%)
Saccades in the incorrect direction (83.1% anticipatory)	195 (3.47%; 0.23 – 9.95%)	4603 (81.96%)
Anticipatory saccades (correct direction)	357 (6.36%; 1.16 - 10.88%)	4246 (75.61%)

Table 4.4; Pre-processing of saccadic analysis. Details of the data removed from further analysis, and the reasons for removing them. Percentage of initial number of saccades is included in brackets, followed by the range across participants. The five participants that were excluded from analysis are not included in this table.

Of the saccades directed to the incorrect side, 83.1% had a latency of 85ms or less and these were assumed to be anticipatory (Table 4.4). In addition to reflect this anticipatory criteria all saccades with reaction times 85ms or less in the correct direction were excluded. Saccades with negative response times (due to the saccade being ongoing during the target onset) were present in the anticipatory/incorrect data. These saccades were included in the anticipatory analysis as they still reflect an anticipation of the target appearing on a particular side. After removing the invalid, anticipatory and error saccades, the total number of analysed saccades was 4246 (75.61%).

There was no significant effect of target probability or reward on saccadic response times. The data showed a trend towards an effect of probability in the high and equal probability conditions, although this was not evident in the low reward condition (Figure 4.5).

The correct anticipatory saccade trials were analysed by frequency within reward condition and probability sides, and the percentages of the total possible trials were calculated for each participant. There was a significant effect of probability on the percentage of correct anticipatory saccades, whereby more anticipatory saccades were made towards the higher probability target (Repeated Measures ANOVA: [$F(1, 12) = 14.33$, $p = 0.003$]; Effect size (partial ETA) = 0.54). There was no effect of reward on the percentage of correct anticipatory saccades, nor an effect of either reward or probability on the percentage of anticipatory saccades in the incorrect direction.

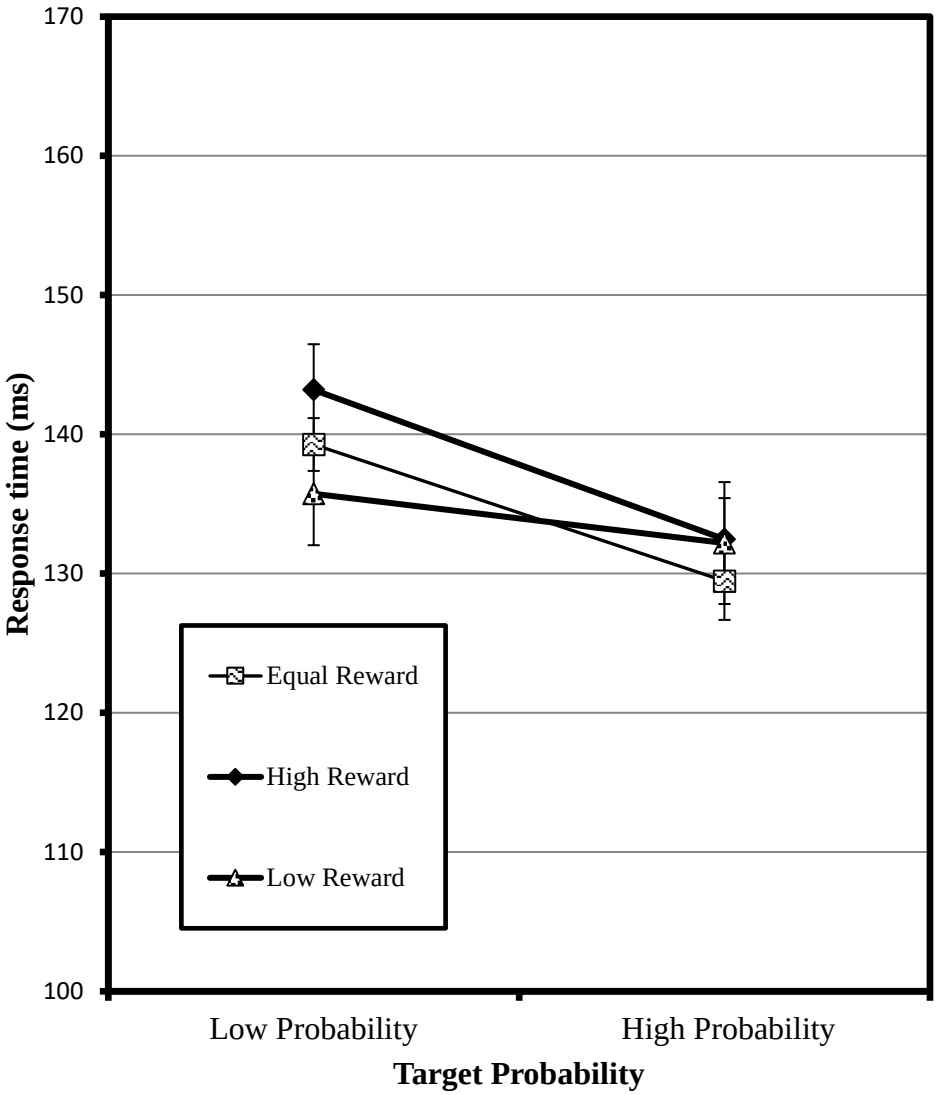

Figure 4.5; Graph of the mean saccadic response time across the medians of 13 participants. The x-axis gives the probability associated with the target, and the three lines denote the three reward conditions. The within subject error bars are the standard error of the mean.

4.2.3 Discussion

Across experiments 7a and 7b there was a generally reliable effect of target probability on manual and saccadic responses: participants' response times were faster to targets associated

with higher probability. However, there was no significant effect of probability on the saccadic responses in experiment 7b. There was a trend for faster responses to higher probability and slower responses to lower probability in the high and equal reward conditions, but this effect was completely extinguished in the low reward condition. In experiment 7a, the probability effect was only present between the high/equal and the low probability conditions.

There was no significant effect of reward in either experiment 7a or 7b, and no evidence to suggest that reward rate has any effect on saccadic or manual responses. In the manual results of experiment 7a, some evidence was found to suggest that a small reward effect was present only when probability was equal across targets.

Although there was an effect of reward in a similar paradigm in Chapter 3, these results suggest that this effect is completely extinguished when there are unequal probabilities of the targets that rewards are associated with. It could be that the strength of the probability effect completely dominates the modulation in behaviour and thus these processes do not combine in a simple manner. Our results suggest that there are differences between the two processes governing reward and probability effects despite the similarities they have on behaviour in isolation.

I now report an experiment investigating the effects of reward and probability in isolation, using the same paradigm for both effects and a within-subjects design. This was to allow for a direct comparison of the reward and probability effect without combining them together, and examine whether the two effects are correlated. Given the smaller and less reliable effect of probability (and reward in Chapter 3) on saccadic responses in comparison to manual responses in Experiment 7, only manual responses have been recorded in Experiment 8. This decision is also supported by the results of the final experiments of Chapter 2 and Chapter 3, where there was no correlation between the saccadic and manual responses for the reward and

probability effect. Additionally, the same two keys were used to respond to targets on the left and right-hand side of the screen so that participants only used one hand to respond. Both these adjustments are advantageous for future experiments with Parkinson's patients: eye tracking is more complex and restrictive for these patients partly due to increased head movements and often their Parkinsonism affects one side of their body more severely than the other (Djaldetti, Ziv & Melamed, 2006).

In addition it is not clear at what stage in processing the manual response advantages reported previously occur. In the previous experiments one side of the display was associated with either a higher reward or an increased probability and this led, under some circumstances, to a reduction in manual reaction time. As each side was unequally associated with a particular hand it is entirely possible that the speeding up was a result of some low level motor readiness associated with one hand rather than the other. By having both responses (left or right) being made by the same hand this allows a test of whether these effects are more central than this explanation suggests.

