The modulation of information processing by reward expectation and spatial attention

Stephanie Baines

The Queen's College

Michelmas Term, 2010

A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy at the University of Oxford

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Abstract

Reward expectation and spatial attention both exert powerful control over behaviour and modulate neural activity. The experiments in this thesis aimed to chart the dynamics of reward expectation effects across the time course of information processing and examine the relationship between reward and attention. Experiments 3.1 and 3.2 parametrically manipulated reward magnitude in the presence or absence of attention and demonstrated reward could influence reaction time (RT) under conditions of time pressure. Experiments 4.1 and 4.2 independently varied reward and spatial probabilities and illustrated independent and interactive effects of reward and attention at late stages of cognitive processing (the P300 potential), as well as modulation of detection sensitivity (d') by reward under conditions of uncertainty when reward was able to work through feature-based attention. The experiment of Chapter 5 cued reward and attention trial by trial and showed under these conditions, not only could reward influence late stages of information processing, but expectation of reward reduced peak latency of the visual N1 potential. Reward and attention also modulated motor preparation with both independent and interactive effects. The experiment of Chapter 6 examined the dynamics of reward association with task-relevant targets and irrelevant distracters during visual search and demonstrated that task-irrelevant but motivationally-salient distracter items could capture attentional resources away from the target, guided by endogenous reward association alone. The experiments of this thesis demonstrated the ability of reward expectation to modulate both behaviour and multiple stages of information processing, with effects predominantly independent from those of attention. Reward could influence processing from early visual analysis and target detection stages. Interaction between the two systems occurred at late processing stages, whereby reward and attentional information may have been integrated to provide a cohesive representation of the stimulus given the current environmental conditions.

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List of Abbreviations

ACC	Anterior cingulate cortex
ANOVA	Analysis of variance
BOLD	Blood-oxygen-level-dependence
CNV	Contingent negative variation
D'	Detection sensitivity
EEG	Electroencephalogram/Electroencephalography
EOG	Electrooculogram
ERP	Event-related potential
FEF	Frontal eye fields
fMRI	Functional magnetic resonance imaging
HEOG	Horizontal electrooculogram
IPS	Intraparietal sulcus
ITI	Inter-trial interval
LIP	Lateral intraparietal area
LRP	Lateralised readiness potential
MEG	Magnetoencephalography
OFC	Orbitofrontal Cortex
PET	Positron emission tomography
PFC	Prefrontal cortex
PPC	Posterior parietal cortex
RF	Receptive field
RT	Reaction time
SOA	Stimulus-onset asynchrony
TMS	Transcranial magnetic stimulation
VEOG	Vertical electrooculogram

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Chapter 1: General Introduction

1.1 Attention: Resolution of Competition for Processing Resources

The limited processing capacity of the brain necessitates the prioritisation of currently-relevant stimuli in the competition for these processing resources (Desimone & Duncan, 1995). The attentional system uses current task requirements and expectations to bias allocation of these resources towards those stimuli currently most relevant for behaviour. This can occur by reflexive capture of attention via bottom-up stimulus features, or through voluntary allocation in a top-down manner (Desimone & Duncan, 1995; Kastner & Ungerleider, 2000, 2001). Attentional signals derive from a network of regions in frontal and parietal cortex (Gitelman, et al., 1999; Kim, et al., 1999; Mesulam, 1981a; Nobre, et al., 1997). This section will discuss the ways in which attentional priority is allocated, and the network of brain regions responsible for such deployment of attention.

1.1.1 The mechanisms of attentional bias

Prioritisation of processing can be achieved by allocation of attention to a given stimulus. A stimulus may gain attentional priority by means of its inherent properties. Stimuli more salient in terms of colour, luminance or abrupt onset of motion capture attention in an entirely reflexive manner, by means of their physical stimulus properties alone. This is known as bottom-up or stimulus-driven attentional capture (Desimone & Duncan, 1995; Gottlieb, Kusunoki, & Goldberg, 1998; Kastner & Ungerleider, 2000, 2001; Treue, 2003; Yantis, 2008). Such a capture of attention is observed in singleton or ‘pop-out’ visual search, where a highly

salient target stimulus appears to pop out from the surrounding, non-salient stimuli (Lamy, Leber, & Egeth, 2004; Luck, 1994; Luck & Hillyard, 1994b; Treisman & Gelade, 1980). Pop out is robust, with the addition of an increasing number of distractors typically failing to increase target detection time (Treisman & Gelade, 1980). In addition, if a search array contains a non-salient target accompanied by salient non-targets, electrophysiological data suggest the salient non-target evokes a response before the non-salient target, despite the salient stimulus having no relevance for task performance (Hickey, Di Lollo, & McDonald, 2008, 2009; Hickey, McDonald, & Theeuwes, 2006; Hickey, van Zoest, & Theeuwes, 2010b). A salient non-target produces an N2pc component, an index of visual search, which precedes that produced to a less-salient target (Hickey, et al., 2006). The capture of attention via bottom-up factors may be mediated by regions of the parietal cortex, where neuronal firing in response to highly salient stimuli is observed (Gottlieb, et al., 1998). The role of the parietal cortex in attention will be further discussed in a later section.

Bottom-up capture is not the only means by which attention may be allocated, however. Current behavioural goals and expectations may establish top-down biasing signals, which act upon visual processing regions (Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Kastner & Ungerleider, 2000, 2001; Serences & Yantis, 2006). At increasing levels of processing in the visual hierarchy, the receptive fields (RFs) of neurons increase in size as well as the complexity of information contained therein (Kastner & Ungerleider, 2000). Competition for processing resources within the RF of a neuron therefore increases at successive stages within this hierarchy. Top-down biases act through multiple mechanisms to lead to selection of only those stimulus locations, features or objects of most relevance to the current task goals (Desimone & Duncan, 1995; Kastner & Ungerleider, 2000, 2001). At the behavioural level, cues indicating the likely location of an upcoming target stimulus lead to increased speed of

response and greater accuracy and detection sensitivity (Posner, 1980; Posner, Snyder, & Davidson, 1977). Selective attention to a specific stimulus attribute results in greater sensitivity to change in that feature than when attention is divided across multiple stimulus attributes (Reynolds & Chelazzi, 2004). In addition, selective attention in such a case causes sensitivity to be unaffected by changes in unattended features, suggesting a sharpening in perception that is specific to the attended attribute (Reynolds & Chelazzi, 2004). Attention may thus serve to produce a coherent percept across the visual hierarchy by giving greater competitive weight to those stimuli currently of greater relevance to the fulfilment of behavioural goals and expectations (Serences & Yantis, 2006). One mechanism through which the competition for processing within a neuron's RF may be resolved it through a filtering out of information related to the task-irrelevant item(s). The response of a neuron to a given stimulus differs depending on that neuron's preference. If a pair of stimuli, one effective at evoking a response, the other ineffective, is presented together in a neuron's RF, the response is scaled to a level intermediate to the effective and ineffective responses. When attention is directed to one or other of these stimuli, the response is driven by the attended stimulus, almost as though that stimulus was presented in isolation. Firing to the pair thus increases with attention to the effective stimulus and decreases when allocated to the ineffective stimulus (Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985; Reynolds, Chelazzi, & Desimone, 1999). This mechanism appears to depend on competition between stimuli within the RF. If one stimulus of the pair is presented inside the RF and the other outside, direct competition between the two for the RF disappears and attentional modulation is no longer observed (Luck, et al., 1997; Moran & Desimone, 1985; Reynolds, et al., 1999). Consistent with this argument, functional magnetic resonance imaging (fMRI) studies with humans have demonstrated greater blood-oxygen-level-dependence (BOLD) activation in visual processing regions from striate cortex through to temporal visual processing regions

when four stimuli are presented sequentially, in isolation, compared with simultaneous presentation (Kastner, De Weerd, Georgopoulos, Desimone, & Ungerleider, 1998b). In accordance with increasing competitive interference at higher levels of the visual hierarchy, BOLD activation differences between the sequential and simultaneous conditions increase progressively at each successive stage of the visual processing hierarchy (Kastner, et al., 1998b).

In addition to the filtering of irrelevant stimulus information, top-down signals also induce the enhancement of activity related to the location or features of the task-relevant item. This is achieved by increasing the baseline or tonic firing rate of neurons coding the task relevant spatial location or stimulus features. Single-unit studies have observed an increase in baseline tonic firing rates in neurons coding an attended spatial location or stimulus feature in anticipation of stimulus presentation (Chelazzi, Miller, Duncan, & Desimone, 1993; Hillyard, Vogel, & Luck, 1998; Luck, et al., 1997). This attentional modulation of expectation-related firing has been observed in multiple regions of the monkey visual processing hierarchy, from V1 to V4, the parietal lateral intraparietal area (LIP) and motion-sensitive middle temporal region (Chelazzi, et al., 1993; Colby, Duhamel, & Goldberg, 1996; Hillyard, et al., 1998; Luck, et al., 1997; Treue & Maunsell, 1996). These findings were also observed in neuroimaging studies with humans. Increases in BOLD activation were observed in cortical visual processing regions coding retinotopically for a spatial location to which attention was directed in expectation of a stimulus or middle temporal region in expectation of moving stimuli (Hopfinger, Buonocore, & Mangun, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Shulman, et al., 1999). The combined results of the single-unit and neuroimaging studies suggest top-down attentional control signals may target the processing regions coding the attended spatial location of stimulus attributes and modulate the activity such that only those

stimuli most relevant to the current task are selected for further processing. This would allow these stimuli to overcome the competitive interactions with non-relevant items within the visual field (Desimone & Duncan, 1995; Kastner & Ungerleider, 2000). It is possible that top-down sources of bias other than attention may also modulate processing in this way. The experiments of this thesis will investigate whether motivation is also able to bias information processing in this direct, targeted manner.

A further mechanism by which attention aids selection of relevant stimuli for processing is by the modulation of firing synchrony between populations of neurons coding the attended location or stimulus features (Womelsdorf & Fries, 2007). An increase in the synchrony of high-frequency gamma-band activity in V4 neurons is observed in response to stimuli presented within the attended location. Moreover, gamma synchronisation is correlated with behavioural performance (Taylor, Mandon, Freiwald, & Kreiter, 2005; Womelsdorf, Fries, Mitra, & Desimone, 2006). When monkeys were required to detect a change in one of two visual stimuli, an increase in gamma synchronisation in V4 prior to and following change in the target was associated with faster change detection. When gamma-band synchronisation was enhanced with respect to the task-irrelevant distractor, reaction speed was slower (Womelsdorf, et al., 2006). A similar pattern was observed in monkeys performing a shape-tracking task. An increase in gamma-band synchronisation was associated with correct detection of the second presentation of a target shape at the attended location, whereas increases in gamma synchronisation in response to distractor items corresponded with distractor-induced false alarms (Taylor, et al., 2005).

In addition to the increased gamma-band synchrony, desynchronisation in the alpha band is typically observed for neurons coding an attended location (Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Womelsdorf, et al., 2006). Spatial cues lead to alpha desynchronisation contralateral to the attended visual field in the human electroencephalogram (EEG). Consistent with this desynchronisation reflecting successful deployment of attention to the cued locations, and in accordance with the results of gamma-band activity, alpha desynchronisation correlated with behavioural performance. Target detection was faster when stimuli were presented to the location corresponding with enhanced alpha desynchronisation (Thut, et al., 2006). The modulation of oscillatory synchronisation in gamma and alpha frequency bands may bias processing such that only those attended stimuli are selected and processed. The increased communication between populations of neurons coding attributes of the relevant stimulus at lower-level visual areas may determine the relative access to later processing. This may be achieved by exclusive communicative access to higher processing regions for task-relevant items, effectively blocking the influence of irrelevant items at later stages of processing (Fries, 2009).

Effects of attention observed in event-related potentials (ERPs) are broadly consistent with the single-unit findings. Attention modulates activity at multiple points in the information processing time course, with the first cortical effects evident upon visual processing in extrastriate visual cortex. Amplitude of the P1 and N1 potentials, thought to reflect visual processing within separable regions of extrastriate visual cortex, is larger for attended compared to unattended stimuli (Eimer, 1998; Luck, Woodman, & Vogel, 2000; Nobre, Sebestyen, & Miniussi, 2000b; Nobre & Silvert, 2008). These changes in sensory-evoked activity in ERP studies may represent a gain control or amplification mechanism of attention. Enhancement of activity by attention may increase the signal-to-noise ratio of an attended

stimulus, leading to enhanced visual processing (Luck, et al., 2000). The form, latency and topography of the P1 do not differ for attended and unattended stimuli. This is consistent with sensory amplification of the same underlying signal, rather than activation of different populations of neurons. Amplitude modulations of early visual potentials by attention also correlates with behavioural performance (Mangun & Hillyard, 1988). Presentation of stimuli successively further from the locus of spatial attention results in attenuation of P1 and N1 potentials. This is accompanied by a commensurate decrease in detection sensitivity (d'), indicating amplitude enhancement of early visual potentials by attention reflects a greater processing of stimuli occurring at the attended location (Mangun & Hillyard, 1988).

It is important to note that the P1 and N1 attention effects, rather than being the continuation of one process, are likely the result of separate underlying processes. This is evident in the differing pattern of effects of P1 and N1 amplitude with differing task requirements, in addition to the distinct neural sources of the two potentials (Hillyard, et al., 1998; Luck & Hillyard, 1995; Luck, et al., 1994). In a cued attention task with valid and invalid spatial cues as well as neutral cues that did not specify a likely target location, both P1 and N1 amplitudes were modulated by attention, but the nature of this modulation differed. P1 amplitude was attenuated on invalid relative to neutral trials, whereas N1 amplitude was enhanced for valid compared with neutral trials (Luck, et al., 1994). In a visual search task requiring target discrimination, a similar result was observed. A smaller P1 was observed if a probe stimulus was presented at a non-target location relative to the target location or to an array without a target. A larger N1 was present for probe stimuli presented at the target location, compared with a non-target location or a target-absent array (Luck & Hillyard, 1995). When simple target detection was required, N1 amplitude continued to be modulated by attention, but effects of attention on P1 amplitude disappeared. The results suggest distinct roles for the P1 and N1

potentials with respect to attention (Luck & Hillyard, 1995). P1 is suggested to reflect suppression of potentially distracting information at unattended locations. N1, in contrast, may reflect a "limited-capacity discriminative process" that is allocated to the attended location (Hillyard, et al., 1998). Attention may therefore operate at multiple stages of visual processing through manifold different mechanisms.

Neuroimaging data are also consistent with an amplification of sensory-related activity by attention. Regional cerebral blood flow is observed to increase when attention is directed to a specific stimulus attribute, compared with when it must be divided across the visual scene (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990). In addition to this increased activity with attention, activation changes are specific to distinct brain regions, depending upon the stimulus attribute attended (Corbetta, et al., 1991; Corbetta, et al., 1990). This suggests that attention to specific stimulus attributes leads to increased activity in sensory cortical regions specialised for processing the attended feature. Attention to a specified location also evokes increased BOLD activity in extrastriate regions coding the attended location prior to any stimulus presentation (Kastner, et al., 1999).

In addition to the influence upon sensory processing, attention is able to modulate later stages of information processing relating to cognition and action. Indeed, the magnitude of attention effects increases at successive levels of the visual processing hierarchy (Kastner, De Weerd, Desimone, & Ungerleider, 1998a). Amplitude of the P300 potential is modulated by attention, though the precise nature of the modulation is dependent on task goals and parameters (Donchin & Coles, 1988a; Eimer, 1998; Johnson, 1986; Nieuwenhuis, Aston-Jones, & Cohen,

2005a). In visual search, pop-out targets elicit a larger P300 than non-target pop-outs or homogeneous arrays (Luck & Hillyard, 1994a). In addition, the P300 is highly sensitive to other task parameters such as probability, uncertainty and WM requirements. A larger P300 is produced for less probable targets, or under conditions of uncertainty, such as with difficult to discriminate stimuli or when target identity changes from one trial to the next, and may reflect changes in WM demands (Johnson, 1986; Luck & Hillyard, 1994a).