4.3 Experiment 8: Isolated reward and probability

4.3.1 Methods

Participants

Eighteen participants (eleven female) were recruited from the student population of the University of Bristol (mean: 22.8, range: 18 - 40). All had normal or corrected-to-normal vision. Participants were reimbursed £6 for their time and received a variable performance related reward (£0, £2, £6 or £10) as outlined below. They were asked to use their self-reported

dominant hand to do the experiment (14 right-handed). The study was approved by The Faculty of Science Human Research Ethics Committee at the University of Bristol.

Procedure

The sequence of events in a single example trial is illustrated in Figure 4.6. The task as in previous experiments was to respond to the "T" stimuli that appeared to the left or right of a central fixation point. The response required was to indicate the orientation of a letter with a manual button press. Regardless of which hemifield the target was presented in, the same two buttons on the keyboard were used to indicate the orientation of the letter T. The experiment consisted of a practice phase (10 trials), a pre-test phase (36 trials), and then 12 blocks (36 trials each) of the testing phase.

In the testing phase correct responses in each trial were associated with a reward. The reward value was displayed on each trial at the location of the target after the response was given. A trial from the testing phase was selected at random at the end of the experiment and the participant received that reward. If the manual response was too slow or incorrect then a message was displayed after the trial. Participants were informed at the outset of the experiment that they would receive no reward if one of these error trials was selected at the end of the experiment. The participants were explicitly told the reward distribution at the start of each block.

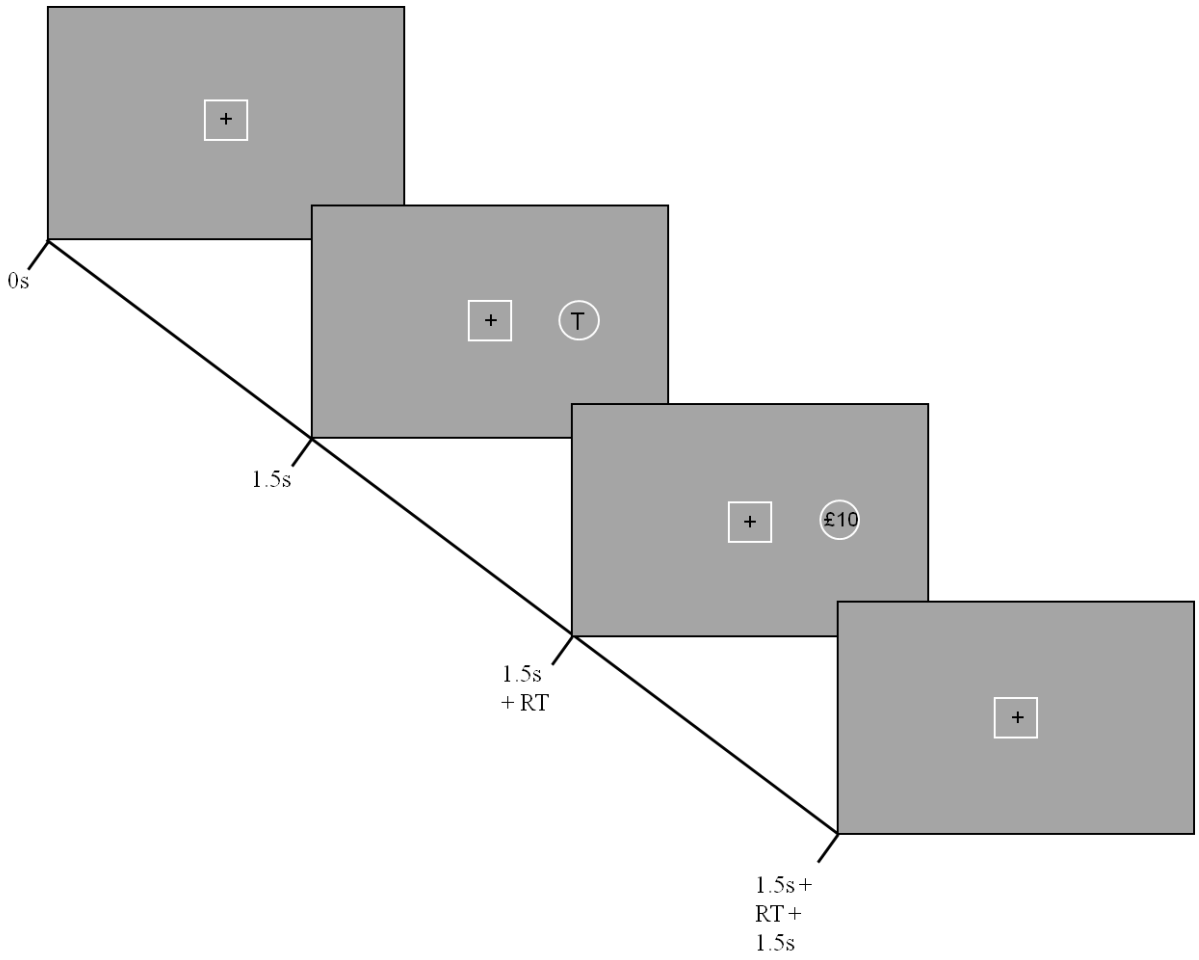

Figure 4.6; Diagram of the experimental procedure in the testing phase. The figure depicts an example trial from a 'reward' block in the 'high reward right' condition with a target appearing on the right-hand side.

Stimuli

All stimuli and the fixation point were white (16.4 cd/m^2) and displayed on a grey background (10.4 cd/m^2). A trial commenced with a centrally presented fixation square (1.65^o x 1.65^o; 0.18^o thick) which was presented for 1.5s. The fixation square contained a single cross in the presented in red (15.8 cd/m^2) and in font size 17. This was immediately followed by the

circle target with a T or inverted T in the centre. The target had a diameter of 1.85^{o} and a line thickness of 0.18^{o}. The letter T subtended 0.3^{o} as in all previous experiments. This ensured that participants had to make an accurate target directed saccadic eye movements towards the target to complete the task. The target was presented on the left or right of fixation at 6^{o} eccentricity: in the reward manipulation the target was presented on either side in an equal number of trials across all conditions, whereas the frequency changed in different conditions of the probability manipulation.

The testing phase was split into two sections – the reward manipulation and the probability manipulation. Half the participants were exposed to the reward conditions first, and half to the probability. In the reward manipulation, there were three conditions: high reward right (£2/£10), high reward left (£10/£2), and equal reward (£6/£6). In the probability manipulation, there were again three conditions: high probability right (0.17/0.83), high probability left (0.83/0.17) and equal probability (0.5/0.5). Each condition consisted of two consecutive blocks of 36 trials. These probabilities were chosen as they are the closest match to £10/£2 reward proportions. To ensure motivation within the probability conditions was not decreased compared to the reward conditions, rewards were fixed at £6 across the whole section. This meant that the equal reward and equal probability conditions were exactly the same. The reward values (including the pound sign) were presented inside the corresponding target after a successful manual response to the target in each trial. The rewards were presented in a golden yellow colour (19.8 cd/m^{2}). If the participant was too slow, or made an incorrect response, no reward value was shown and a message appeared in the centre of the screen reading 'Wrong! No reward' or 'Too slow! No reward' (2.5^{o} above fixation and white). The reward value (or error message) stayed on the screen for 1.5 seconds.

A pre-test block was included in the experiment to set an individual criterion for each participant for the time-out for the testing phase. In the practice and pre-test phases the fixation

square contained an X which was also presented in the targets after response to the letter T, as no rewards were given on these trials. The distribution of manual response times from the pre-test block of the experiment were used to calculate a 70th percentile of each participant's reaction time (ms) distribution. Unknown to the participants, their individual 70th percentile values were used as the length of time the target and letter T would be visible for in the testing phase trials after which they would receive the time-out notice and forfeit the chance of gaining the reward on that trial. This ensured motivation to respond quickly.

Apparatus

The experiment was controlled by Psychophysics Toolbox (Brainard, 1997) running within Matlab 2014b running on Windows 7 The display was 17" running at 75Hz and with a resolution of 1600 x 1200 pixels, and the viewing distance was 57cm. The participants were provided with a chin rest to keep the viewing distance constant. Manual responses were recorded via the keyboard – the up arrow for correct orientation of the letter T, the down arrow for an inverted letter T.

Design

There were two within participant repeated measure binary factors: probability (high, low or equal) and reward (high, low or equal) leading to six conditions: High probability, low probability, equal probability; High reward, low reward, equal reward. The order of the blocks were counterbalanced across participants. The dependent measure was the manual response time.

4.3.2 Results

Manual Responses

A total of 7776 trials were recorded (432 x 18 participants). I analysed the remaining manual reaction times excluding 588 time-out and 470 response errors, leaving a total of 6718 data points. The distribution of errors is shown in Table 4.5. The range of the total percentage of time-out/response errors of each participant's responses was 0.9% - 27.78%.

Side	**Condition**			
	Probability		Reward	
	Time-Out	Response Errors	Time-Out	Response Errors
High	5.05 (0-9.17)	4.86 (0.83-19.17)	6.67 (1.39-16.67)	6.85 (0-15.28)
Low	18.87 (0-33.3)	9.23 (0-25)	10.34 (1.39-23.6)	8.91 (0-27.78)
Equal	8.3 (1.39-20.83)	7.84 (0-18.06)	7.68 (0-18.06)	7.64 (0-16.67)

Table 4.5; The mean percentage of errors (of the total number of possible trials in each condition), for both types; time-outs and response errors. The range across 18 participants is given in brackets.

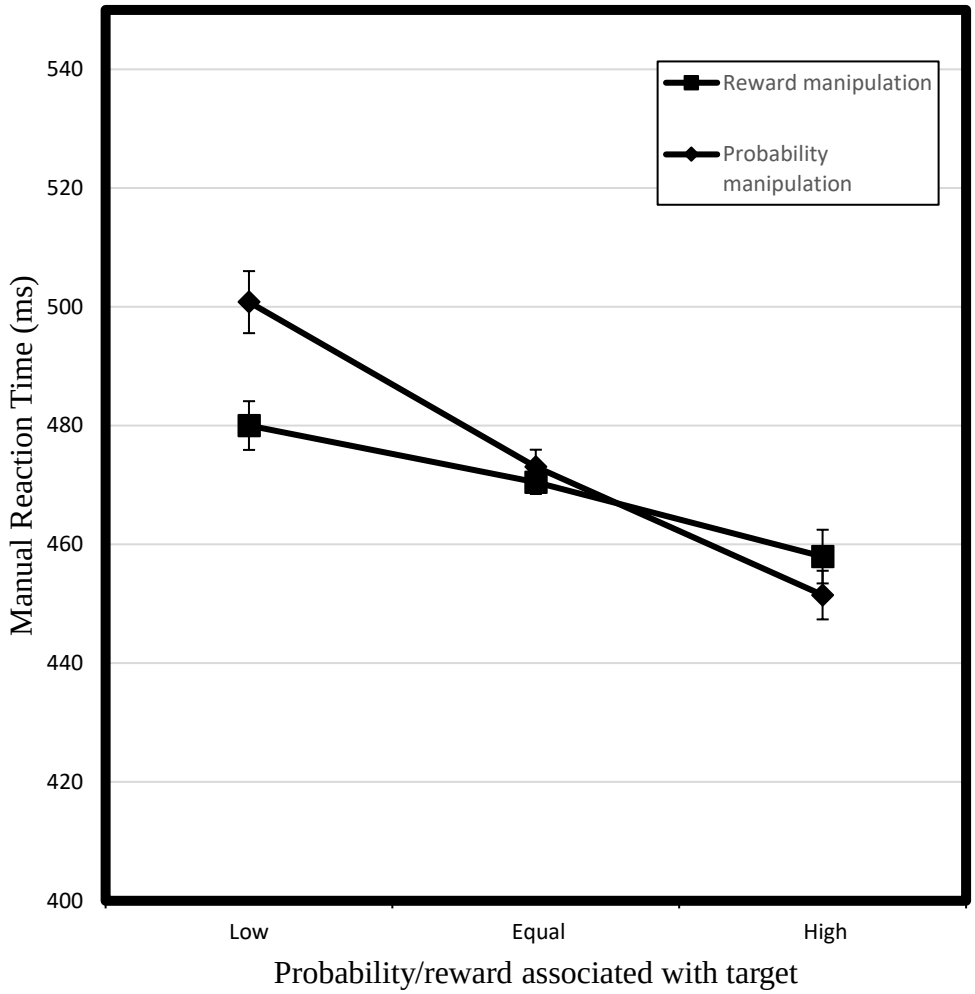

Figure 4.7; Graph of mean manual response times across medians of all 18 participants. The two lines show the two different conditions (reward and probability) and the three x-axis points denote the level of reward or probability associated with the target. The within-subject error bars are the standard error of the mean.