1.1.2 Origin of Top-down Control Signals: the fronto-parietal network

Attentional signals appear to originate in a distributed network of highly interconnected brain regions in fronto-parietal cortex (Corbetta, Miezin, Shulman, & Petersen, 1993; Gitelman, et al., 1999; Kim, et al., 1999; Mesulam, 1981b, 1990; Nobre, et al., 1997). This network of regions is consistently activated during diverse attention tasks, irrespective of requirements such as reflexive or non-reflexive allocation of attention, central or peripheral cues or the requirement to respond (Corbetta & Shulman, 1998; Gitelman, et al., 1999; Nobre, Gitelman, Dias, & Mesulam, 2000a; Nobre, et al., 1997). This suggests the network is involved in a general orienting of spatial attention, rather than separate regions governing different types of spatial attention (Mesulam, 1999). The resultant attentional signals allow the identification and representation of behaviourally relevant stimuli from multimodal sensory information and the planning and enacting of motor plans for exploration of and interaction with such stimuli (Mesulam, 1999). The fronto-parietal attention network possesses extensive reciprocal connections with visual cortical processing regions. This allows the biasing signals generated in fronto-parietal cortex to directly modulate visual processing from the earliest stages.

The frontal eye fields (FEF), a region of prefrontal cortex (PFC) that is heavily interconnected with extrastriate visual cortex and also parietal region LIP/intraparietal sulcus (IPS), is implicated as a likely generator of top-down attention signals. In addition to a vital role in the programming and initiation of saccades, covert direction of attention to peripheral locations in the absence of saccade requirements leads to increased activation of the FEF (Corbetta, et al., 1998; Corbetta, Kincade, & Shulman, 2002; Corbetta, et al., 1993; Corbetta & Shulman, 1998; Gitelman, et al., 1999; Kastner, et al., 1999; Kim, et al., 1999; Mesulam, 1990; Nobre, et al., 1997). FEF neurons produce target-detection related increases in firing during top-down visual search that precedes firing increases in LIP, as well as preceding saccade initiation (Armstrong, Fitzgerald, & Moore, 2006; Armstrong & Moore, 2007; Buschman & Miller, 2007; Goldberg & Bruce, 1985; Moore & Armstrong, 2003; Moore & Fallah, 2004). Subthreshold FEF stimulation elicits increased firing rates in V4 neurons whose RFs contain a given visual stimulus (Armstrong, et al., 2006; Armstrong & Moore, 2007; Moore & Armstrong, 2003; Moore & Fallah, 2004). These changes in V4 firing mirror the results of allocation of attention to a visual stimulus (Luck, et al., 1997; Reynolds, et al., 1999). In addition, microstimulation leads to a selective enhancement of responses to stimuli aligned with the endpoint of the planned saccade, relative to stimuli appearing at a misaligned location. No such favouring of saccadic endpoint alignment occurs in the absence of FEF microstimuation. This suggests FEF microstimulation leads to an increase in the competitive weight of a stimulus at the saccadic endpoint, consistent with the FEF having role in top-down attention (Armstrong, et al., 2006). FEF microstimulation also influences V4 firing rates for pairs of stimuli occurring within the RF, such that the response was driven by the stimulus appearing at the aligned location rather than reflecting the average of the response to each stimulus in isolation (Armstrong, et al., 2006). This effect mirrors that of directing attention to one of a pair of stimuli (Luck, et al., 1997; Reynolds, et al., 1999). Furthermore, FEF microstimuluation leads to improvements in

the ability of V4 neurons to discriminate between two orientation stimuli, due to increased magnitude of firing for the preferred stimulus, an effect also observed with the allocation of attention (Armstrong & Moore, 2007; Reynolds & Chelazzi, 2004). This improvement was specific to stimuli at the saccadic endpoint (Armstrong & Moore, 2007). These results suggest that FEF microstimulation elicits changes in firing in visual cortex in the same manner as allocation of attention, consistent with the FEF having a role in top-down attentional control.

Application of transcranial magnetic stimulation (TMS) to the FEF influences activity in visual processing regions in a manner that is immune to current stimulus context, consistent with a role in generation of top-down control signals (Ruff, et al., 2008; Ruff, et al., 2006; Taylor, Nobre, & Rushworth, 2007a). Delivering TMS pulses to the right FEF following a spatial cue in an attentional-orienting task results in a negative EEG deflection over ipsilateral occipital electrode sites. This negativity begins prior to and persists after stimulus presentation (Taylor, et al., 2007a). The effect does not occur after TMS delivered to a right-hemisphere control site located closer to the occipital electrodes. Similarly, FEF TMS causes changes in BOLD activation in retinotopic visual regions V1 to V4. Activity in visual cortical regions decreased with increasing TMS intensity for regions representing centrally-presented stimuli, whilst the reverse was true for regions representing peripheral stimuli (Ruff, et al., 2006). This effect did not differ as a function of stimulus presence or absence. It is important to note that this differs from the effects of IPS TMS, where effects were dependent upon stimulus context (Ruff, et al., 2008). These context-invariant changes to visual processing as a result of FEF TMS illustrate the direct, causal relationship between FEF activation and that of visual cortex. This is consistent with the FEF as an origin of top-down attentional signals.

Parietal activation during attentional orienting is observed in the posterior parietal cortex (PPC) the most vital component of which, for attention, appears to be IPS (the human homologue of monkey LIP) (Mesulam, 1999). Activation is also observed in the superior and inferior parietal lobules, and medial parietal cortex. The parietal components of the spatial attention network display properties of both extrastriate processing and higher-level activity, thus PPC has been proposed to act as a bridge between sensory and motor aspects of extrapersonal space (Gottlieb, et al., 1998). Many aspects of activity in LIP/IPS reflect characteristics of that exhibited by extrastriate visual processing regions. Stimulus salience, such as abrupt motion onset, increases firing rates (Bisley & Goldberg, 2003; Gottlieb & Goldberg, 1999; Gottlieb, et al., 1998). A further illustration of the bridging role of LIP is observed during visual search. Both LIP and the FEF fire prior to saccade to a target in a visual search array. The relative timing of firing in these regions, however, is governed by the factor guiding visual search. LIP neurons fire early, and prior to frontal regions, when bottom-up salience governs visual search (in "pop-out" search). When search is guided by top-down rules (in memory-guided search), LIP activity is later, following frontal firing. Thus whilst the two regions display similar patterns of activity, the extent to which each is guided by exogenous or endogenous factors differs (Buschman & Miller, 2007).

In addition to these extrastriate-resembling effects, IPS/LIP also displays characteristics akin to those of higher-order frontal regions such as the FEF. Though the timing of activity in PPC and PFC may differ, there is a remarkable similarity in the pattern of firing characteristics of neurons in these regions (Buschman & Miller, 2007; Chafee & Goldman-Rakic, 1998). The spatial tuning and temporal duration characteristics, for example, are virtually indistinguishable. Firing in these regions displays a high level of synchrony. There was significant coherence between LIP and FEF firing during visual search, indicative of firing

synchrony (Buschman & Miller, 2007). Furthermore, systematic deactivation of area 7ip in PPC or area 8a in PFC led to a commensurate decrease in neuronal firing in the other region (Chafee & Goldman-Rakic, 2000). Both regions are involved in the guidance of eye and limb movements within extrapersonal space (Barash, Bracewell, Fogassi, Gnadt, & Andersen, 1991; Brotchie, Andersen, Snyder, & Goodman, 1995; Niki & Watanabe, 1976). Furthermore the regions targeted by PPC and PFC, such as extrastriate visual cortex, are similar. This suggests the top-down bias signals of both these regions are used to target processing of visual information and the guidance of motor behaviour with respect to modulation of activity within similar brain regions (Chafee & Goldman-Rakic, 2000).

Taken together, the results implicate parietal cortex as an intermediary between stimulus processing in extrastriate visual cortex, exogenous attentional capture and endogenously guided attention in higher-order regions. The anatomical connections between LIP/IPS and both extrastriate regions and frontal regions like the FEF would allow for such a role (Andersen, Asanuma, & Cowan, 1985; Andersen, Asanuma, Essick, & Siegel, 1990; Petrides & Pandya, 1984). Neurons in LIP/IPS may encode incoming stimulus information and integrate this into salience-based representations stored as retinotopically coded coordinate systems (Bisley & Goldberg, 2003; Gottlieb & Goldberg, 1999; Gottlieb, et al., 1998; Mesulam, 1999). These maps code objects according to their current behavioural salience, with task irrelevant objects and locations eliciting little neuronal response (Gottlieb, et al., 1998; Mesulam, 1999). Specific regions within PPC then translate these salience maps into different action plans. Saccades to motivationally relevant locations appear to be guided by LIP whereas reaching or grasping movements are the responsibility of more anterior regions (Bushnell, Goldberg, & Robinson, 1981; Gottlieb, et al., 1998). The PPC also guides attentional shifts in the absence of overt motor responses, displaying activation by cues that direct covert attention toward a

specific spatial location or between salient stimuli (Robinson, Bowman, & Kertzman, 1995). The use of TMS demonstrates a direct, causal relationship whereby parietal neurons modulate activity in visual processing regions. This is done so in a manner that is dependent upon the current stimulus context (Ruff, et al., 2008). The area has recently been proposed as a potential region in which motivational information, in addition to physical salience, may be integrated into these salience maps (Bendiksby & Platt, 2006). LIP neurons have been demonstrated to increase rates of firing for rewarded stimuli, or scale their firing rates to the weight of evidence toward a decision likely to result in reward (Bendiksby & Platt, 2006; Gold & Shadlen, 2002; Yang & Shadlen, 2007b). Motivational signals originating in the anterior cingulate cortex (ACC) may be incorporated into the salience maps in this region (Mesulam, 1999).

The ACC may therefore act as an important point of integration between the attention and reward systems. The ACC is activated during visuospatial attentional tasks and may be important in maintenance of effort required for task execution and attentional shifting, given the correlation of activity with efficiency of shifts of attention (Gitelman, et al., 1999; Kim, et al., 1999; Mesulam, 1999; Nobre, et al., 1997). In addition to connections with other potential sources of top-down attentional biases, such as FEF and area7a, the ACC is highly interconnected with the limbic system (Pandya, Hoesen, & Mesulam, 1981). This pattern of connectivity may allow the ACC to integrate signals regarding attentional and motivational significance, which information is then used to bias visuospatial processing of and interaction with those stimuli of current relevance.

Subcortical regions are also involved in the spatial attention network (Gitelman et al., 1999; Mesulam, 1999; Nobre et al., 1997). Activity in the lateral geniculate nucleus of the thalamus has been demonstrated to be modulated by attention via multiple means. A neuroimaging study demonstrated increased BOLD activation in the lateral geniculate nucleus for attended relative to unattended stimuli (O'Connor, Fukui, Pinsk, & Kastner, 2002). In addition, when task demands were engaged with a secondary task, there was a relative decrease in BOLD activity produced in response to ignored stimuli, suggesting activation of lateral geniculate nucleus by task-irrelevant items decreases when attention is directed elsewhere. The lateral geniculate nucleus also exhibited an increase in baseline activity in expectation of a stimulus presented to an attended location, akin to the baseline shifts observed in extrastriate visual regions of the cortex (O'Connor, et al., 2002). The superior colliculus is another subcortical region with a role in attention that is highly related to that of the FEF. The superior colliculus has been implicated in the planning and initiation of saccades (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Müller, Philiastides, & Newsome, 2005; Schiller & Stryker, 1972; Wurtz & Goldberg, 1972). Stimulation of the superior colliculus in monkeys induces saccades that bring the fovea in line with the stimulated neuron's RF (Schiller & Stryker, 1972). Superior colliculus neurons fire prior to saccade production (Schiller & Stryker, 1972). This firing can be modulated by attention, with a greater neuronal response to stimuli that are the target of a saccade (Wurtz & Goldberg, 1972). Visuomotor neurons in the superior colliculus fire at the time of a covert shift of attention in addition to preceding saccadic onset (Ignashchenkova, et al., 2004). In accordance with studies of the FEF (Moore & Armstrong, 2003; Moore & Fallah, 2004), microstimulation of the superior colliculus improves stimulus discriminability of stimuli presented in the RF of the stimulation site. This suggests that activation of superior colliculus neurons can induce an orienting of attention to the cell's RF, and suggests the function of the superior colliculus is highly related to the FEF (Müller, et al., 2005).

This network of interconnected brain areas is activated under most conditions of visuospatial attention. As such, these regions likely comprise the core spatial attention network. In addition to this core network, additional regions are selectively recruited depending upon task requirements and the nature of expectations established. For example, lateral orbitofrontal cortex (OFC) is activated by a violation of expectation (Nobre, Coull, Frith, & Mesulam, 1999) and lateral prefrontal areas are recruited during spatial orienting to mental representations (Nobre, et al., 2004). Regions in addition to those of the core spatial attention network might be expected to be recruited with the additional task component of reward expectation.

1.2 Reward expectation – influences upon decision making and choice behaviour

Attentional signals are unlikely to be the only source of bias upon behaviour and neural processing. Motivational factors, such as the attainment of reward, are powerful driving forces in the learning process. An action associated with a favourable outcome is increasingly repeated, whereas one associated with an aversive outcome diminishes in incidence (Skinner, 1966). Stimuli associated with reward elicit approach behaviour (Robbins & Everitt, 1996; Schultz, 2000). Novel or otherwise attention-inducing events relating to reward delivery influence the firing of midbrain dopamine neurons in a manner reminiscent of the effects of stimulus salience on attentional signals in regions such as LIP (Maunsell, 2004; Schultz, 2000). The mechanisms and brain circuitry underlying the effects of reward expectation are discussed in the following section.

1.2.1 Reward expectation

The ability to anticipate delivery of a reward with respect to current stimulus information is an important factor in shaping behaviour before an action is executed. Reward expectation signals are observed in the ventral striatum and caudate nucleus (Fiorillo, Tobler, & Schultz, 2003; Hollerman, Tremblay, & Schultz, 1998; Robbins & Everitt, 1996; Romo & Schultz, 1990; Schultz, 1986; Schultz, Apicella, Scarnati, & Ljungberg, 1992). In a go/no-go task, neurons were observed to produce a sustained increase in firing in response to visual stimuli that indicated impending reward delivery. Activity increased above baseline upon presentation of reward-predicting stimuli, enduring until reward delivery, upon which time activity sharply diminished. The activity demonstrated a close relationship with time of reward delivery; sustained activity persisted until reward delivery even when the timing of delivery was altered to be earlier or later than expected (Hollerman, et al., 1998). This activity was motivationally specific, occurring for rewarded but not non-rewarded movements (Hollerman, et al., 1998). A diverse set of visual stimuli elicited activity similar in nature, with differences related only to the motivational association of the stimuli, not visual features (Hollerman, et al., 1998). Furthermore, this could not be dismissed as motor preparation, as similar sustained activity was observed for rewarded non-movements (Hollerman, et al., 1998). This sustained activity may depend on the level of certainty in which stimulus-outcome associations occur. Activity magnitude increased with growing uncertainty, with maximal magnitude for stimuli that had a 0.5 probability of reward delivery, and near-absent activity with probability of 0 or 1 (Fiorillo, et al., 2003). The sustained activity of dopamine neurons may thus represent an expectation signal detailing the degree of certainty with which a reward can be expected, as well as the time of expectation. This may add an additional layer of sensitivity in driving the learning process, when coupled with the prediction error signal. Though differences between the

precise mechanisms exist, these sustained reward signals are reminiscent of the baseline shifts associated with attentional expectations (Chelazzi, et al., 1993; Hillyard, et al., 1998; Kastner, et al., 1999; Luck, et al., 1997). It is possible the brain uses common mechanisms across different cognitive systems to establish expectations with respect to stimuli of current importance.