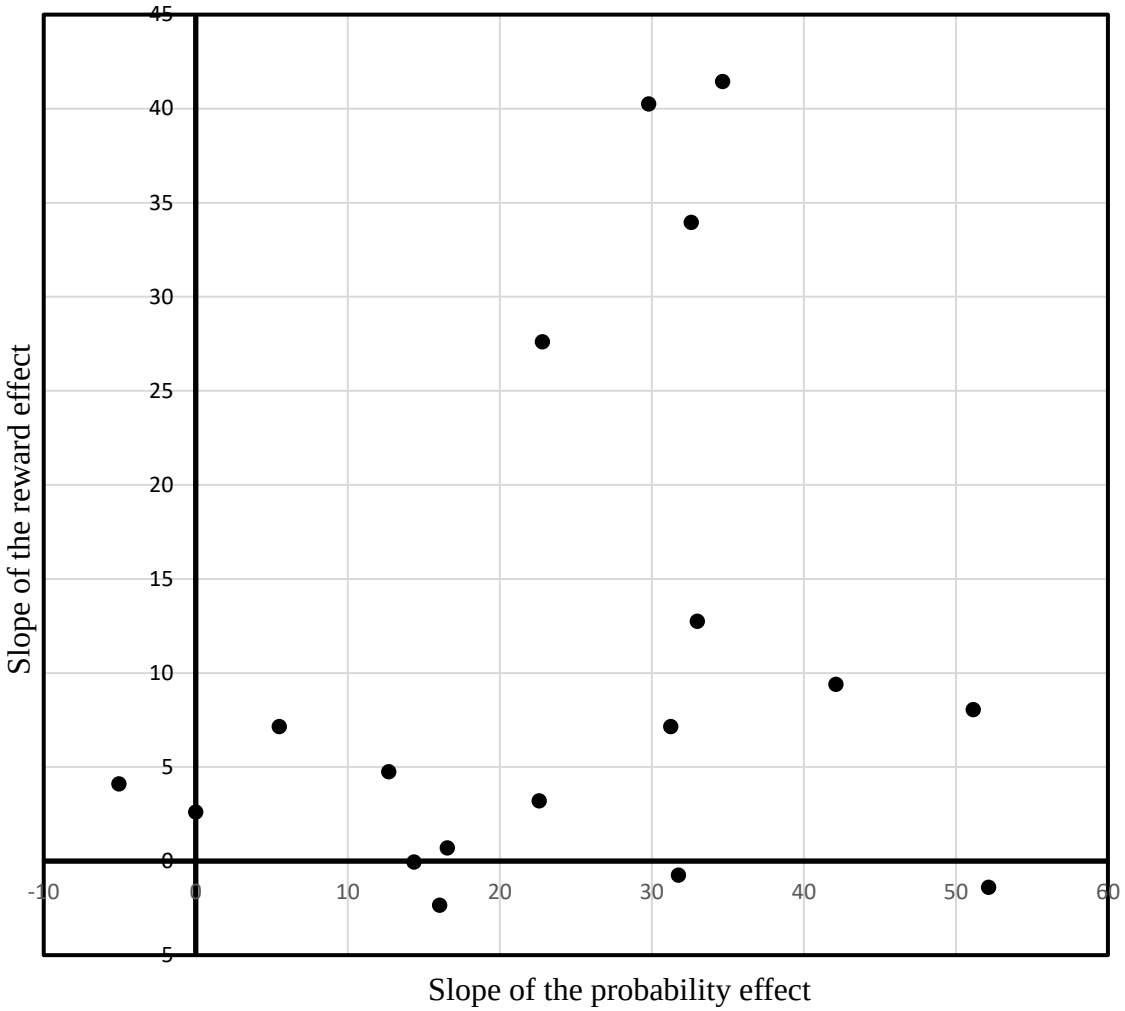

Figure 4.8; Scatter plot of the slope of the probability effect against the slope of the reward effect in manual responses across all participants.

I found that reward value had a significant effect on manual reaction times, and exhibited a linear relationship across the three conditions (Figure 4.7) (Repeated Measures ANOVA: [$F(2,17) = 7.55$, $p = 0.002$]; Effect size (partial ETA squared) = 0.31). Probability also had a significant effect on manual reaction times, and a linear relationship can also be seen in Figure 4.7 (Repeated Measures ANOVA: [$F(2,17) = 28.03$, $p < 0.001$]; Effect size (partial ETA squared) = 0.62). As expected, there was no difference between reward and probability in the

equal condition; these were identical besides from the participants experiencing them within the reward or probability manipulation of the experiment.

There were significantly more time-out errors made the lower the probability or reward value was across the experiment (Probability: Repeated Measures ANOVA: [$F(2,17) = 27.03$, $p < 0.001$]; Effect size (partial ETA squared) = 0.61; Reward: Repeated Measures ANOVA: [$F(2,17) = 6.13$, $p = 0.005$]; Effect size (partial ETA squared) = 0.27). However, there was no effect of reward or probability on the frequency of response errors.

There was only a weak non-significant positive correlation between the effect of reward and probability across all participants (Figure 4.8; correlation coefficient = 0.24, N.S. [p=0.34]). Analysing the data together from both manipulations, overall there was no significant difference between the reward and probability conditions across the three levels (Repeated Measures ANOVA: [$F(1,17) = 2.7$, $p = 0.12$]; Effect size (partial ETA squared) = 0.14), suggesting a similar effect on responses. There was a significant effect of level of probability/reward (Repeated Measures ANOVA: [$F(2,17) = 31.45$, $p < 0.005$]; Effect size (partial ETA squared) = 0.65), and a significant interaction between level and manipulation (reward/probability) (Repeated Measures ANOVA: [$F(1,17) = 5.43$, $p = 0.01$]; Effect size (partial ETA squared) = 0.24), reflecting a larger effect of level on probability than reward.

Additionally, the data was split for the 14 right-handed participants into manual responses made to the left or the right-hand target. This was in order to ascertain if there was any effect of using the same button presses for responses to both hemifields. I ran two repeated measures ANOVAs (three by two) for both reward and probability conditions, and found that there was no significant difference between manual responses made to the left or right targets.

4.3.3 Discussion

Reward and probability had a significant linear effect on the manual reaction times, whereby responses were faster to targets associated with higher reward and probability. This modulation in responses was larger in the probability manipulation. It was found that the lower the reward or probability, the greater the frequency of time-out errors; this suggests, as some studies discussed in Chapter 1 have suggested, that both high reward and probability could lead to increased motor preparation (Basso & Wurtz, 1997; Dorris & Munoz, 1998; Koval et al., 2004). Additionally, it was found that there was no difference between responses made to targets on the right or the left-hand side of the screen. It could be concluded from this that spatial mapping of visual stimuli to manual responses is not an important aspect of the effect of reward and probability on reaction times.

There was no correlation between reward and probability in our data, suggesting different processes governing these effects. This also supports the results of Experiment 7 where we did not see these processes combining in a simple manner. This could be partly due to the differences in the nature of reward and probability; the probability of events or objects appearance in our environment is inherent and continues to exist (albeit fluctuating) even if not observed. The reward value attributed to an event or object relies on the way in which we perceive it, and is thus dependent on many other factors that can differ between individuals (utility, internal state etc).

The next experiment I report is an investigation into the effect of reward and probability on the manual responses of healthy older adults. The purpose of this experiment was to understand how these effects change with age, and to provide a control study for further research with Parkinson's patients who have deep brain stimulators (DBS). As we observed

both the reward and probability effects in isolation in Experiment 8, I have used the same paradigm in Experiment 9 with some small adjustments.

4.4 Experiment 9: Reward and probability with healthy older adults

4.4.1 Methods

Participants

Six participants (four female) were recruited from the BRACE charity (supporting dementia research) volunteer network in Bristol. The average age of participants was 74.3 and the range was 62 – 90. All had normal or corrected-to-normal vision. Participants were reimbursed £6 for their time/expenses/travel and received a variable performance related reward (£0, £2, £6 or £10) as outlined below. They were asked to use their self-reported dominant hand to do the experiment (all participants right-handed). The study was approved by The Faculty of Science Human Research Ethics Committee at the University of Bristol.

Procedure

The sequence of events in a single example trial is illustrated in Figure 4.9, and was exactly the same as in the Experiment 8. The task as in previous experiments was to respond to the "T" stimuli that appeared to the left or right of a central fixation point. The response required was to indicate the orientation of a letter with a manual button press. The two lower buttons on a Cedrus response pad (RB-830) turned sideways were used to indicate the orientation of the letter T, regardless of which hemifield the target was presented in. The experiment consisted of an initial practice phase (10 trials), a pre-test phase (36 trials), and then 12 blocks (36 trials

each) of the testing phase.

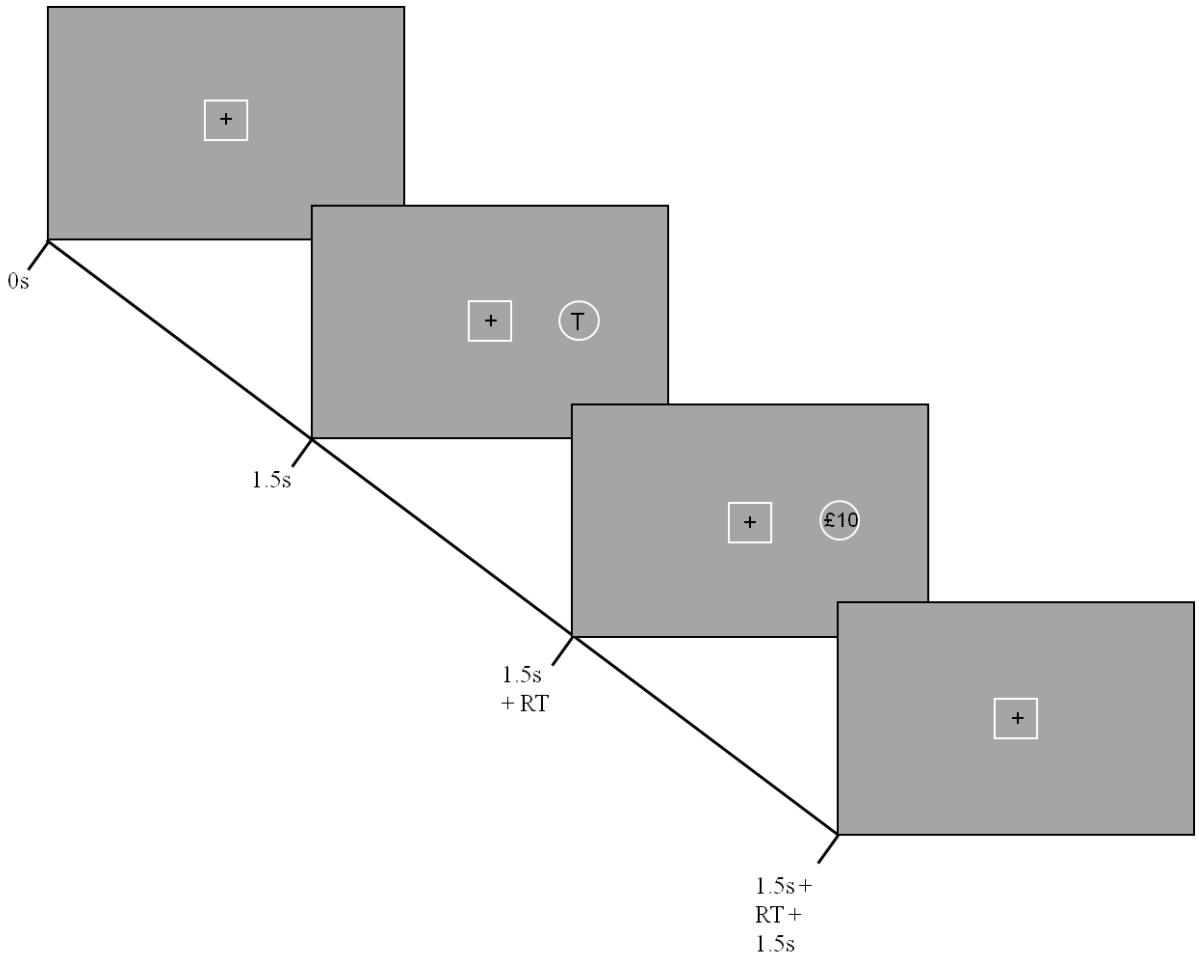

Figure 4.9; Diagram of the experimental procedure in the testing phase. The figure depicts an example trial from a 'reward' block in the 'high reward right' condition with a target appearing on the right-hand side.

In the testing phase correct responses in each trial were associated with a reward. The reward value was displayed on each trial at the location of the target after the response was given. If the manual response was too slow or incorrect then a message was displayed after the trial. Participants were informed at the outset of the experiment that they would receive no reward if one of these error trials was selected at the end of the experiment. However, due to ensuring that these participants had their travel and expenses covered, a £10 reward was

consistently given to participants. The participants were explicitly told the reward distribution at the start of each block.

Stimuli

All stimuli and the fixation point were white (16.4 cd/m^2) and displayed on a grey background (10.4 cd/m^2). A trial commenced with a centrally presented fixation square (1.65^o x 1.65^o; 0.18^o thick) which was presented for 1.5s. The fixation square contained a single cross presented in red (15.8 cd/m^2) and in font size 17. This was immediately followed by the circle target with a T or inverted T in the centre. The target had a diameter of 1.85^o and a line thickness of 0.18^o. The letter T subtended 0.3^o as in all previous experiments. This ensured that participants had to make an accurate target directed saccadic eye movements towards the target to complete the task. The target was presented on the left or right of fixation at 6^o eccentricity: in the reward manipulation the target was presented on either side in an equal number of trials across all conditions, whereas the frequency changed in different conditions of the probability manipulation.

As in the previous experiment, the testing phase was split into two sections – the reward manipulation and the probability manipulation. Half the participants were exposed to the reward conditions first, and half to the probability. In the reward manipulation, there were three conditions: high reward right (£2/£10), high reward left (£10/£2), and equal reward (£6/£6). In the probability manipulation, there were again three conditions: high probability right (0.17/0.83), high probability left (0.83/0.17) and equal probability (0.5/0.5). Each condition consisted of two consecutive blocks of 36 trials. To ensure motivation within the probability conditions was not decreased compared to the reward conditions, rewards were fixed at £6 across the whole section. This meant that the equal reward and equal probability conditions were exactly the same. The reward values were presented inside the corresponding target after

a successful manual response to the target in each trial. The rewards were presented in a golden yellow colour (19.8 cd/m^2). If the participant was too slow, or made an incorrect response, no reward value was shown and a message appeared in the centre of the screen reading 'Wrong! No reward' or 'Too slow! No reward' (2.5^o above fixation and white). The reward value (or error message) stayed on the screen for 1.5 seconds.

Unlike in the previous experiment, responses from the pre-test phase were not used to calculate a time-out criterion for each participant. This is primarily because this experiment was a control for an experiment with Parkinson's patients; I have been advised by clinicians that the time-out aspect would be too stressful for the participants. Additionally, the healthy older adults and patients are likely to be much more variable in their responses than in previous experiments with young students. This variability would make setting the time-out criterion at the 70th percentile of the participants' responses less effective. In the practice and pre-test phases the fixation square contained an X which was also presented in the targets after response to the letter T, as no rewards were given on these trials.

Apparatus

The experiment was controlled by Psychophysics Toolbox (Brainard, 1997) running within Matlab 2014b running on Windows 7 The display was 17" running at 75Hz and with a resolution of 1600 x 1200 pixels, and the viewing distance was 57cm. The participants were not required to use a chin rest as I decided this would be too uncomfortable for them. Manual responses were recorded via using a button box – one button for correct orientation of the letter T, and a button below the first button for an inverted letter T.

Design

There were two within participant repeated measure binary factors: probability (high, low or equal) and reward (high, low or equal) leading to six conditions: High probability, low probability, equal probability; High reward, low reward, equal reward. The order of the blocks were counterbalanced across participants. The dependent measure was the manual response time.

4.4.2 Results

Manual Responses

A total of 2592 trials were recorded (432 x 6 participants). During the testing session for one participant, the response box stopped working so the experiment was carried out using the keyboard as in experiment 8. This meant that the participant did in fact have a calculated 'time-out' criterion. However, given only 39 time-out errors were made, I included this participant in the analysis. The manual reaction times were analysed excluding the 39 time-out errors and 22 response errors; 16 trials that had reaction times of greater than 2 seconds were also excluded. This left a total of 2515 data points. As there were so few errors, I did not analyse the frequencies across the conditions.