The reward expectation signals of the ventral striatum are relayed to the OFC of the PFC (Tremblay & Schultz, 1999, 2000b). In addition to this striatal input, the OFC is highly interconnected with cortical sensory regions, receiving information with regards to all of the primary senses (gustation, olfaction, somatosensation, audition and vision) as well as visceral sensory information (Kringelbach, 2005). As such, the OFC is well placed to integrate multimodal sensory information with reward expectation, to allow for the dynamic tracking of subjective reward value of current behavioural options (Kringelbach, 2005; Schultz, 2000).

Neurons of the OFC elicit motivationally-specific sustained firing increases that resemble the reward expectation signals of the ventral striatum. As with the striatal signals, these are observed specifically for reward-predicting stimuli, irrespective of visual stimulus features or motor requirements and exhibiting a tight temporal linkage with reward delivery (Tremblay & Schultz, 1999, 2000a, 2000b). Furthermore, these expectation signals are influenced by the learning process. When new sets of stimuli are introduced, with animals required to learn the correct stimulus-response-outcome associations, reward expectation signals adapt to the new associations learned for the stimuli, mirrored by changes in behaviour. Initially reward is expected on each trial, but as learning progresses, increased selectivity in response is observed, with expectation activity only for those trials on which it is learned to be expected

(Tremblay & Schultz, 2000a). Changes in neural reward expectation signals with learning are similar to those learning-related changes observed in behaviour, thus may be a neural correlate of the learning process.

Stimulus information signalling current outcome likelihood is of particular importance to the activity of the OFC. This region is observed to be active when participants must monitor an externally-guided action to determine the outcome. This is not the case when switches necessitate individuals to choose which action to select and monitor the outcome (Walton, Croxson, Behrens, Kennerley, & Rushworth, 2007). It is thus monitoring of outcomes associated with stimuli rather than actions that are important in OFC function. This is consistent with the observation that damage to the OFC leads to an inability to learn new stimulus-outcome associations during reversal learning (Dias, Robbins, & Roberts, 1996). The OFC thus appears to construct stimulus-outcome representations which can be used to guide choice behaviour to the most relevant action in the current environment, an important aspect of adaptive behaviour.

In addition to OFC activity reflecting expectation of a reward, activity in this brain region appears responsible for dynamic tracking of relative value of the expected reward under changing reinforcement conditions. Neuronal firing in response to a predictive stimulus reflects the relative value of that stimulus with respect to other options within the current reinforcement environment, with firing to the same stimulus dependent on the other alternatives (Kringelbach, 2005; Tremblay & Schultz, 1999). Furthermore, BOLD activity in OFC diminishes when the same food reward becomes less desirable, such as when fed to satiety with that item. No comparable decreases in activation are observed for unrelated odours or

different food items. (Kringelbach, O'Doherty, Rolls, & Andrews, 2003; O'Doherty, et al., 2000). The OFC thus appears responsible for the updating of relative reward value, in order to construct dynamic stimulus-outcome representations that reflect the current reinforcement environment. Optimisation of behaviour depends upon the ability to compare reward options and evaluate the most desirable option at a given time. The increase in risky decisions with OFC lesions illustrates the important evaluative role played by this brain region (Bechara, Damasio, Damasio, & Anderson; Bechara, Damasio, Tranel, & Anderson, 1998).

These reward expectation signals are heavily dependent upon incoming stimulus information. Outcomes are evaluated on the basis of predictive stimuli, and representations associating these stimuli with reward outcomes constructed and updated (Hollerman & Schultz, 1998; Hollerman, et al., 1998; Kringelbach, 2005; Schultz, 2000; Tremblay, Hollerman, & Schultz, 1998; Tremblay & Schultz, 2000b). It is therefore possible that the ventral striatal-OFC system may be able to influence sensory processing regions, biasing stimulus processing by means of reward expectation systems.

1.2.2 Violations of expectation

These sustained reward expectation signals do not appear to be the only mechanism by which reward information influences decision making processes and choice behaviour. As with the attention system, it appears multiple mechanisms are utilised to signal an impending reward. Phasic changes in firing rate with respect to reward likelihood are also observed. Dopamine neurons of the midbrain, principally the substantia nigra pars compacta and ventral tegmental area appear to signal a reward prediction error through such phasic changes in firing rates.

Reward prediction error refers to the difference between expected and obtained reward (Montague & Berns, 2002; Schultz, Dayan, & Montague, 1997). An unconditioned stimulus followed by reward delivery elicits a burst of increased firing. Such reward delivery is unexpected, thus results in a positive prediction error (Bayer & Glimcher, 2005; Fiorillo, et al., 2003; Hollerman & Schultz, 1998; Leon & Shadlen, 1999; Ljungberg, Apicella, & Schultz, 1992; Montague, Hyman, & Cohen, 2004; Robbins & Everitt, 1996; Romo & Schultz, 1990; Schultz, 1986, 2000; Schultz, et al., 1997; Schultz & Romo, 1990; Schultz, Tremblay, & Hollerman, 1998). As stimulus-outcome associations are learned, changes in firing are observed which mirror the changes in expectation. A stimulus that fully predicts a reward, a reward prediction error of zero, no longer elicits a change in firing at the time of reward delivery. There is instead a shift to firing at the time of the earliest stimulus predictive of reward, the conditioned stimulus. The magnitude of this activity is scaled to the probability signalled by this stimulus, with greater rates of firing observed for stimuli predicting lower probability of reward, when prediction errors are higher (Fiorillo, et al., 2003). The speed of this shift in neural activity is mirrored by behavioural learning. Firing rates in response to reward delivery (and a shift to firing at the time of the conditioned stimulus) decrease faster for more rapidly learned stimulus-reward associations (Hollerman & Schultz, 1998). This implicates the prediction error signal as a neural correlate of the learning process.

Comparable with the sustained expectation signals, phasic firing is contingent upon motivational relevance of the conditioned stimulus. No firing is observed for presentation of these stimuli outside of the reward task context. Furthermore activity is modality non-specific and observed under differing motor-response requirements (Romo & Schultz, 1990; Schultz, 1986; Schultz & Romo, 1990).

As with sustained expectation signals, phasic activity appears tightly linked to the temporal aspects of reward delivery. Omission of an expected reward, a negative prediction error, results in suppression of firing at the time of expected reward. Shifting delivery time also alters firing activity. Predicted rewards delivered earlier than expected produce a burst of firing, commensurate with a positive prediction error. Those presented later than anticipated result in suppressed firing at the expected time of delivery (negative prediction error), followed by phasic firing increase at the later time of actual delivery (positive prediction error) (Hollerman & Schultz, 1998; Montague, et al., 2004). The observed activity of midbrain dopamine neurons closely matches that predicted by a temporal difference model of the reward prediction error (Montague, et al., 2004; Schultz, 2000; Schultz, et al., 1997). These models suggest the predicted value of an expected reward is approximated at a given point in time by integrating information about previously received rewards. Past rewards are weighted such that more recent rewards are valued more highly than those received further in the past (Montague, et al., 2004; Schultz, 2000; Schultz, et al., 1997). The integration of this timing and history information with the quantitative probability of reward provides a highly sensitive means of tracking actual reward outcome with respect to expectations. This allows for continuous updating of expectations with respect to current reward context.

The prediction error signals of the midbrain dopamine neurons allow updating as to the appropriateness of a given response in terms of the current reward contingencies with respect to the discrepancy between expected and actual outcome. The sustained signals of the striatum and OFC, in contrast, allow for the control of behaviour based on expectations with respect to upcoming outcomes. The combination of these two dissociable signals provides an

exquisite flexibility to allow the optimisation of behaviour in response to events in a dynamically changing environmental context (O'Doherty, 2004; Rushworth & Behrens, 2008).

These teaching signals of midbrain dopamine neurons are subsequently relayed to the ACC in the PFC (Montague, et al., 2004). Innervation with the limbic system also ensures the ACC is in receipt of information pertaining to current behavioural goals. The ACC is connected with the primary motor cortex and spinal cord, providing the means to directly influence motor behaviour. It is in this region, therefore, that reward prediction signals are integrated with action plans, reinforcement history and behavioural goals to guide choice to the most profitable action alternative in the current environmental context (Walton, et al., 2007). The convergence of these reward teaching signals of the dopaminergic midbrain and top-down attentional goals and expectations ensures the ACC is optimally placed for interaction and integration between the reward and attention systems.

Consistent with a role in monitoring reward probability and predictability, neurons of the ACC produce activity reminiscent of the reward prediction error signals of the midbrain. ACC neurons fire in response to behavioural errors resulting in the absence of anticipated reward. The error-related negativity, an ERP thought to derive from the ACC, is also observed when individuals make response errors (Debener, et al., 2005; Holroyd & Coles, 2002). As with midbrain dopamine neurons, the magnitude of this activity is scaled to the value of the expected reward. ACC neuronal activity in monkeys is of greater magnitude for larger volumes of expected juice reward (Amiez, Joseph, & Procyk, 2005). ACC activity is also able to track reward value of action alternatives accurately based on probabilistic allocation of reward to different response options. Magnitude of neuronal firing is scaled according to the average

value of reward, indicating which of a pair of stimuli is the optimal choice (Amiez, Joseph, & Procyk, 2006). In addition, when a sequence of three actions must be produced to earn reward, error-related ACC activity is greater for errors made further into the sequence (Amiez, et al., 2005). This may also be a function of reward expectation, as the expectation of correctly completing the sequence and earning reward increases with each successfully performed action. Furthermore, ACC activity is not observed in the absence of reward with successful performance of the first or second action in the sequence. This is also consistent with a reward prediction error account of this activity. Reward is not expected after the first or second action, thus the reward prediction error term is zero and no activity should be observed. The activity of ACC neurons is thus consistent with tracking the difference between expected and obtained reward (Amiez, et al., 2005).

Feedback-related responses in the ACC are also consistent with a close tracking of reward prediction error (Matsumoto, Matsumoto, Abe, & Tanaka, 2007). Initial positive feedback, associated with a large positive prediction error, elicits a large response from positive feedback-preferring ACC neurons. Each successive correct response is associated with a smaller positive prediction error and thus elicits increasingly small neuronal responses. Negative feedback-preferring neurons respond only to error trials, demonstrating specificity for negative prediction error (Matsumoto, et al., 2007). Increases in BOLD activation are also observed when action-outcome associations are reversed and individuals must monitor the outcomes of internally-guided actions in order to learn the new associations (Walton, Devlin, & Rushworth, 2004). Correct and incorrect feedback are equally informative in such a situation, and as such the magnitude of BOLD activation is equivalent following both feedback types. Response conflict can be ruled out as an explanation, as switch costs do not differ from a condition in which individuals are instructed as to the response to make, but ACC activity

does. ACC neurons are thus able to signal reward prediction error by the magnitude of the response of separable populations of cells within this brain region. These signals demonstrate an outcome-monitoring process, where deviations from expectation are indicated by changes in phasic firing rates (Matsumoto, et al., 2007; Walton, et al., 2004).

Rather than simply monitoring the outcome of the current action, the ACC appears to update expectations with respect to recent reinforcement history. Deactivation of the ACC by lesion or muscimol injection impairs choice behaviour in monkeys in a manner that highlights the importance of the ACC in integrating reinforcement history (Amiez, et al., 2006; Hadland, Rushworth, Gaffan, & Passingham, 2003). In a simple choice task, control animals are able to optimise behaviour by selecting the largest reward based on reinforcement history. ACC deactivation, however, leads to a tendency to repeat the choice of the stimulus chosen on the previous trial, even if such choice results in obtainment of the smaller reward. This deficit is not observed for stimulus pairs in which the optimal stimulus has been learned prior to ACC deactivation (Amiez, et al., 2006; Hadland, et al., 2003). A similar inability to use reinforcement history to guide behaviour is reported in a response-switching task, though the nature of the deficit somewhat differs. Only one response is rewarded at a given time, with sustained choice of the rewarded response required until reward assignment is reversed. ACC lesions lead to an inability of animals to sustain the rewarded choice (Kennerley, Walton, Behrens, Buckley, & Rushworth, 2006). Multiple regression analysis demonstrates this is due to decreased impact of previous reinforcement history upon current action choice. Whilst control animals use the information from the previous four or five trials, only the most recent outcome is used by ACC lesioned animals. There is no impairment on the trial following an error, which accounts for a similar response of lesioned and control animals at the time of a switch (Kennerley, et al., 2006). In dynamic foraging tasks, rewards are probabilistically allocated to two response

options, such that once allocated they remain available until collected. Optimal performance thus depends on dynamically tracking the potential value of each option in the context of reinforcement history and switching responses when the alternative action value exceeds that of the currently-chosen option. Whilst control animals are able to optimise reward, ACC lesions result in significantly more trials required to reach optimal behaviour (Kennerley, et al., 2006). As with the study of Amiez and colleagues (2006), if reward is allocated deterministically no deficit is observed. Furthermore, ACC lesioned animals are still able to maximise reward in choice between differing values of reward or the option requiring the least amount of work (Kennerley, et al., 2006). ACC lesions thus do not impair the ability to track reward value as such, but the ability to integrate reward value and reinforcement history to update action-outcome associations that guide choice behaviour to optimise performance.

The midbrain dopamine prediction error signals thus appear to be integrated with motor plans in the ACC. The outcome of an action is compared to expectations and integrated into recent reinforcement history. To date, most research of this nature has focused on the influence of reward allocation and expectation with respect to motor behaviour. The experiments of this thesis aim to extend the literature by examining the effects upon perceptual processing, as well as the way in which expectation of a reward and violations of these expectations relate to the expectations associated with top-down attentional control signals.

1.2 Toward an integrated examination of reward and attention

More recently, studies have begun to investigate the effects of reward and attention in connection with one another. This section will examine the research focusing on reward expectation and spatial attention in single-unit animal research and behavioural and neuroimaging studies with human participants.

1.3.1. Single-unit and lesion studies

Single-unit and lesion studies with animals have uncovered brain regions in which activity appears to be modulated by both reward and attention signals. LIP is one such region in which stimulus salience and attentional signals as well as reward expectation have been demonstrated independently to modulate neuronal activity (Bisley & Goldberg, 2003; Colby, et al., 1996; Gottlieb & Goldberg, 1999; Gottlieb, et al., 1998; Platt & Glimcher, 1999). The convergence of the reward and attention systems in LIP has recently been directly investigated (Bendiksby & Platt, 2006). A peripherally-cued saccade task was used. Two cues at separate spatial locations were successively illuminated at the start of each trial and monkeys were required to produce a saccade to a third target location upon detecting stimulus dimming ('flicker') in one of the cues. A greater likelihood of flicker of the first (probability 0.8) compared with the second (probability 0.2) cue was used to bias attention towards the location of the first cue. Production of a saccade to the target stimulus upon cue flicker could result in a large or small reward, which was manipulated in blockwise fashion. Expectation of a larger magnitude reward evoked greater firing rates in LIP neurons as well as increased accuracy and faster responses. Also observed was a positive correlation between LIP firing rates and reaction times (RTs), which was invariant to reward magnitude. This was argued to

be a modulation of firing by attention, with longer RTs when reorienting of attention was required, independent from the effects of reward (Bendiksby & Platt, 2006). This manipulation may have been problematic, however. Monkeys may have endogenously allocated attention to the cue more likely to flicker, but alternatively attention may have been exogenously captured by the abrupt onset of the second cue, or divided across the two cues. Indeed the authors note there was only a weak bias towards the first illuminated cue, and there was no effect of which cue flickered upon detection accuracy (Bendiksby & Platt, 2006). Therefore though the authors argue the results demonstrate an independence of reward and attention, there may simply have been no or minimal attentional manipulation, at least not in the form of a systematic bias in the allocation of spatial attention. It is possible that the results obtained in this study may not be an accurate depiction of the relationship between reward and attention systems.

In contrast to this proposed independence, results of another study suggest that reward expectation can selectively bias the allocation of attention toward the location of a reward-associated stimulus (Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009). When target stimuli followed peripheral cues associated with reward (RC+) or no reward (RC-) at the same or opposite location, presaccadic LIP firing rates were higher and saccades faster and more accurate for RC+ than RC- cues. Congruent cue-target location resulted in excitatory firing and greater saccade accuracy for RC+ cues but inhibitory firing and impaired accuracy for RC- cues. Furthermore, presentation of an RC+ within the cell's RF induced sustained excitation of firing during the cue-target delay period, whilst RC- cues resulted in a sustained inhibition, suggestive of an inhibition of return mechanism (Tipper, Driver, & Weaver, 1991). The results indicate cue-reward association instigated biased allocation of attention towards RC+ and away from RC- cues despite the fact that cues signalled reward expectation but not likely

target location. Maintaining attention at or away from the cued location was therefore not optimal for behaviour. Reward expectation information appears to capture attention despite potential disruption to behaviour (Peck, et al., 2009).

Moreover, overtraining with stimulus-reward associations led to a visual plasticity effect (Peck, et al., 2009). New cue-target trials were conducted, but with the addition of the presentation of a former RC stimulus opposite to the target saccade location during the cue-target interval. These probe stimuli were task irrelevant, with no indication of reward expectation. The new RC stimuli determined presence or absence of anticipatory licking behaviour, indicating the monkeys did learn the new stimulus-reward associations. Probe presentation did, however, induce a valence-specific disruption to performance. Saccades to the target location were slower in the presence of RC+ compared with RC- probes. No such disruption was observed with novel stimuli acting as probes. This suggests task-irrelevant stimuli that were formerly, but no longer, associated with reward could capture attention via bottom-up salience, perhaps similar to the automatic capture of attention by fearful stimuli ('threat capture') (Peck, et al., 2009).

1.3.2. Human studies of behavioural and neural activity

Studies with human participants have recently demonstrated the ability of reward expectation to influence behaviour on tasks manipulating attentional state. Expectation of a reward, or a reward of higher value, can improve detection sensitivity, speed RTs, increase effectiveness of distractor inhibition or overcome attentional bottlenecks, with the precise effects upon behaviour dependent upon the task parameters (Della Libera & Chelazzi, 2006; Engelmann,

Damaraju, Padmala, & Pessoa, 2009; Engelmann & Pessoa, 2007; Mohanty, Gitelman, Small, & Mesulam, 2008; Raymond & O'Brien, 2009; Small, et al., 2005). In many cases, an interaction between reward and attention has been reported, leading to the hypothesis that reward expectation enhances behavioural performance by acting through the attention system (Della Libera & Chelazzi, 2006; Engelmann, et al., 2009; Engelmann & Pessoa, 2007). In the experiments of Della Libera and Chelazzi (2006) participants were presented with a prime stimulus, containing an ignored (such as shape) and an attended dimension (such as colour), followed by a probe stimulus. They were required to judge whether the probe matched the prime on one of the stimulus dimensions. Negative priming (slower RTs and lower accuracy when the probe judgement dimension matched the ignored dimension of the prime) was observed following high reward. Residual suppression of the irrelevant dimension from the time of prime presentation influenced performance with respect to probe judgement. This effect was reversed following low reward, such that a positive priming-like effect was observed. This suggested distractor inhibition was lifted more rapidly when behavioural performance was poorly rewarded (Della Libera & Chelazzi, 2006). Engelmann and colleagues (2009) presented a valid or invalid spatial cue as to the likely location of a target stimulus, followed by bilateral presentation of degraded visual stimuli. Human participants were required to discriminate which of the two stimuli contained a degraded face image. Incentive value differed across blocks, with neutral ($0) blocks, the possibility to win $1 or $4 or avoid losing $2.50. There was an interaction between reward and attention upon RT, with a significant slowing in the $1 condition when cues were invalid and a significant speeding of responses with the larger incentive values ($2.5 and $4). It is possible reward information in tasks of this nature has a greater effect in the absence of attention, thus modulating RTs only on invalidly-cued trials. It must be noted, however, that behavioural measures lack the ability to chart the activity of the two systems at different stages of processing, but are rather a

measure at the endpoint of processing. As such, behavioural measures are unable to elucidate whether, at earlier stages of processing, the two systems act independently.

In addition to effects on behaviour, reward expectation is able to modulate BOLD activation. Manipulating a primary reinforcer (food) or monetary incentive has shown that motivation positively correlates with BOLD activation in brain regions such as the ACC, posterior cingulate cortex, OFC, parahippocampal cortex and amygdala (Engelmann, et al., 2009; LaBar, et al., 2001; Mohanty, et al., 2008; Small, et al., 2005). Several brain regions show differential activation in response to both reward and attention manipulations. Cingulate cortex shows activation in response to orienting of attention that is influenced by the motivational value of stimuli to which attention is being allocated (Engelmann, et al., 2009; Mohanty, et al., 2008; Small, et al., 2005). Small and colleagues (2005) used a spatial cueing paradigm in which monetary rewards or losses (relative to a no-incentive condition) could result. The posterior cingulate was activated during visual spatial orienting, as evident in the greater BOLD activation for valid compared with neutral spatial cues. This attention-related activation was greater for win or loss trials compared with no-incentive trials (Small, et al., 2005). Mohanty and colleagues (2008) cued participants to the location of food or tool items during hunger or satiation and observed comparative effects in the posterior cingulate. The posterior cingulate showed greater BOLD activation in expectation of food items when hungry than full and compared with expectation of tools. Furthermore, BOLD activity level correlated more highly with the benefit from the spatial cue (faster RT for valid compared with neutral cues) when cued to food items in the hungry versus satiated condition. In addition, cingulate activation in response to spatial cues increased linearly as a function of absolute incentive value in the study of Engelmann and colleagues (2009). These results suggest the cingulate cortex is a region in which reward and attention information may be integrated.

Regions of parietal cortex are also activated by both reward and attention (Engelmann, et al., 2009; Mohanty, et al., 2008; Small, et al., 2005). Small et al. (2005) observed increased activation in inferior parietal cortex during attentional reorienting, with greater activation on invalid than neutral trials. BOLD activity was also greater in this region for win or lose trials relative to no-incentive trials. A similar pattern was observed by Mohanty et al. (2008) in the IPS and posterior parietal sulcus. A stronger correlation between BOLD activity and cue benefit was observed in expectation of food items when hungry than satiated or in expectation of tools. Cue-related activity was also was linearly scaled to incentive value in a similar manner to that observed in cingulate regions (Engelmann, et al., 2009). The results of these studies suggest that regions of the attention network, such as parietal and cingulate cortices, may also be influenced by reward information. As such, the potential exists for integration of reward and attentional signals in these regions.

The way in which the reward and attention systems relate to one another is also of particular interest to the studies of this thesis. There are two main possible routes through which reward prediction could influence perception. The reward system could modulate visual activity indirectly, by acting through the attention system. Several brain regions appear to encode both reward and attention factors. It is therefore possible that in regions such as cingulate and parietal cortices (though note the hypothesised independence speculated by Bendiksby and Platt, 2006), reward and attention signals are integrated (Bendiksby & Platt, 2006; Engelmann, et al., 2009; Mohanty, et al., 2008; Peck, et al., 2009; Small, et al., 2005). A top-down signal including biases from both systems would then act upon visual cortex to modulate perceptual processing. Alternatively, the direct connections existing between the reward network and sensory areas, such as those between the amygdala and extrastriate cortex, may enable direct

perceptual modulation by reward, independent of the attention system (McDonald, 1998). Prefrontal regions such as the OFC or cingulate cortices may be the origin of signals that act upon this pathway (Kringelbach & Rolls, 2004; Mohanty, et al., 2008; Small, et al., 2005). Some combination of the two is also plausible, with interaction between reward and attention systems at some stages of processing and independence at others. The modulation of BOLD activation in visual cortex by reward suggests such modulation may be possible (Engelmann, et al., 2009; Mohanty, et al., 2008; Small, et al., 2005). The temporal resolution of fMRI, however, is insufficient for determining whether such modulatory effects occur early during active stages of perceptual analysis or later via re-enterant feedback. The studies of this thesis employ the ERP method, which has the fine temporal resolution necessary to examine the time point(s) at which reward expectation influences processing.

The experiments of this thesis aim to examine the effects of reward expectation across the time course of human information processing. This will allow examination of the way in which reward influences successive stages of processing. The use of ERP methodology, which will be discussed in the following chapter, will provide the rich temporal information to allow such an investigation. The relationship between reward expectation and spatial attention will also be examined.

Chapter 2: General Methods

The experiments in this thesis combine the use of behavioural methods with non-invasive recordings of neural activity in human participants. This chapter reviews the physiological basis of the EEG and its derived ERP measures, as well as the procedures for processing and analysing EEG and ERP data.

2.1 ERP methodology: Introduction

The EEG methodology provides a means of measuring neural activity, in the form of voltage changes over time, from the scalp of normal, awake humans. Waveforms representing the neural processes triggered by various sensory, cognitive or motor events can be derived from this signal, known ERPs (Coles & Rugg, 1995; Eimer, 1998; Luck, 2005; Luck, et al., 2000). By comparing the ERP waveforms produced under differing experimental conditions, one is able to study the influence of changing experimental factors on cognitive processing in real time.

2.2 Physiological basis of the EEG signal

Two types of electrical signals arise from neurons. The first of these is the rapid action potential, the in- and out-flow of current that travels down the axon. These take the form of rapid, discrete spikes. The other is the postsynaptic potential. The flow of ions induced by binding of neurotransmitters to the postsynaptic neuron causes a change in electrical potential across the membrane. Postsynaptic potentials are orders of magnitude slower than action potentials, lasting between tens and hundreds of milliseconds. Both action potentials

and postsynaptic potentials can be recorded extracellularly. These electrical signals can furthermore propagate through the conductive medium of the brain according to the laws of physics, decaying over distance (Coles & Rugg, 1995; Luck, 2005).

If and when a large number of neurons within a population (on the order of hundreds of thousands or millions) are activated synchronously, the potential generated becomes sufficiently strong to be detectable at the scalp. Because of their slower time course, postsynaptic potentials summate over the population of co-activated neurons, contributing significantly to the signal measured in the EEG. Action potentials, on the other hand, tend to cancel out due to their transient and moving nature and imperfect alignment across the population of neuronal axons and thus contribute little to the EEG signal (Allison, Wood, & McCarthy, 1986; Coles & Rugg, 1995; Luck, 2005).

Neurotransmitters released by presynaptic neurons act primarily upon the apical dendrites of the postsynaptic cell. If a sufficient level of stimulation depolarises the postsynaptic neuron to the firing threshold, an inflow of current results. This induces net negative charge in the surrounding extracellular space, provoking an outflow of current primarily in the basal dendrites and cell body, with resultant positive charge. This separation of positive and negative charges creates a dipole. Though individual dipoles are small, the summation of dipoles from aligned populations of cells provides a strong enough signal to be read at the scalp (see Figure 2.1). Cortical pyramidal cells tend to be aligned in parallel with one another perpendicularly to the scalp, in what is known as an ‘open-field’ configuration (Lorente De No, 1947; Luck, 2005; Luck, et al., 2000). Due to their optimal alignment and their proximity to the

scalp, these pyramidal cells provide the basis of the EEG signal (Allison, et al., 1986; Coles & Rugg, 1995; Eimer, 1998; Luck, 2005; Luck, et al., 2000).

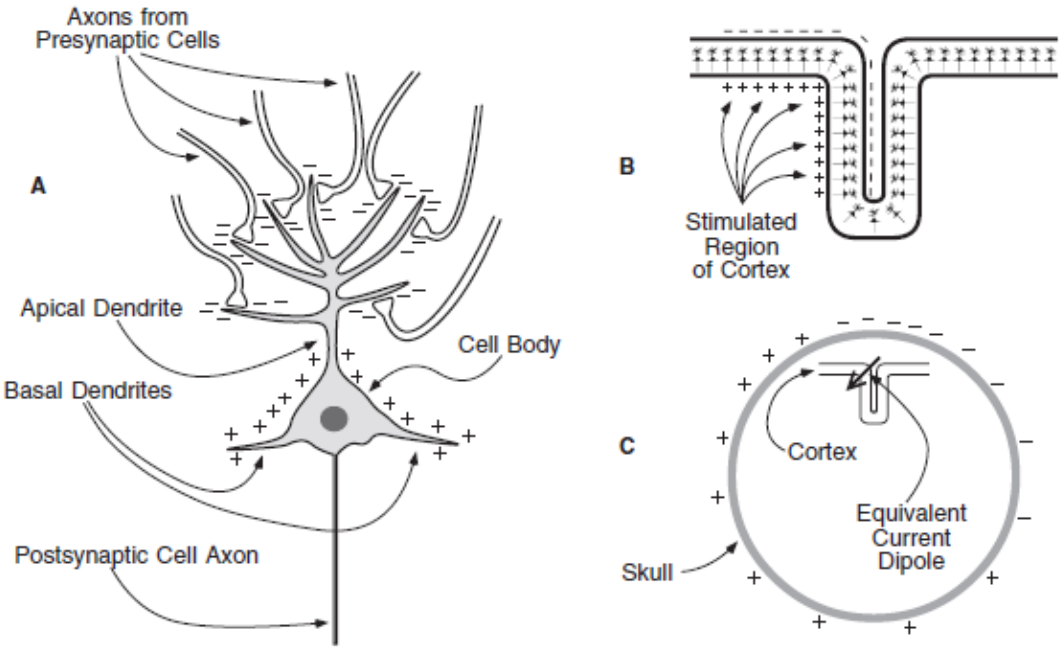

Figure 2.1: A schematic of the conditions necessary for generation of the EEG signal. (A.) Representation of a cortical pyramidal cell during a postsynaptic potential. The presynaptic neuron releases an excitatory neurotransmitter, which binds to the apical dendrites of the postsynaptic neuron. Positive ions flow into the cell, causing a net negative charge in the extracellular space. A commensurate positive charge occurs at the basal dendrites and cell body. This separation of negative and positive charge in space is a dipole. (B.) When a section of cortex is stimulated, the dipoles produced by closely aligned cells summate. (C.) An equivalent current dipole is the approximation of the summated dipoles of a region of cortex, as illustrated in B. This distribution of positive and negative charge produced by an aligned population of neurons has sufficient strength to be detected at the scalp. Figure adapted from Luck (2005).

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2.3 Recording ERPs

Voltage is measured as a difference in charge between two sites. In measuring the voltage at a given scalp site of interest, the charge at this active electrode must be compared to a second, reference electrode. To record neural activity at the scalp, and for this recording to be as free from noise and distortion as possible, a reference site must be relatively free from neural activity ('neutral') and electrical noise ('silent'). The choice of reference can critically alter the shape of waveforms, such that potentials may be visible only with certain reference choices. The variance around a given potential also changes. As such, the shape and consequently amplitude and latency information pertaining to an observed potential applies only to the given choice of reference. Reference choice thus introduces a source of experimenter bias (Murray, Brunet, & Michel, 2008). Though there is no ideal reference, options include the nose, earlobes and mastoid bones (Coles & Rugg, 1995). The average voltage across the active recording electrodes can also be used (Desmedt & Tomberg, 1990; Murray, et al., 2008). This 'average reference' is particularly sensitive to distortion, however. It does not fulfil the requirement of neutrality and is particularly prone to contamination by artefacts occurring in the recorded activity at the active electrodes contributing to this measure (Murray, et al., 2008). The mastoid bones, used for the experiments of this thesis, are a good solution. This region is relatively free from muscle activity artefacts. Converting the reference to "linked mastoids" offline, the average of the two mastoid bones, gives a reference site from which left and right hemisphere electrodes are equidistant (Coles & Rugg, 1995).