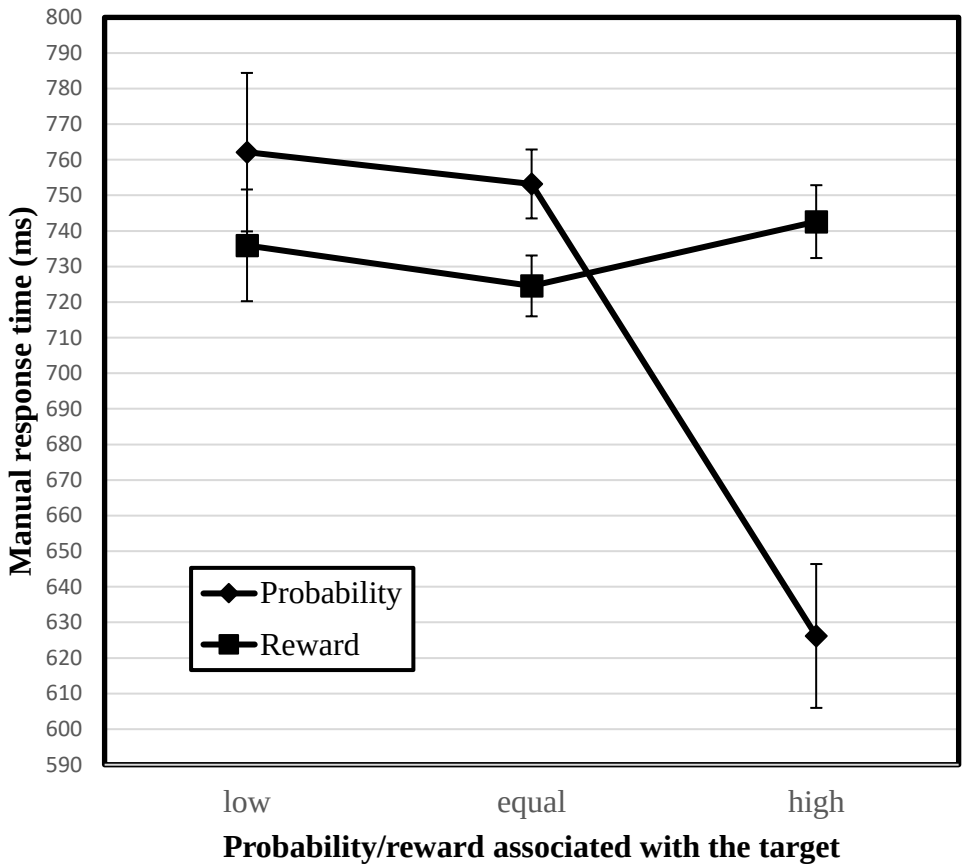

Figure 4.10; Graph of mean manual response times across medians of all 6 participants. The two lines show the two different conditions (reward and probability) and the three x-axis points denote the level of reward or probability associated with the target. The within-subject error bars are the standard error of the mean.

There was a significant effect of probability on the manual reaction times across the six participants (Repeated measures ANOVA: [$F(2, 5) = 15.96$, $p = 0.001$]; Effect size (partial ETA squared) = 0.76). Reward value did not have a significant effect on manual reaction times; the difference between the low and equal conditions however was very similar to the difference between those conditions in the reward manipulation. Crucially, although the average difference between the low and equal conditions was 11.4 ms in the reward manipulation and 8.93ms in the probability manipulation, the 95% confidence intervals for the differences were

-21.31 to 44.11 and -62.96 to 80.83 respectively. The only reliable effect within the conditions was found to be between the equal (and thus low) probability condition and the high probability condition. Although there was high variability in these data (mean = 127.02, CI 95%: 55.94 – 198.09), five out of six participants showed a clear decrease in manual reaction times as the probability increased.

4.5 Discussion

There was an effect of probability overall on the manual response times in older adults, but this effect was only reliable between the low/equal and the high probability condition. Given the variability of responses across the experiment, this could indicate an effect of practice; the number of responses in the 0.5/0.5 condition may not have been sufficient to cause a decrease in response times. However, the huge variability in responses means that some participants did show an effect between low and equal probability conditions; thus with results from only six participants a reliable conclusion cannot be drawn from this.

There was no effect of reward on the manual response times of older adults. This could reflect the instability of the reward effect, which in Experiment 7 of this chapter is clear: not all participants show the effect even when it is present, and any effects are extinguished by manipulations of probability. As there are only six older adult participants in this experiment, it is not that surprising that no reward effect is seen. Additionally, it could be the difference between the inherent qualities of reward and probability that lead to the absence of the reward effect. Specifically, as discussed in the introduction, the reward value of events or objects in the environment can be defined by their relative value to an individual and thus depend on the utility and internal state of the individual. In comparison, the probabilities of events occurring

in the environment are not dependent on the observer. Given this, it is not surprising that the reward effect is weaker than the probability effect, is extinguished by concurrent manipulations of probability and is not seen in the data of every participant (as in Experiment 7 and 8). In the older adults experiment, half of the participants did not want to keep the £20 they received for participating, and donated it to the BRACE charity. This was made clear by the participants from the outset of their testing session. Firstly, this could have meant that they were not motivated to respond quickly/accurately as their reward system was not engaged. Additionally, the magnitude difference in the reward values may have had no effect on their reward processing, to ensure they were more likely to gain a higher reward value. The differences in sensitivity to reward is supported by studies discussed in the discussion of the Chapter 3, where Hickey and colleagues (2010b) measured trait reward-seeking using a personality index, and found a correlation with the magnitude of reward priming in a visual search task. Even the participants who did accept the payment for the experiment may have a different utility, economic background or may be less motivated by reward at that stage of their life in comparison to the student population. As they were recruited from a volunteer database of a charity supporting dementia research, the older adult participants were likely to have different motivations to take part in the experiment than the participants in the previous experiments.

The theory around differences in reward sensitivity also supports the findings in Experiment 8, where there was no correlation in manual responses between the slope of the reward and probability effect. The difference between the nature of reward and probabilities in the environment could mean that it is unlikely that those participants that show particular sensitivity to the reward manipulation show a similar magnitude of sensitivity to the probability distributions of the environment. Additionally, in Experiment 7 it was found that the effects of reward and probability do not combine in a simple manner, and that the reward effect is extinguished by modulations in probability. These results could suggest that in an accumulator

model framework, reward and probability may act separately on different accumulators to produce an effect on responses.

An alternative theory for the absence of the reward effect in older adult participants could be related to the effect of reward on motor systems over time, if the reaction time effect is driven by dopamine activation. As discussed in Chapter 3, the dopamine reward signal is rapid and activations in dopamine neurons have latencies of 60-100ms and endure for less than 200ms (Schultz, 2007). This could explain the weak effect of reward on saccadic compared to manual responses seen in Chapter 3, as the saccadic response is initiated too early to be affected by the activation. Additionally, the manual responses in the older adults study are substantially slower than the manual responses in the previous experiments in the student population; it could be postulated that these responses are too slow for the endurance of the dopamine activation to affect response times. However, given the evidence to support the response slowing in aging being manifested in the motor-response generation phase of processing, it is relatively unlikely that this theory could hold true. It is more probable that the reward-related activity in the dopamine system affects the earlier stages of processing, such as activation in the anterior cingulate eventually leading to changes in sensory representation (Hickey et al., 2010a). This would suggest that the reward system, if activated, should still cause modulations in the manual reaction times of older adults.

Together the three experiments in this chapter suggest that although reward and probability modulate response times in apparently similar ways, they do not combine in a simple manner. This was shown directly in Experiment 7. The results of Experiment 8 also show that the effect of probability and reward are also not correlated across participants. In conjunction with the finding in Experiment 7, that the reward effect is less reliable than the probability effect, and extinguished by unequal probability distributions across targets. The results of this chapter together suggest that different neural and functional processes support

these two factors. As discussed, intuitively this may be explained by the inherent differences of how reward and probability are perceived in the environment. Additionally, the absence of reward effect in healthy older adults in Experiment 9 supports the reliance of the reward effect on properties of the individual: the way in which reward is processed depends on the individual and so depends on personal factors such as utility, age, internal state and economic background. This is very different to the probabilistic distributions in the environment, which are not dependent on individual interpretation but is instead a physical property of the environment.

CHAPTER 5

5.1 General Discussion

In the previous three chapters I have reported experiments that investigate how manipulations of probability and reward affect different response modalities and how these effects interact. Generally I have employed a similar paradigm across all experiments: participants are required to saccade to and respond manually to a simple perceptual task at a target to the left or right of a central fixation. The probability and reward value of the two targets have been manipulated singularly or concurrently in the experiments.