Electrodes are typically placed according to the 10-20 system. Electrode location is classified in terms of its region (frontal, central, parietal, temporal and occipital) and laterality (odd number signifying a location over the left hemisphere, z for midline, and even number for

right). Oz, for example, is the occipital midline electrode location, whereas F4 is a right-side frontal electrode (Coles & Rugg, 1995; Society, 1994). This system of electrode placement can be extended to create a high-density array of up to 345 electrodes in the 10-5 system (Oostenveld & Praamstra, 2001). The experiments in this thesis use two electrode montages for ERP recording. The experiments in chapters 4 and 6 use an array of 40 electrodes arranged on the scalp according to the 10-20 system, as shown in Figure 2.2. The Neuroscan NuAmps amplifiers and software were used for these EEG recordings (Neurobehavioural Systems, CA). The experiment in Chapter 5 uses a high-density array of 128 electrodes arranged on the scalp according to the 10-5 placement system as shown in Figure 2.3. The Biosemi Active-Two amplifier (www.biosemi.com) and software were used for these recordings.

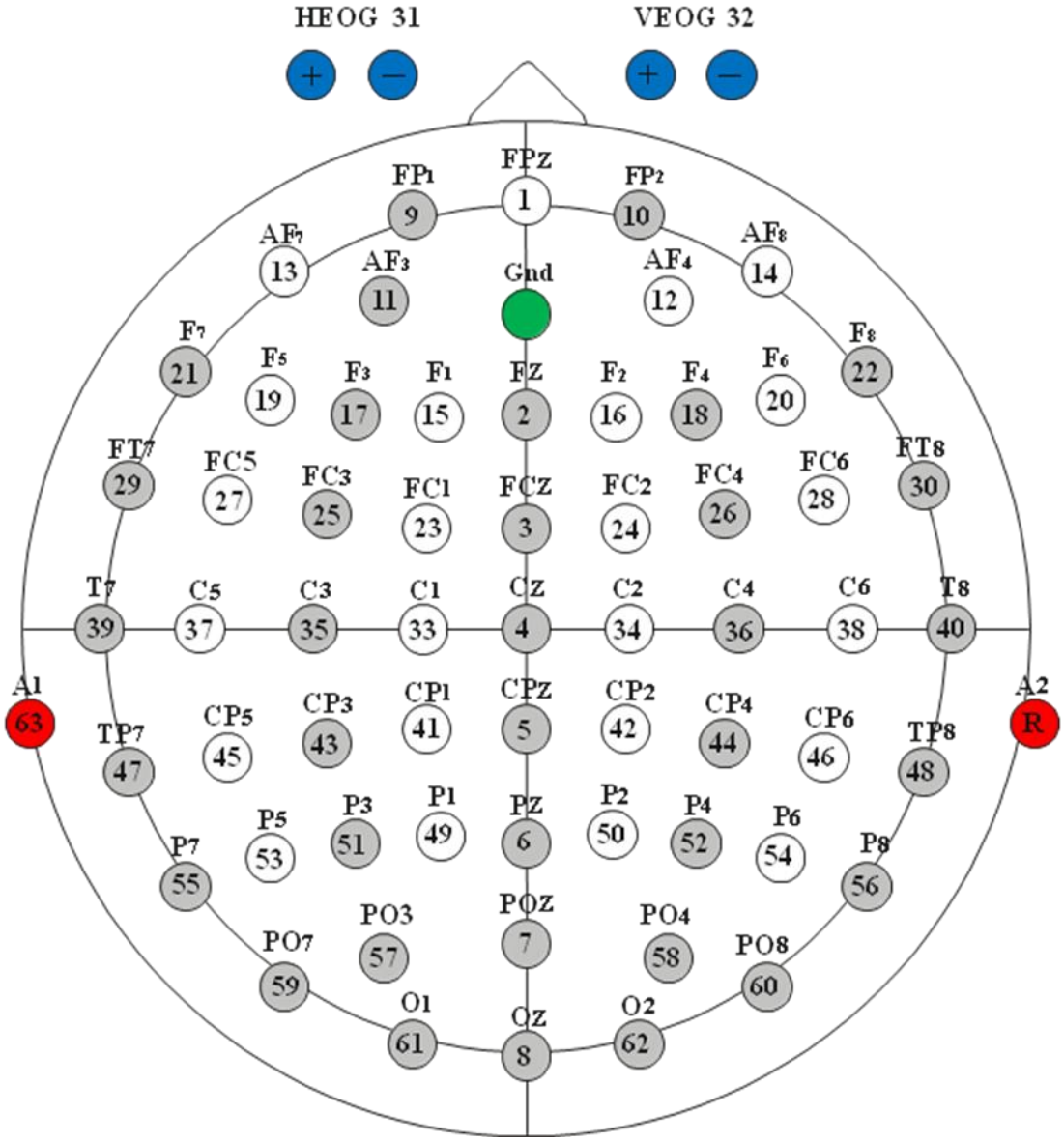

Figure 2.2: The 10-20 system for electrode placement. Gray circles show the electrode locations that were used for recording in Chapters 4 and 6. POz was used in Chapter 6 only. The mastoid sites, used as reference, are coloured red. The blue electrodes are those used to derive the HEOG and VEOG bipolarly. The green electrode is the ground site.

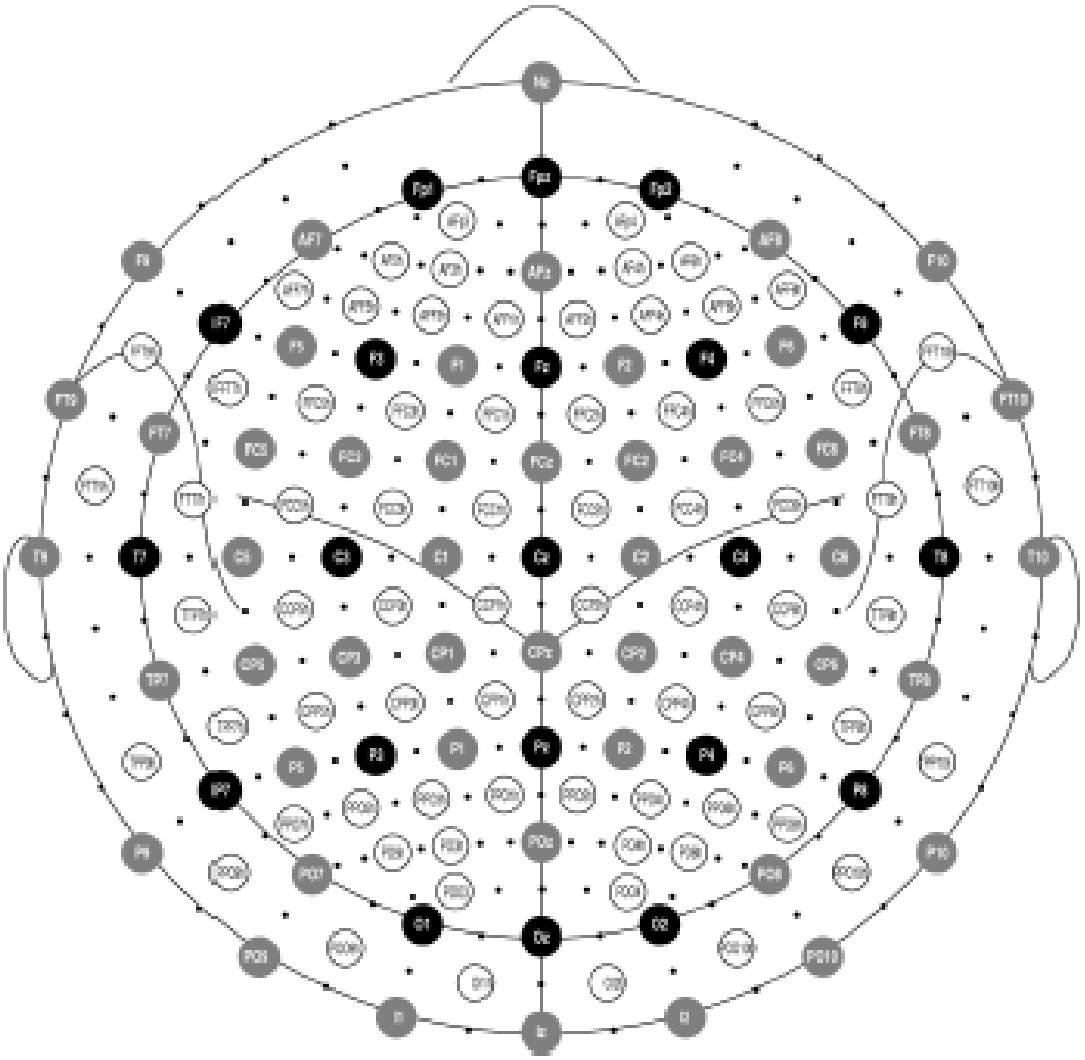

Figure 2.3: The 10-5 system of electrode placement used by the Biosemi system. This electrode array was used for the experiment in Chapter 5. Black and gray electrodes are those of the standard 10-20 system, with the additional electrodes of the 10-5 system shown in white. Figure from Oostenveld and Praamstra (2001).

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Once recorded, the ERP potentials of interest must be extracted from the noise of the multi-frequency EEG trace. “Epoching”, the time-locking of data around the stimulus event of interest, is the procedure by which this is achieved (see Figure 2.4) (Coles & Rugg, 1995; Eimer, 1998; Luck, 2005; Luck, et al., 2000). Artefacts arising in the signal can be removed at this stage. The electrooculogram (EOG) recording of eye-related activity can be used to remove artefacts related to blinks and eye movements. The eye acts as a dipole, thus movements and blinks produce large voltage deflections (+/- 70μV) that interfere with potentials of interest. Eye movements and blinks are particularly troublesome as they occur at the same frequency as the activity of interest (Coles & Rugg, 1995). Trials containing drift exceeding a predefined limit (such as +/- 50μV) can also be removed. Filtering may be utilised to remove excessively high or low frequency noise that is not relevant to the neural activity of interest, such as the noise from mains electricity. Excessive filtering of frequencies carrying relevant neural activity can distort the shape of the waveform, however, so filtering must be applied with caution (Coles & Rugg, 1995; Luck, 2005).

Once artefact-free epochs have been extracted from the raw EEG signal, the epochs relating to each experimental condition are averaged together to generate an ERP waveform. This is necessary due to the small size of the potentials of interest relative to the background signal. The noise, which is not time-locked to the event of interest, will tend to average toward zero and thus be removed during the averaging procedure, leaving mainly activity time-locked to the event of interest (Coles & Rugg, 1995; Luck, 2005; Luck, et al., 2000). It must be noted, however, that averaging may alter a waveform’s appearance. Differences in the time point at which peaks occur in individual subjects leads to averaged waveforms that are smaller in amplitude than those of individual subjects. Latency differences, furthermore, are often lost or altered (Coles & Rugg, 1995; Luck, 2005).

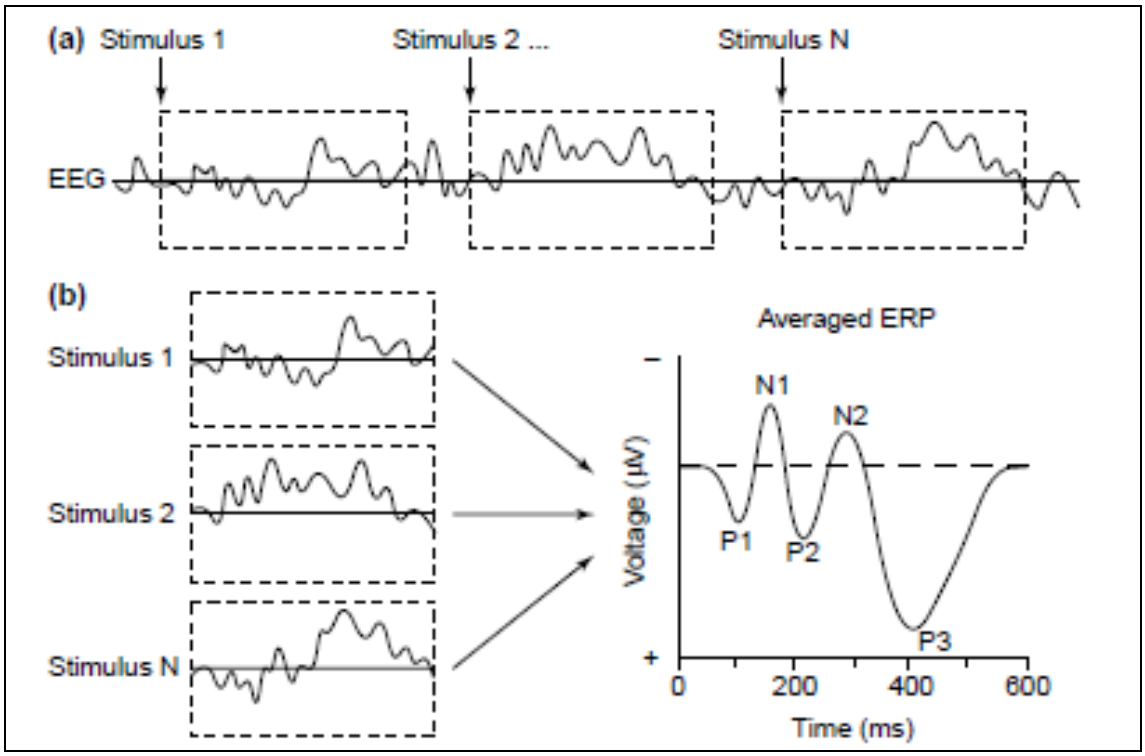

Figure 2.4: A representation of the procedure of epoching and signal averaging used to derive the ERP. (A) Epochs time-locked to the event of interest are extracted from the continuous EEG recording. (B) The epochs from all trials pertaining to a given experimental condition are averaged together to produce the resultant average ERP waveform, shown on the right. Figure from Luck et al. (2000).

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2.4 Interpreting ERPs

The effects of different experimental variables upon information processing can be examined by comparing the amplitude and/or latency of specific potentials in the ERP waveforms. In addition to this analysis of potentials, topographical analysis can be performed with ERP data. The following sections will discuss the processing and analysis procedures employed in this thesis.

2.4.1 ERP potential analysis

The ERP waveform is composed of a series of characteristic peaks and troughs termed "potentials" (Coles & Rugg, 1995; Luck, 2005). Two main means of classifying potentials exist. The first is according to amplitude, latency, scalp topography and sensitivity to certain task factors (Coles & Rugg, 1995; Luck, 2005). Alternatively, ERP potentials can be viewed as processing markers. This second approach categorises potentials according to neural origin and the processes they reflect (Coles & Rugg, 1995; Eimer, 1998; Luck, 2005). In this thesis, potentials are characterised in terms of their latency and polarity, but the focus is upon the underlying processing their activity represents. ERP analysis provides the means to examine the effects of experimental manipulations at multiple time points along the information-processing time course (Coles & Rugg, 1995; Eimer, 1998; Luck, 2005).

In this thesis, experiments using visual stimuli were used to test whether reward expectation could influence perceptual, cognitive and motor stages of information processing and to compare and contrast the modulatory effects of reward expectation with those of spatial

attention. Accordingly, ERP potentials reflecting visual processing, target selection, and motor preparation were used as the primary dependent measures of interest.

2.4.1.1 Visual potentials

Subcortical activity evoked by stimuli in the early stages of the visual hierarchy is typically not evident in the visual ERP. This is owing to the fact that the neurons of the thalamus, to which the retina projects, are distant from the recording electrodes and not aligned to form the open field required for measurement of the EEG signal (Coles & Rugg, 1995). The C1 wave generated in primary visual cortex is thus the earliest observed visual potential (Coles & Rugg, 1995; Eimer, 1998; Luck, 2005; Luck, et al., 2000). Its polarity differs depending on the position of stimuli within the visual field due to the folding of the calcarine fissure, around which V1 is organised. C1 is typically positive for stimuli in the lower visual field and negative for stimuli in the upper visual field. This makes the C1 difficult to observe with stimuli placed on the horizontal meridian, such as those used in the ERP experiments of this thesis. For this reason, the earliest potential upon which effects of reward expectation are likely to be apparent in these experiments is the P1 potential. This has an onset of 60-90ms and peaks at 100-130ms post stimulus. There is a fair amount of spatial and temporal overlap between C1 and P1, thus the two may be difficult to disentangle (Clark, Fan, & Hillyard, 1994). Inverse dipole modelling using the Brain Electric Source Analysis algorithm to estimate the sources of activity from the scalp-recorded voltage, as well as combination of dipole modelling with structural and fMRI data and positron emission tomography (PET), implicate the P1 to originate from lateral or ventral extrastriate cortex including the fusiform gyrus (Clark, et al., 1994; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Heinze, et al., 1994). P1 is affected by sensory features, such as stimulus contrast, as well as top-down factors such as arousal (Di Russo, et al., 2002;

Hillyard & Anllo-Vento, 1998; Hillyard, et al., 1998; Luck, et al., 2000). P1 is also the first point at which attentional modulation is observed, with amplitude enhancement in response to attended stimulus features, objects or locations (Di Russo, et al., 2002; Eimer, 1998; Heinze, et al., 1994; Hillyard & Anllo-Vento, 1998; Hillyard, et al., 1998; Luck, et al., 2000).

The next component of import is the N1 potential, thought to be comprised of multiple subcomponents with distinct topographical distributions (Clark, et al., 1994; Coles & Rugg, 1995; Di Russo, et al., 2002). The earliest subcomponent is anterior in distribution and peaks 100-150ms post-stimulus (Clark, et al., 1994; Coles & Rugg, 1995). This may originate in a distributed set of frontal regions or a frontally-projecting region of parietal cortex (Clark, et al., 1994). Two later posterior subcomponents arise from parietal and lateral occipital cortex, peaking 150-200ms post stimulus (Clark, et al., 1994). Like P1, N1 is likely to reflect primarily perceptual elements of processing, possibly that of a discriminative nature (Eimer, 1998; Hopf, Vogel, Woodman, Heinze, & Luck, 2002). The N1 is greatly influenced by top-down spatial attention (Hillyard, et al., 1998; Mangun, 1995).

2.4.1.2 Cognitive potentials linked to target detection

The N2 potential, like N1, is comprised of several subcomponents, appearing from 200ms post-stimulus. A later subcomponent of N2 is strongly modulated by task relevance. Task relevant, but not irrelevant, stimuli elicit an N2 potential (Coles & Rugg, 1995; Eimer, 1998; Luck, 2005). In visual search tasks, target identification and selection has been linked to an enhanced negativity over posterior electrodes located contralateral to the target stimulus starting around 200ms. The potential obtained by subtracting waveforms over ipsilateral

electrodes from waveforms over contralateral electrodes is usually referred to as the N2pc (Eimer, 1996; Luck & Hillyard, 1994a, 1994b). Source localisation and combined EEG/TMS recordings have identified two potential sources of the N2pc, an early posterior parietal source and a later activation deriving from anterior occipital and posterior infero-temporal cortex (Fuggetta, Pavone, Walsh, Kiss, & Eimer, 2006; Hopf, et al., 2000).

The N2pc may reflect suppression of distractor items, necessitated by the potential interference these produce on selection and processing of the target stimulus. N2pc amplitude increases with greater numbers of distractor items, whilst it is absent for single-stimulus displays. The N2pc is similarly absent when target identification is unnecessary, as in discrimination of a feature of the global array (Luck & Hillyard, 1994a, 1994b). Alternatively, the N2pc may reflect target selection and processing. An N2pc is evident even with a two-stimulus display with target and distractor in opposite hemifields. Suppression is unnecessary under such minimal competition but target selection demands are greater, as the target can no longer pop out from an homogeneous display (Eimer, 1996). Furthermore, no difference in N2pc amplitude is observed with changing proximity of distractors from the target despite this changing target-distractor competition (Mazza, Turatto, & Caramazza, 2009a). Also, when distractors are necessary to identify the target, discouraging suppression, results are inconsistent. Some evidence suggests this does eliminate the N2pc (Luck & Hillyard, 1994b), whilst others show an N2pc invariant to the manipulation (Mazza, et al., 2009a; Mazza, Turatto, & Caramazza, 2009b). This may depend upon specific task demands; insufficient power or changes in task difficulty between conditions in the manipulation of Luck and Hillyard (1994b) may have led to the lack of an observable N2pc (Mazza, et al., 2009a, 2009b).

Alternatively, the N2pc may consist of a summation of neural activity related to two separate attentional processes (Hickey, et al., 2009). A target negativity with lateral ventral topography is observed contralateral to the target, likely an index of target processing. This is followed by a distractor positivity over medial and dorsal sites contralateral to a distractor stimulus. This may reflect suppressive mechanisms acting upon the representation of the distractor stimulus. This may also account for the observation of an N2pc even in the case of distractors being used in target identification (Mazza, et al., 2009b). Distractors may aid selection of the target then subsequently be suppressed. Such a supposition is consistent with single-unit recordings. Target-related enhancement of neuronal firing and the suppression of firing in relation to distractor stimuli are both apparent. Ventral regions such as V4 demonstrate a larger stimulus-evoked response to attended target stimuli (Luck, et al., 1997). This attention-related enhancement is larger when several stimuli are presented simultaneously, demonstrating the necessity of target-related firing to overcome the competition from distractor items (Luck, et al., 1997). Neurons in monkey LIP show decreased firing in relation to ignored distractor items, in addition to target-related firing increases (Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006). Neuronal responses elicited when saccades are made to distractor stimuli are significantly smaller than those observed when saccading to target stimuli during visual search, with this differentiation of response developing around 90ms post stimulus. Furthermore, an inability to suppress saccades to distractor items is associated with a lack of suppressed distractor-related firing. This suggests that when firing suppression does not occur, distractors are not suppressed and thus interfere with task performance (Ipata, et al., 2006). The use of balanced visual displays and derivation of the N2pc by the subtraction process may thus produce a waveform containing both distractor-related positivity and target-related negativity (Hickey, et al., 2009). It is noteworthy that the topographies of the subcomponents identified by Hickey

and colleagues (2009) are consistent with the sources localised by Hopf et al. (2000). The order of the two processes, however, is reversed.

N2pc amplitude is strongly modulated by top-down task set. An N2pc is observed to salient non-targets or task-irrelevant cues preceding target arrays when of the same feature dimension as the target. No N2pc is observed when they differ in feature dimension (Eimer & Kiss, 2008; Hickey, et al., 2006; Kiss, Jolicaeur, Dell'Acqua, & Eimer, 2008a). Furthermore, non-targets difficult to distinguish from the target (differing in only one feature) produce an N2pc, whilst easily distinguishable items (differing on all dimensions) do not (Luck & Hillyard, 1994b). Modulation by task set may be scalar, as the N2pc is smaller for task set-matched non-targets than targets (Luck & Hillyard, 1994b). Amplitude may depend upon the similarity between a stimulus and the target template (Kiss, et al., 2008a). This indicates task set modulates the degree of attentional capture by non-target items, and this is reflected in a modulation of N2pc amplitude. In addition, the N2pc is qualitatively similar, in terms of latency and topography, for search guided by perception or WM. This suggests the N2pc may reflect a spatially-specific selection of task relevant and/or suppression of irrelevant features or objects that is modulated by top-down attention in a manner invariant to the representation used to guide visual search (Kuo, Rao, Lepsien, & Nobre, 2009). Items appearing at non-attended locations that share task-relevant dimensions produce an N2pc indistinguishable from those appearing within the focus of spatial attention, however, suggesting the attentional processes reflected by the N2pc may be at least partially independent from spatial attention (Brignani, Lepsien, & Nobre, 2010; Kiss, Van Velzen, & Eimer, 2008b). The N2pc will be examined in Chapter 6 to determine whether reward association can influence the selection of task-relevant features or objects from within a cluttered array as well as whether associating irrelevant stimuli with reward can override selection of the task-relevant stimulus.

Another set of subcomponents related to target processing is the P300 complex. This refers to a slow positive potential over parieto-central scalp sites, emerging from 300ms, typically peaking between 300 and 500ms post stimulus (Coles & Rugg, 1995; Donchin & Coles, 1988a; Johnson, 1986; Luck, 2005; Nieuwenhuis, et al., 2005a). Multiple sources are likely to contribute to the P300, but intracranial recordings suggest the later subcomponent of relevance for the present thesis is generated in parieto-occipital cortex and medial temporal lobe, a set of regions implicated in visual processing and the orienting of attention (Halgren, et al., 1995; Kiss, Dashieff, & Lordeon, 1989; Nieuwenhuis, et al., 2005a; Smith, et al., 1990). Consistent with an attentional influence, task relevance is of vital importance to manifestation of the P300. Stimuli elicit a P300 only when attended. No P300 is observed if identical stimuli are actively ignored or processing resources are occupied by a secondary task. The more demanding the secondary task, the greater the P300 attenuation (Nieuwenhuis, et al., 2005a). Response-requiring target stimuli produce larger P300s than non-targets when frequency of occurrence is equated. This suggests the P300 reflects attention-dependant processing (Nieuwenhuis, et al., 2005a).

The P300 has been hypothesised to reflect the maintenance of environmental context (Donchin & Coles, 1988b; Nieuwenhuis, et al., 2005a). The relationship between P300 amplitude and maintenance activity is evident in the larger P300 for subsequently recalled items of a memorised list (Donchin & Coles, 1988b). Rather than a static maintenance of stimuli, however, stimulus representations must be continually updated with each new piece of information in order to accurately represent the context of a dynamically changing environment. Rare or novel stimuli produce a larger P300. Amplitude is inversely related to

stimulus probability, such that less likely stimuli evoke a larger P300 (Donchin & Coles, 1988b; Johnson, 1986; Nieuwenhuis, et al., 2005a). Probability is important in that information regarding less frequently presented items is gathered more slowly than for frequent items. Each presentation thus provides a greater opportunity for learning the context of presentation and outcome information than presentation of frequent items. Furthermore, there is a greater likelihood of environmental change between successive presentation of infrequent than frequent items, requiring further updating of representations. This may explain the observation of greater P300 amplitude for an infrequent target presented in a stream of frequent non-targets than two successive frequent targets (Donchin & Coles, 1988a). This importance of recent presentation history has parallels with the integration of current outcome and recent reinforcement history by the ACC described in Chapter 1. This suggests the brain may employ similar mechanisms for different cognitive subsystems and processes.

Expectation also plays an important role in P300 modulation. Using confidence ratings as an index of participants' expectation of outcome, P300 amplitude is larger on trials with greater discrepancy between expected and actual outcome (Donchin & Coles, 1988b). Violations of expectation also necessitate contextual updating. It is possible that violations of reward and spatial expectancies, as manipulated in this thesis, will influence P300 amplitude. As such, the effects of the experimental factors on this potential will be of great interest.

The information processing indexed by the P300 is related more closely to stimulus and attention-related factors, as changing motor demands or requirements do not always alter P300 amplitude, though this may be heavily dependent upon task demands (Donchin & Coles, 1988a; Johnson, 1986; Nieuwenhuis, et al., 2005a). Contextual updating reflected by the P300

may, however, be used to guide action selection on subsequent trials. Incorrect responses to infrequent targets that produce a P300 of larger amplitude are more likely to lead to correct responses for the next infrequent event than those eliciting a small P300. Furthermore, these large P300-eliciting errors also result in slower RTs on subsequent trials (Nieuwenhuis, et al., 2005a). A larger P300 may therefore indicate updating of correct stimulus-response associations for the infrequently encountered stimulus, where learning is less complete than for frequent targets. Successful updating results in improvements in performance for subsequent encounters with similar stimuli (Donchin & Coles, 1988a; Nieuwenhuis, et al., 2005a). This is also reminiscent of the ACC-guided learning described in Chapter 1.

Of particular interest to this thesis is the observation of an influence of motivational salience on P300 amplitude. The P300 produced in response to outcome information increases with magnitude of monetary incentive. No influence of valence is observed, however, with wins and losses producing comparable effects (Yeung & Sanfey, 2004). This may be due to an increased incentive to update representations when a larger value outcome is at stake. Alternatively the P300 may index active tracking and maintenance of the reward value of available options or the state of current monetary gains. Accurate stimulus-outcome representations are constructed by the integration of current outcome into reinforcement history, with greater importance placed on large-outcome trials (Johnson, 1986; Nieuwenhuis, et al., 2005a; Yeung & Sanfey, 2004). With the influence of both motivational and attentional factors on P300 amplitude, the relationship between reward expectation and attention with respect to P300 amplitude will be of particular interest in the subsequent experimental chapters of this thesis.

2.4.1.3 Expectation-related potentials

A further potential of interest in Chapter 6 is the contingent negative variation (CNV). This potential is a slow negative wave of ramp-like shape, with a fronto-central distribution (Coles & Rugg, 1995; Luck, 2005; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The potential is observed when a warning stimulus is followed by an imperative stimulus. The CNV is proposed to reflect expectation and preparatory processes related to preparation for the impending target, rather than sensory processing alone, as it is observed only when the second stimulus of the pair necessitates a response (Coles & Rugg, 1995; Luck, 2005; Walter, et al., 1964). Given the necessity of expectation for the emergence of this potential, the CNV will be of interest in anticipation of a multi-stimulus search array in Chapter 6.

2.4.1.4 Motor potentials

Given the prolific demonstration of the effects of reward factors upon motor processing, it will be important to examine the relationship between reward expectation and attention upon motor-related potentials. This can be achieved by examination of the lateralised readiness potential (LRP). The LRP refers to a negative deflection at fronto-central electrode sites C3/C4 contralateral to the hand of response (Coles, 1989). Intracranial recordings confirm the primary motor cortex as the source of the LRP (Arezzo & Vaughan, 1975). The LRP is derived by an averaging process according to the following equation (see also Figure 2.5):

$$LRP = [mean(C4\text{-}C3)_{\text{left-hand movement}} + mean(C3\text{-}C4)_{\text{right-hand movement}}]/2$$

(Coles, 1989).

Activity unrelated to preparation of motor response will average to zero. The resultant potential will thus reflect activity related to motor preparation and execution in the contralateral effector. The LRP is observed in warned RT tasks when the required response to an imperative stimulus is known in advance, allowing motor preparation prior to cue presentation (Coles, 1989).

Motor expectations greatly influence the LRP. In a choice RT task in which likely hand of response is cued, the LRP indicating preparation of the expected movement is observed. The LRP is thus negative with a valid cue, where expectation and required action are the same. The LRP is positive for invalid cues, where the incorrect action is prepared and has to be overcome. This preparatory activity correlates with validity benefit and invalidity cost in RTs (Coles, 1989). In addition, response biases are observed on a proportion of neutrally-cued trials. Fast RTs are likely due to performance based on guessing which response will be required. In fact this does appear to be the case; a negative LRP is observed for fast correct responses and a positive potential for fast incorrect responses (Coles, 1989). It will be of interest to examine the LRP with respect to the reward and spatial expectations manipulated in this thesis.