Although a probability effect was established in Chapter 2 in both saccadic and manual responses, this effect was not correlated and was sensitive to the exact structure of the paradigm. Manipulating probability modulated saccadic response times when the inter-stimulus interval (ISI) was short (less than 1 second) which was consistent with the existing literature (Antonaides et al., 2014; Carpenter & Williams, 1995). Conversely, an effect of probability was found on manual responses when the ISI was longer and there was clear motivation to respond quickly and accurately. The results of the experiments on reward manipulations in Chapter 3 showed a stronger effect of reward on manual than saccadic responses. Again, this was linked to a clear motivation on manual responses to respond quickly and accurately to the targets, and a long ISI. However, the reward effect was also sensitive to the reward structure in the paradigm; it was apparent that small increments of reward values are not salient enough to modulate response times. This was corroborated within the paradigm where a reward effect was seen, as response times were affected by the global magnitude of reward as well as the relative magnitude of reward associated with a particular stimulus in comparison to the other. As in the experiments investigating probability in Chapter 2, no correlation was found between the two response modalities. In Chapter 4 I investigated the

interaction between the reward and probability effect and found that the reward effect was extinguished as soon as there was an unequal probability manipulation across the two targets. This suggests that there are different processes governing the effect of reward and probability on response times, and that the probability effect is more dominant. It was also found that mapping the manual responses to spatial position of the targets was not a determining factor in the manifestation of the reward effect on manual responses. This suggests that the manual effect is not produced by increased low-level motor preparation to one side of the body. Additionally, the results of the final experiment in Chapter 4 show that in older adults the reward effect in manual responses is not present, highlighting the inherent differences between the features of information about reward value and probability in the environment.

Both the effects of reward and of probability on different response modalities seem to be sensitive to the time course of the stimulus presentation. Generally, stronger probability effects are seen on saccadic responses when the ISI is shorter; as discussed in Chapter 2, this could reflect an effect of IOR on inhibiting response generation to more likely targets over longer inter-stimulus intervals. This hypothesis does not hold for manipulations of reward, as no effect in either modality is seen in the experiments where the ISI is shorter; this is likely due to the reward schedule of those three experiments rather than any other aspect. In the final experiment of Chapter 3 where a reward effect was found in both saccadic and manual responses, I have suggested that the stronger effect on manual responses could be linked to the time course of dopamine activation (Schultz, 2007). Activations in dopamine neurons to reward-predicting stimuli are very fast and have latencies of 60-100ms and endure for less than 200ms (Schultz, 2007). Fast saccadic responses may be initiated too early to be affected as strongly by the dopaminergic activation, in comparison to manual responses.

Perhaps more pertinent to the differences across response modalities is the effect of negative feedback on manual response speed and accuracy. Across all experiments in Chapters

2 to 4 where a fixed time window specific to each participant was deployed for manual responses, a stronger effect of probability/reward was seen on manual responses than saccadic. The motivation to respond is more clearly focussed on the manual response to the target, which is explicitly goal-oriented and directly linked to the speed and accuracy of the response and thus the feedback received on each trial. This could explain why we see a stronger effect of reward and probability on manual responses compared to saccadic: the purpose of the saccade is primarily to gather information (Hickey et al., 2010a). With regards to this point, and the absence of correlation between saccadic and manual responses across all experiments, it is unlikely that both response modalities could be explained by a decision-making model where all signals across pathways are brought together with different decision thresholds for different responses (Bompas & Sumner, 2008). However, it is important to note that the difference in the purpose and execution of the saccadic and manual response in these experiments could be the significant factor that sets the two response modalities apart and leads to no correlation. As discussed in Chapter 1, the pre-motor theory of attention suggests a common source of information is used for all types of motor responses and that the same decision threshold would apply to all responses (Bompas & Sumner, 2008). The decision threshold for the saccadic latency in the experiments reported here relates to the side on which the target has appeared. Conversely, the decision threshold for the manual response additionally encapsulates the time taken to reach a binary perceptual decision at the location of the target; this is unrelated to the spatial position of the target. Thus it follows that these two responses may be too different to be able to combine as a common source of information. Research suggests a common target detection stage for both response modalities; this might not be reflected in the reported experiments due to all the other factors intrinsically linked to the differences in the nature of the saccadic and manual responses required (Taylor et al., 2006). It is possible that further work investigating both response modalities in a paradigm where the perceptual task requires a

similar goal-oriented fast and accurate saccadic and concurrent manual response (e.g. a saccade up or down to indicate the orientation of a letter T) could clarify this issue.

The short saccadic latencies recorded could provide an alternative explanation as to why the effect of probability and reward is weaker in the saccadic system. It has been discussed in the existing literature whether there are a separate distribution of saccades that are very fast and termed 'express saccades'; these fast saccades do not consistently form a different distribution (Wenban-Smith & Findlay, 1991). Although the mean latencies seen are still above the general distribution for express saccades (a mean of between 70-100ms), in some experiments across the thesis they are towards the lower end of the latency distribution of the 'fast regular' saccades (Wenban-Smith & Findlay, 1991). The fast latencies observed could suggest a 'floor effect' whereby the probability/reward manipulation cannot decrease the latencies beyond a certain point as they are already very fast (Wenban-Smith & Findlay, 1991). This is specifically supported by the absence of an effect between the high and equal probability conditions in Experiment 2 and Experiment 7a. Slowing down to less likely targets is apparent, but the speeding up of saccadic responses to more likely targets may be inhibited by a floor effect. This effect is not systematic across the experiments presented, nevertheless it is possible that the 'floor effect' could be a factor in the weak saccadic effect in general compared to the manual effect of reward and probability modulations. One way in which our experiment could be adapted to see if slowing down saccadic latencies increased the influence of probability or reward would be to change the nature of the targets. For example, the contrast of the targets could be modulated so that the process of detecting the location of the target before making a saccade takes longer. This would slow down the decision process and overall increase saccadic latencies, such that 'floor effects' should not influence the results.

Although an effect of reward has been established on both manual and saccadic responses, this has generally been a weaker and more unstable effect than probability has on these response modalities. I have hypothesised that this difference could lie in the properties of reward value and inherent probabilities in the environment. Reward value (specifically secondary rewards) depends on features of the individual (internal state, utility, economic background), whereas the probability that an event will occur in the environment is not dependent on the observer. This theory supports the absence of a reward effect in healthy older adults (Chapter 4), given that most of the participants were not motivated by reward to take part and some donated the money received in the experiment to charity.

The influence of probability and reward also differ across the experiments in the way that they affect the ocular drift/offset at fixation. As discussed in Chapter 2, a systematic offset at fixation towards the higher probability target was only present when the ISI was longer and constant, suggesting top-down temporal preparation developing over time (Weinbach & Henik, 2012). There was no reliable effect of reward on the offset at fixation in any of the experiments presented where reward value was manipulated. However, the probability manipulation consistently had an effect on the offset, with the exception of Experiment 1 where ISI was shorter. This suggests differences between the ways that these two factors affect the saccadic system. It could be that due to the nature of the probability manipulation requiring more saccades to the higher side, the effect of practice increases motor preparation/saccadic readiness to that side. A drift at fixation has been suggested to reflect intentions to make an eye movement (Kowler & Steinman, 1979), and the intention to make an eye movement to either hemifield is naturally going to be more affected by a probability bias (repeated saccades to one side) than a reward bias. This offset would not affect the latency to the target (Kalesnyka & Hallett, 1994), but highlights another way in which processing of reward and probability differ.