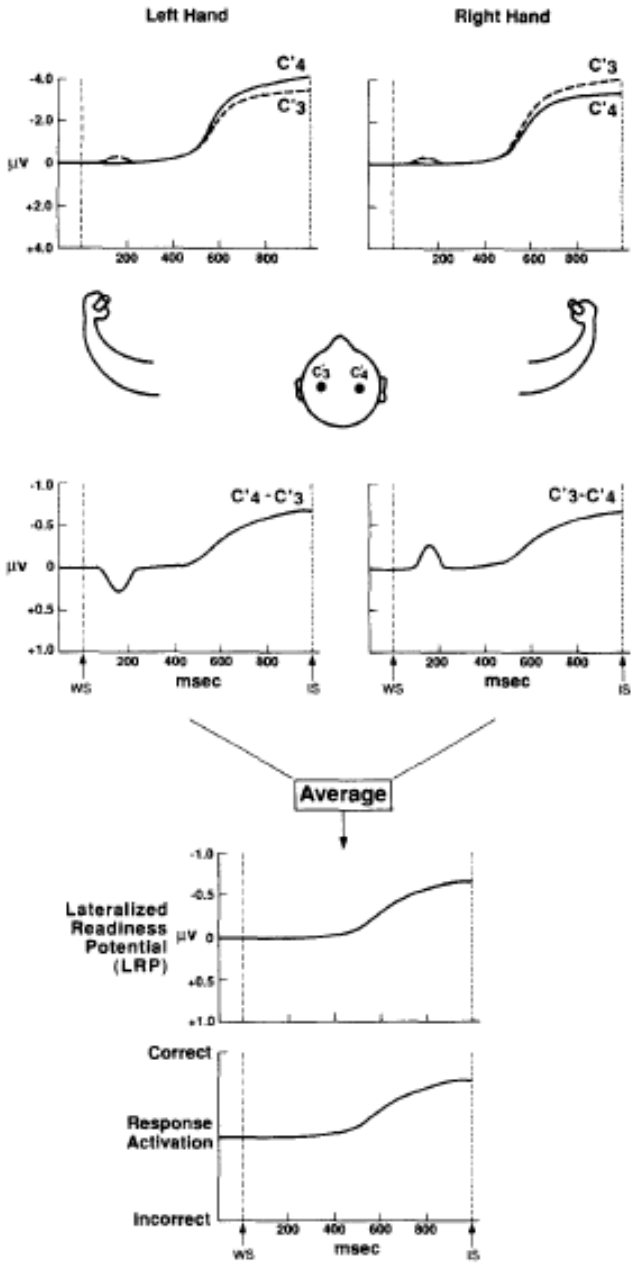

Figure 2.5: Derivation of the LRP. The potentials observed for left and right hand movements (top panels) are subjected to a subtraction, whereby potentials recorded from the ipsilateral scalp are subtracted from those at the contralateral electrode (middle panel). These are then averaged together to derive the LRP (third panel). The bottom panel shows the relationship between the LRP and response activation. Since the LRP is derived with respect to the correct response, preparation of the correct response results in a negative LRP, whereas preparation of the incorrect response results in positive deflection. WS refers to the warning stimulus, IS to the imperative stimulus. Figure taken from Coles (1989).

Coles, M. G. H. (1989). Modern Mind-Brain Reading - Psychophysiology, Physiology, and Cognition. Psychophysiology, 26(3), 251-269. © 1989 by The Society for Psychophysiological Research, Inc. Reprinted with permission from John Wiley & Sons.

2.4.2 Scalp topography

Although the spatial resolution of ERPs is poor, the topographical distributions can be used to gain additional information to that obtained with waveform analysis. Topographical analysis provides a reference-independent means to examine differences within and between conditions, in terms of the spatial distribution of voltage changes across time. This method allows inference of the underlying neural generators of neural activity (Murray, et al., 2008). Topographic analysis with CarTool software (http://brainmapping.unige.ch/cartool.htm) uses clustering algorithms with group-averaged data to determine periods of stable topography from the electrical field measured at the scalp. This can be used to determine time periods in which topographies differ between experimental conditions. Differences between conditions may be used to infer a difference in the configuration of contributing intracranial sources of neural activity. Alternatively, differences between conditions may be due to differences in the relative weightings of intracranical sources (Murray, et al., 2008). The results with the group-averaged data can be "fitted" back to that of individual subjects' data to test the validity of experimental manipulations and their effects upon individuals (Murray, et al., 2008).

2.5 Advantages and disadvantages of the ERP technique

It is always important to be aware of the limitations of any methodology. A primary disadvantage of the ERP technique is the poor spatial resolution. It is difficult to determine the source(s) of a voltage signature recorded at the scalp. This derives partly from the "inverse problem". Inferring the source of the ERP recorded on the 2D scalp surface from the 3D brain is a mathematically underdetermined problem. For an observed signal recorded at the scalp there exist an infinite number of possible dipole configurations (Coles & Rugg, 1995; Luck,

2005; Luck, et al., 2000). Volume conduction contributes to this issue. The brain is a conductive medium, thus current spreads as it flows through the brain along the path of least resistance, rather than travelling directly along between the poles of the dipole. The voltage is further blurred when it reaches the resistant medium of the skull, where it spreads laterally (Luck, 2005). The spatial and temporal summation of activity from multiple separate sources results in a signal recorded at one point at the scalp that may result from activation of a spatially distant source. This temporal summation can also create difficulty in isolating specific potentials of interest, which may overlap (Luck, et al., 2000). It is possible to minimise the spatial resolution problems of ERPs by constraining dipole-modelling solutions with knowledge gained from other methods. Biophysical principles suggest ERPs are generated in cortical grey matter (Luck, et al., 2000). Furthermore, the characteristics of a given brain region observed with single-unit recordings, such as the retinotopic organisation of V1, can be used to determine whether a potential originates from that region (Clark, et al., 1994). Converging anatomical information can also be gained from using functional neuroimaging methods such as fMRI (Di Russo, et al., 2002; Heinze, et al., 1994; Hillyard & Anllo-Vento, 1998).

Despite the poor spatial resolution, ERPs are a highly advantageous and non-invasive method for the study of attention. The major advantage of the ERP technique over other methods is its exquisite temporal resolution (Coles & Rugg, 1995; Luck, 2005; Luck, et al., 2000). ERPs are a powerful tool for the measurement of online changes in neural signal occurring in real time. This allows the study of effects occurring at successive stages of processing. The temporal resolution of ERPs also provides high sensitivity to the measurement of short-lived neural changes (Coles & Rugg, 1995; Luck, 2005; Luck, et al., 2000).

Of particular importance to the study of attention is the fact that ERPs allow examination of neural activity without requirement of an overt response. This is essential for the study of unattended stimuli. Behavioural measures do not allow for this (Luck, 2005; Luck, et al., 2000). Furthermore, response-based measures are relatively polluted. They may be influenced by neural processing at a number of stages, including perceptual processing, cognitive operations and response selection and execution, which cannot be distinguished. ERPs can provide information that may not be evident in behavioural measures, such as differences in neural activity where no differences in behaviour exist, and can pinpoint the stage of processing at which experimental manipulations take effect (Eimer, 1998; Luck, 2005).

Another important advantage is the ability of ERPs to record neural activity directly. fMRI and PET use indirect measures of blood flow and oxygenation levels as correlates of the brain activity mediated by metabolic demands. In addition to providing a sluggish measure, the way in which these hemodynamic methods represent changes in underlying neural activity is not entirely clear (Huettel, Song, & McCarthy, 2004). The advantages of ERPs make them an ideal method for the study of the manipulations of attention and reward expectation in this thesis.

Chapter 3: Spatial attention and parametric manipulation of reward

Reward expectation has been demonstrated to influence behaviour in attention tasks. The results of Della Libera and Chelazzi (2006) suggested that attempts to obtain reward may enhance attention in order to overcome potentially distracting stimuli. Negative priming effects, a disruption in behaviour when irrelevant cues matched subsequent targets, were reversed following a lower rewarded outcome. This implied the attention system was more swiftly reset when outcomes were less desirable in an attempt to gain a higher reward on the next trial (Della Libera & Chelazzi, 2006). d' was also observed to increase with the absolute value of obtainable incentive (Engelmann, et al., 2009; Engelmann & Pessoa, 2007). Improvements were more pronounced when target location was invalidly cued. This suggested reward information may have been more heavily relied upon in the absence of accurate spatial information. This may have been because valid spatial cues had already provided sufficient information to optimise performance, with additional information becoming redundant. Alternatively, reward information may have been utilised to a greater degree by the reorienting attention system, in action following invalid cues, rather than the orienting system, active with valid cues (Engelmann, et al., 2009; Engelmann & Pessoa, 2007).

Attentional processes may be influenced differentially by different types of reward information. When attention was unrestrained, the motivational salience of a stimulus, the probability of a win or loss associated with that item, appeared to determine stimulus recognition (Raymond & O'Brien, 2009). Stimulus recognition was higher for stimuli associated with a high probability outcome, regardless of whether the outcome was a win or loss. Under conditions of reduced attention, however, association with positive valence appeared to prioritise stimuli in the competition for processing resources. A clear deficit in recognition (an

"Attentional Blink") was observed for loss or no-outcome stimuli (negative valence) when the time between successive target stimuli was short. The deficit was abolished for stimuli associated with a win. Even under these conditions, outcome probability modulated performance in the same manner as with unrestricted attention. This suggested a dissociation between the effects of valence and salience. Whilst valence prioritised allocation of attention to a given stimulus, outcome probability (salience) modulated processes independent from attention. It was therefore possible that multiple top-down signals could influence perceptual awareness, with motivational signals working independently from attention under certain conditions (Raymond & O'Brien, 2009).

The aim of this study was to develop a paradigm under which spatial attention and reward expectation could be manipulated factorially, with the aim of investigating the effects of each upon information processing. It was hypothesised spatial attention and reward expectation would each modulate information processing. Two groups of participants performed two versions of the same task, with instructions emphasising either accuracy (Experiment 3.1) or RT (Experiment 3.2). Neutral cues were used rather than the invalid cues adopted by others within the literature (Engelmann, et al., 2009; Engelmann & Pessoa, 2007). Invalid cues differ qualitatively from neutral ones. They require a host of different processes, such as disengagement of attention from the incorrect location, reorientation to the correct location and error processing (Corbetta, Patel, & Shulman, 2008). This task used neutral cues to allow not only examination of the effects of spatial attention, but also of the effects of reward expectation in the presence versus absence of spatial attention.

Experiment 3.1 – Instructions stressed accuracy

3.1.1 Materials and Methods

3.1.1.1 Participants

Fifteen healthy volunteers with average age of 25.2 years (range 20-43 years, 6 female) were recruited from the University of Oxford community. Individuals participated as paid volunteers, with verbal and written consent obtained. All individuals were right handed, according to self report. Visual acuity was normal or corrected-to-normal. The experimental methods were non-invasive and had ethical approval from the University of Oxford Research Ethics Committee. Participant numbers were determined by counterbalancing considerations. Three subjects were removed from analysis due to failure to perform the task at an accuracy level above chance.

3.1.1.2 Task Design and stimuli

The task was prepared using Presentation software, and is illustrated in Figure 3.1. Participants viewed briefly presented grating stimuli appearing within a peripheral location at one of the four quadrants, and made a forced-choice judgement about their orientation. Spatial expectation about the target location and reward value for each target location were manipulated in a factorial design. Central cues preceding the peripheral target stimuli predicted the location where the target stimuli would occur on half the trials (valid cues) but provided no spatial information on the other half (neutral cues). Stimuli appearing within each quadrant were associated with different reward values (£1.00, £0.50, £0.25, £0.00). The

different magnitude of reward associated with each of four possible target locations was fixed for a block. These values were presented onscreen for participants to memorise before the block began. A new set of associations between reward value and location was given for each block, with the order of these contingencies counterbalanced across participants. Participants were informed they would receive earnings based on one randomly selected block. This was to ensure motivation remained high for the duration of the experiment. A recall test was performed after each block to ensure the reward-location associations had been memorised. Participants were informed this test would be performed prior to commencement of the experiment. Targets were presented to each location [up left, up right, down left, down right] 60 times in each block, with equal numbers of trials for each cue type (valid, neutral) and grating tilt direction (left or right). Order of presentation was randomised. Four blocks of trials were presented, one for each reward-location association, with breaks (with length of participants' choosing) between blocks. A practise block of 16 trials was presented prior to commencement of the four blocks of experimental trials, after which verbal feedback as to accuracy was provided. Total running time approximated 50 minutes.

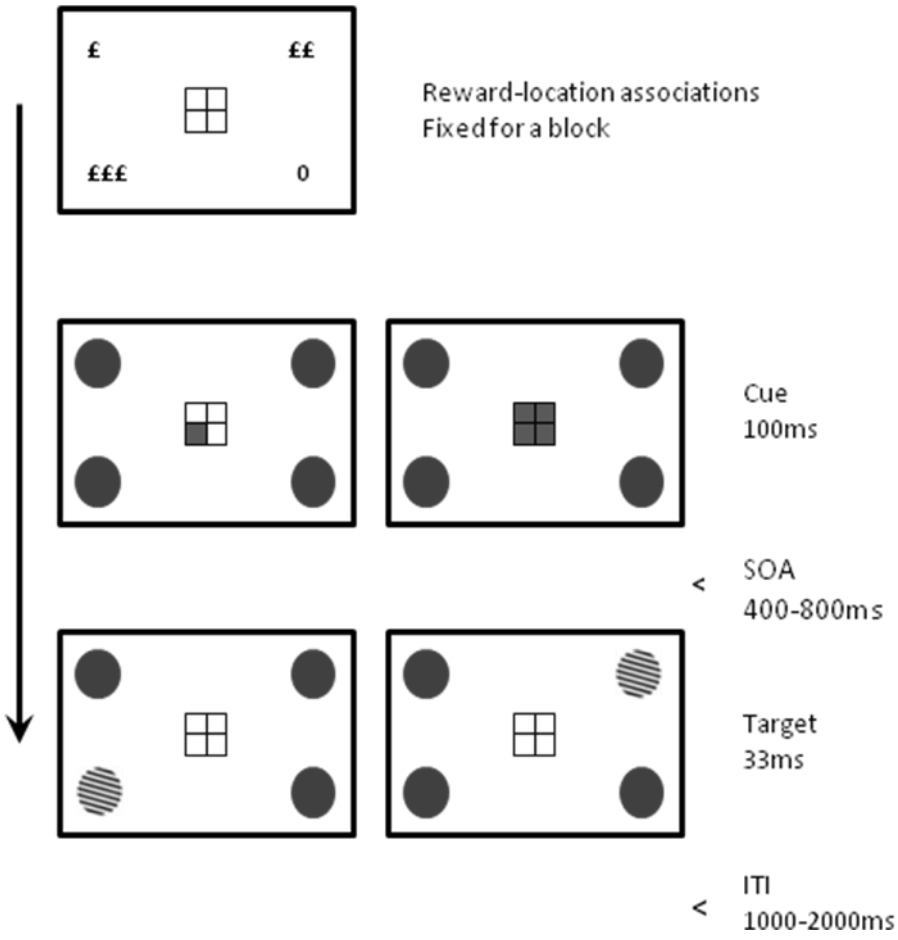

Figure 3.1: Schematic of the task used in Experiments 3.1 and 3.2. Blocks began with presentation of the reward magnitude associated with each potential target location. Trials began with presentation of a valid (50% of trials) or neutral (50% of trials) spatial cue (100ms). Following a variable SOA the target was presented for 33ms. Following response a variable inter-trial interval (ITI) intervened before the next trial. An example of a validly-cued trial is given on the right. The left is an illustration of a neutral trial.

Each trial started with a valid (100% validity) or neutral cue (100ms) (50% spatial and 50% neutral cues). After a variable stimulus-onset asynchrony (SOA, randomised between 400 and 1400ms), the target was presented for ~33ms (two refresh rates). Participants discriminated the tilt of the peripherally presented grating stimulus using covert attention only and were required to make a button-press response as to the tilt direction of the grating, using the index finger of the left (left tilt) or right (right tilt) hand. Participants were instructed to respond as accurately as possible.