The inability for reward and probability to combine in a simple manner could suggest a common accumulator for these factors to act on. In the experiment where reward and probability were studied concurrently (Chapter 4), the reward effect was extinguished; if reward and probability cannot modulate the starting point at the same time, this could suggest that they are both acting on the same accumulator. This is supported by the neurological research, suggesting that bias in the excitability of SC neurons is increased both by prior knowledge of reward and probability and is likely to be reflected in an elevated starting point of an accumulator model such as LATER (Basso & Wurtz, 1997; Dorris & Munoz, 1998; Liu et al., 2011; Nakahara et al., 2006). However, it is also possible that there are separate accumulators for these processes, which could be more likely given the strong connection reward processing has with dopaminergic activation (Schultz, 2007). This is supported by the result in Chapter 4 where reward and probability were manipulated in the same paradigm; when high probability and high reward were associated with the same target, there was no additive effect of reward and probability and the responses were no different from the manipulation where expected values were matched across the targets. If reward and probability bias acted on a common accumulator we would expect to see an additive (or at least sub-additive) effect of combining the two. Reward has been directly linked within the literature to increasing the salience of stimuli; there is less support for the effect of probability on target salience (Fecteau & Munoz, 2006). It could be suggested that the effect of reward on salience is only manifested in response times if the probabilities are equal across the stimuli. Introducing a probability bias could override the effect of salience, and could suggest that reward and probability processes act on separate accumulators; this is supported by the finding in Chapter 4 that the effect of reward and probability are not correlated. Furthermore, the dominance of the probability bias over reward in the combined study could reflect participants' sensitivity to risk. Combining a high probability target with reward naturally increases the probability of receiving a reward;

given that the probability manipulation dominates the effect on behaviour, this could suggest that participants are more risk averse as they are valuing higher probabilities of reward regardless of the reward magnitudes (Moustafa, Cohen, Sherman & Frank, 2008). This is consistent with the non-linear utility function in behavioural economics, where higher magnitude gains are preferred to lower gains at a declining rate (Kahneman & Tversky, 1979; cited in Moustafa et al., 2008). The theory is supported by a model of reward processing in the basal ganglia, where the contrast between reinforcement probabilities is enhanced by subtracting 'Go' learning (speeding up responses for higher probabilities) and 'NoGo' learning (slowing down responses to lower probabilities) associations but large reward magnitudes are underweighted (Frank, 2005; Frank & Claus, 2006; cited in Moustafa et al., 2008).

In modelling the effect of reward and probability on response times using accumulator models, we would typically assume manipulations of probability affect the starting point of the accumulator model. One important question then is if this is modulated on a trial-by-trial basis or is it a global affect set across blocks of trials? As addressed Chapter 1, some research has suggested that successive target location repetitions ('repetition priming') produce search benefits for more probable locations (Walthew & Gilchrist, 2006). However, other studies have shown that both repetition priming and learning of a spatial probability distribution can produce the probability effect independently (Druker & Anderson, 2010). Preliminary research to this thesis, as mentioned in the Introduction of Chapter 2, showed some evidence of response times decreasing over several days suggesting a global process governing the probability effect. However, investigating how response times change from trial-to-trial proves to be an issue in the paradigms used across the experimental chapters. If there are relatively frequent errors made in the experiments by participants, this reduces the number of pairs of trials in which to examine the effect of the location of the previous trial on response time for the current trial.

This is especially true for saccadic data, where there is likely to be some number of trials discarded due to insufficient fixation and anticipatory saccades. In paradigms with manipulations of probability there are smaller numbers of trials for lower probability targets, which further reduces the number of pairs of subsequent trials to analyse. Moreover, response times on consecutive trials could be affected by the spatial location of the target rather than the associated probability. For example, if the target appeared on the right-hand side on two consecutive trials, IOR (inhibition of return) may slow the response time (saccadic or manual) on the second trial regardless of the spatial probability. As discussed in Chapter 2, this could even be hypothesised to be an explanation for the instability of the probability effect, on saccadic responses particularly: the more likely target location could become inhibited on consecutive trials and counteract the facilitation that results from the increased probability. Additionally, if the target appears in the second trial on the opposite side to the first trial, the saccade required is in the same direction and of the same amplitude as the saccade previously made to return to fixation (see Carpenter (2001) for a similar explanation for the occurrence of Express Saccades). This could facilitate the response to the second trial, again perhaps regardless of the spatial probability. This means on a trial-to-trial basis there could be additional factors affecting response times, such that analysing consecutive trials together would be influenced by these confounds. Furthermore, the additional factors affecting responses on a local level could support the research suggesting that modulations of probability (and perhaps reward) affect the starting point within accumulator models of response times via a global, long-term process (Druker & Anderson, 2010; Dunne et al., 2015). In order to understand if there are sequential effects that interact with reward and probability manipulations it could be more illuminating to use a paradigm in which areas/hemifields are associated with higher probability/reward and the exact location of targets is changed.

The final experiment of Chapter 4 addressed how the effect of reward and probability on manual responses changes in healthy older adults, and provides a simple and feasible paradigm to investigate how deep brain stimulation of the STN (subthalamic nucleus) in Parkinson's patients affects processing of these factors. It would be interesting to see if a reward effect was found in this population, as the results from older adults showed no effect of reward on manual responses. There have been instances of Parkinson's patients developing clinical criteria for pathological gambling addiction from increased dopamine replacement therapy (Bandini, Primavera, Pizzorno & Cocito, 2006). In some cases these pathologies have been dramatically improved by deep brain stimulation of the STN and postoperative withdrawal of dopaminergic therapy (Bandini et al., 2006; Witjas et al., 2005). More generally however, impulsivity has been associated with both dopaminergic replacement therapy (e.g. levadopa) and deep brain stimulation (Bódi et al., 2009; Frank et al., 2007; Ondo & Lai, 2008). With regards to the absence of reward effect in older adult participants in Chapter 4, patients on DBS additionally take dopaminergic medication, albeit in lower doses than those without DBS (Frank et al., 2007). Thus a comparison between patients with DBS turned off and the older adult controls could provide an interesting insight into the reward processing in these two populations. The Parkinson's patients might show a reward effect that is more comparable to the results with younger adult participants. It is hypothesised that the STN is not required to value magnitudes of rewards per se, but that it slows down decisions under conflict; in effect this can be seen as 'buying time' to arrive at the correct decision (Frank et al., 2007). It is likely that deep brain stimulation of the STN disrupts this process, as discussed in Chapter 1, which is supported by the trait of impulsivity across this patient group (Frank et al., 2007). It is unclear whether DBS acts like a lesion on the STN as a 'depolarisation block' or whether it induces high frequency firing patterns; it has been posited that both of these mechanisms would prevent the STN from naturally responding to its cortical inputs and would still disrupt conflict induced slowing. This

research suggests that DBS could have a similar effect on both the reward and the probability effect, if we assume that unequal reward schedules or probability distributions both could be categorised as high-conflict decisions. Specifically, it could be hypothesised that as slowing of responses is seen generally to low probability or low reward valued targets, this is the aspect that would be affected by the DBS. This result has been found in Parkinson's patients with DBS for saccadic responses, and given the differences found between manual and saccadic responses in this thesis it would be very interesting to investigate whether the same result is found in manual responses for this patient group (Antoniades et al., 2014). Understanding the cognitive side effects produced by deep brain stimulation is crucial, as increased impulsivity could greatly impact on a patient's quality of life even without the involvement of a pathological addiction. Highlighting this point, one DBS patient in Frank and colleagues (2007) study when asked if he would like to sit on a more comfortable chair across the other side of the room, immediately moved towards the chair unaided despite not being able to walk properly. They suggest that the rewarding prospect of the comfortable chair was not offset by the activation of a functional STN, which would have slowed his responses in this high conflict decision (Frank et al., 2007). This shows that the impulsivity seen in this patient group could be detrimental to their overall quality of life despite alleviating the symptoms of Parkinson's disease.

This thesis provides new insights into how both reward and probability act and interact to shape behaviour. Both factors only affect behaviour under certain conditions and the relationship between these two factors proved to be both complex and revealing. Further work will be required to fully understand both factors, however the work provides an important starting point in trying to understand how the myriad of factors that shape our behaviour combine to produce the optimal behaviour in a given circumstance. What this study makes clear is that the interactions between these factors will be far from simple and will benefit from

an understanding of how these factors are coded in the brain as well as exactly what they signal about the status of the environment.

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