Target stimuli were circular gratings 2.00 degrees of visual angle in diameter, with spatial frequency of 0.25 cycles per degree, presented in one of the four quadrants. The centre of the stimulus was positioned at 3.15 degrees of horizontal eccentricity and 3.15 degrees of vertical eccentricity. Targets were tilted 10 degrees to the left or right of the vertical orientation. Black location markers, with the same dimensions as targets, occupied all potential target locations throughout each task, as well as the unoccupied target locations during target presentation, to avoid visual afterimages. A fixation stimulus was present at the centre of the screen throughout each block of trials. This was a white square separated into four boxes by a central cross (subtending 0.57 degrees). For validly cued trials the square corresponding with target location was replaced with a black square during the cueing period. For neutral trials all four boxes darkened. Stimuli appeared on a grey background.

Participants were seated comfortably in a dimly illuminated, electrically shielded chamber, 100cm in front of a computer monitor. They were given written and verbal task instructions. Head position was stabilised with use of a chin rest. Maintenance of visual fixation was monitored using a video-based infrared RK-464 eye-tracker (ISCAN, Woburn, MA).

3.1.2 Results

For both Experiments 3.1 and 3.2, behavioural measures (accuracy, d', RT) were analysed with repeated-measures analyses of variance (ANOVAs) testing the factors spatial attention (valid cue, neutral cue) and reward magnitude (£1, £0.50, £0.25, £0). To calculate d', the hit rate was defined as the probability the participant responded "tilt left" given the grating was tilted to the left. The false-alarm rate was the probability participants responded "tilt left" given the target was tilted to the right (Green & Swets, 1966). D' was calculated using hit and false alarm rate with the equation:

$$d' = \frac{1}{\sqrt{2}}[z(H) - z(F)]$$

(Engelmann & Pessoa, 2007). The same d' calculated was employed in all subsequent experiments, unless specifically stated otherwise.

Results for Experiments 3.1 and 3.2 are shown in Figure 3.2. All values in this and subsequent chapters were Greenhouse-Geisser corrected and used the Bonferroni adjustment, unless specifically stated otherwise. For this and all subsequent experiments, only correct responses were included in RT analysis.

Accuracy was high overall in the experiment, but was significantly higher in trials with valid (mean=0.97, SD=0.02) compared to neutral spatial cues (mean=0.96, SD=0.03) [main effect of spatial attention ($F(1,11)=7.25$, $p=.02$)]. There was no significant effect of reward on accuracy ($F(3,33)=0.10$, $p=.41$) and no interaction between the two factors ($F(3,33)=1.08$, $p=.37$). D'

measures showed the same pattern of findings, but none of the effects were significant (all p values>.27).

RT data complemented accuracy data. Responses were quicker in the valid (mean=561ms, SD=95ms) than neutral (mean=613ms, SD=90ms) condition [main effect of spatial attention ($F(1,11)=49.62$, $p<.01$)]. There was no significant effect of reward ($F(3,33)=0.81$, $p=.50$) and no interaction between spatial attention and reward ($F(3,33)=0.78$, $p=.52$).

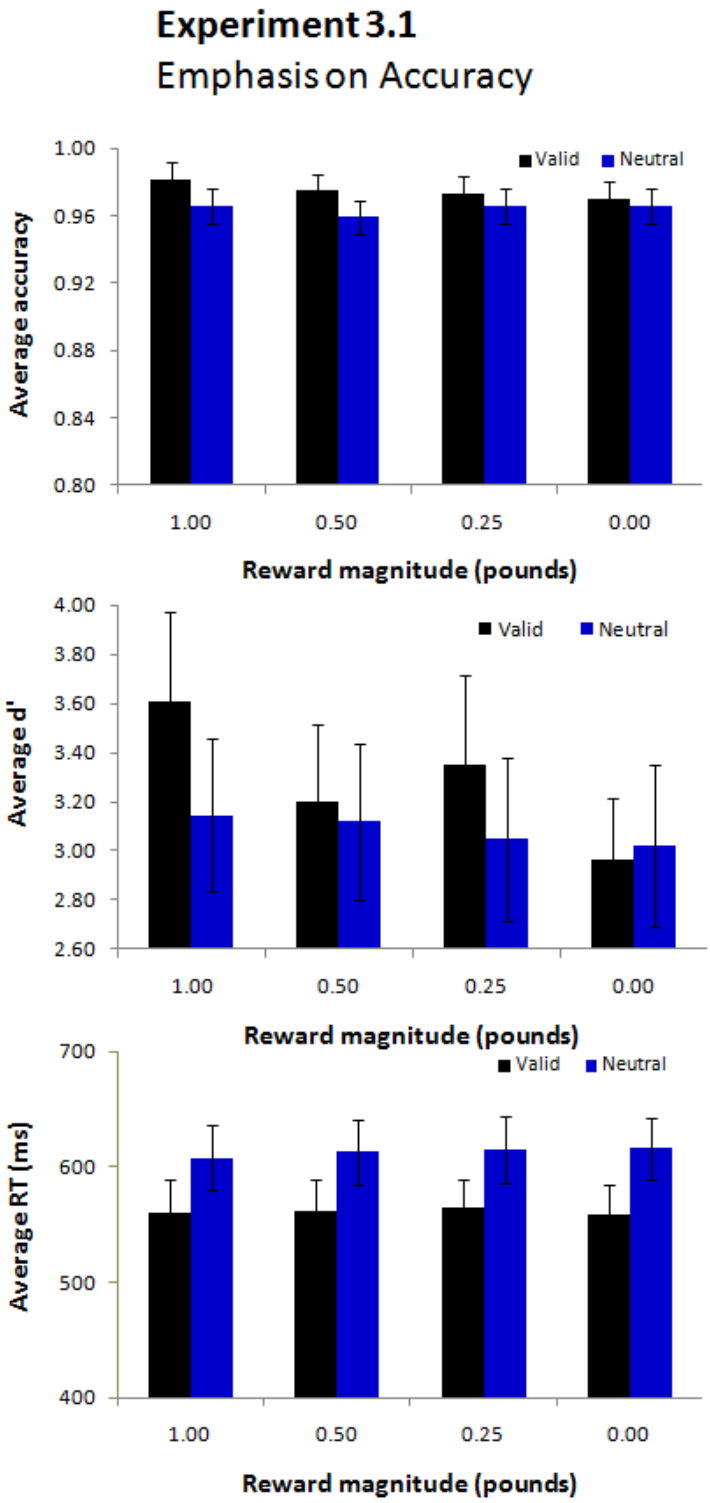

Figure 3.2: Behavioural results for Experiment 3.1. Graphs show average accuracy (top panel), d' (middle panel) and RT (bottom panel) for all participants as a function of reward magnitude. Valid trials are plotted with black bars, neutral trials with blue. The error bars use the standard error of the mean.

Experiment 3.2 – Instructions stressed speed

3.2.1 Materials and methods

All methods were the same as in Experiment 3.1 unless stated otherwise.

3.2.1.1 Participants

Fourteen healthy volunteers with an average age of 24 years (range 18-31 years, 7 females) participated in the task. All participants were right-handed, according to self report. One subject was eliminated from analysis due to inability to perform the task at levels above chance.

3.2.1.2 Stimuli and procedure

Participant instructions accentuated the need to respond as quickly as possible whilst maintaining accuracy. To encourage rapid responses, an RT threshold was introduced. Incorrect responses, or responses that were slower than the mean RT in the preceding block, would not earn reward. The threshold was updated on a block-by-block basis. This procedure was implemented in all later experiments.

3.2.2 Results

Accuracy was significantly higher after valid (mean=0.94, SD=0.05) compared to neutral (mean=0.92, SD=0.05) spatial cues [main effect of spatial attention ($F(1,11)=6.25$, $p=.03$)]. There was no significant effect of reward ($F(3,33)=0.91$, $p=.45$) or interaction between the two factors ($F(3,33)=1.25$, $p=.31$). D' showed the same pattern of effects [main effect of spatial attention ($F(1,11)=8.84$, $p=.01$].

To confirm that introduction of the RT threshold was successful in increasing task difficulty, accuracy in Experiments 3.1 and 3.2 were compared with repeated-measures ANOVA with an additional factor of experiment (3.1, 3.2). There was an effect of experiment ($F(1,11)=6.49$, $p=.03$). Accuracy was higher in Experiment 3.1 (mean=0.97, SD=0.03) than Experiment 3.2 (mean=0.93, SD=0.05). The RT threshold did thus appear to increase task difficulty.

Reward magnitude did significantly modulate RT ($F(3,33)=5.79$, $p<.01$). There was a significant linear trend for reward magnitude ($F(1,11)=5.67$, $p=.04$), with RT decreasing as reward magnitude increased. There was also an effect of spatial attention ($F(1,11)=21.37$, $p<.01$), with responses quicker in the valid (mean=512ms, SD=107ms) than neutral (mean = 548ms, SD=93ms) condition. Furthermore, there was an interaction between reward and attention ($F(3,33)=3.35$, $p=.03$). The interaction between reward and attention was not linear in nature (linear contrast ($F(1,13)=2.37$, $p=.15$). Subsidiary ANOVAs were conducted to test for effects of attention at each level of reward. These showed there was a significant effect of attention for £1 ($F(1,11)=29.15$, $p<.01$), £0.50 ($F(1,11)=21.82$, $p<.01$) and £0.25 ($F(1,11)=34.87$, $p<.01$) reward. There was no effect of attention with no reward [£0 condition ($F(1,11)=0.30$, $p=.59$)].

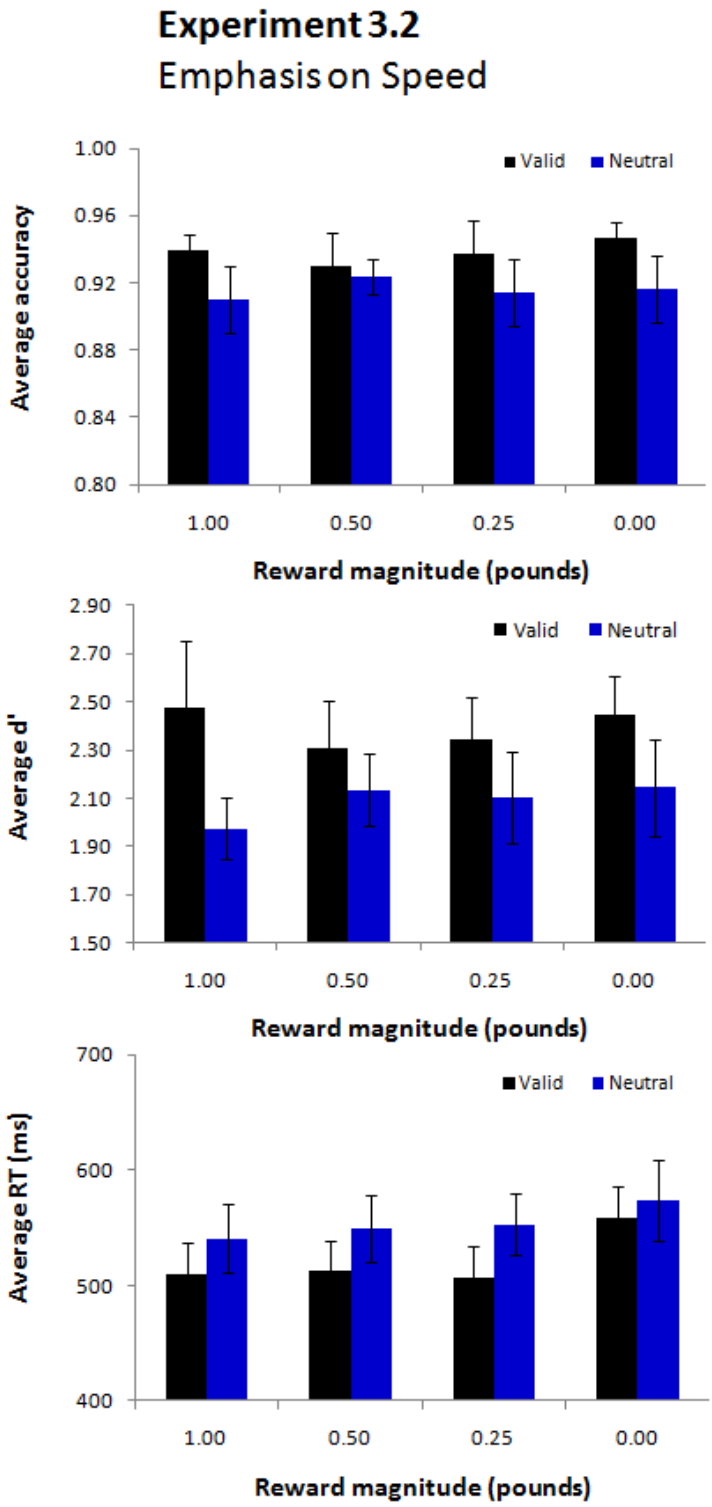

Figure 3.3: Behavioural results for Experiment 3.2. Graphs show average accuracy (top panel), d' (middle panel) and RT (bottom panel) for all participants as a function of reward magnitude. Valid trials are plotted with black bars, neutral trials with blue. The error bars use the standard error of the mean.

3.2.3 Discussion

The primary aim of the experiments of this chapter was to develop a paradigm under which to investigate the effects of reward value in the presence or absence of spatial certainty. The robust effects of attention in both tasks suggested the paradigm was adequate for this. The results of Experiment 3.2 further suggested the task parameters were appropriate in testing for such effects. Tilt discrimination of peripherally presented stimuli did produce behavioural differences with respect to the magnitude of the expected reward, though these effects were smaller than might have been expected, given the strong effects of reward upon behaviour, neuronal firing and BOLD activation (Amiez, et al., 2006; Apicella, Ljungberg, Scarnati, & Schultz, 1991; Bendiksby & Platt, 2006; Della Libera & Chelazzi, 2006; Engelmann, et al., 2009; Engelmann & Pessoa, 2007; Fiorillo, et al., 2003; Hollerman, et al., 1998; Mohanty, et al., 2008; Padmala & Pessoa, 2010; Peck, et al., 2009; Platt & Glimcher, 1999; Raymond & O'Brien, 2009; Schultz & Romo, 1990; Schultz, et al., 1998; Small, et al., 2005; Tobler, Fiorillo, & Schultz, 2005; Tremblay, et al., 1998). RT was the behavioural measure that was sensitive to reward. Responses were faster when produced in the expectation of reward. Though RT decreased linearly with increasing reward, there was little difference between the RT improvements with moderate reward magnitude. Furthermore, the observation of the speeding of responses with reward only with the introduction of an RT threshold suggested time pressure was a necessary precondition for the observation of reward effects. This suggested reward may have acted upon the process most relevant to optimisation of behaviour, in this case speed of response. Alternatively, the motor system, rather than the perceptual system, may be more sensitive to effects of reward.

In addition to the main effect, reward and attention interacted with respect to RT. Attention appeared to speed RT on trials in which reward was obtainable, but failed to do so when no reward was expected. This suggested that reward improved behavioural performance by working through the attention system. This further indicated that on no-reward trials, where there was no longer any potential for monetary gain, participants were not motivated to use the attentional cues to improve performance. In this task, attentional cues and reward information were dissociable, with spatial location indicated by means of the central cues and reward magnitude learned by association with the peripheral target locations at the beginning of each block. This manipulation may have allowed the separable use of reward and attention information, with participants able to utilise or ignore one or the other source of information as desired. Given the disappearance of an attention effect in the no-reward condition, it appears participants exploited the reward information to determine whether or not it was worthwhile to use the attentional cue to optimise performance. When even optimal performance (a fast, accurate response) would not result in reward, attention information was ignored.

Furthermore, the results suggested a categorical, rather than parametric, effect of reward upon behaviour. This was evident in the speeding of RT with valid attentional cues with any level of reward, but no attentional effect on neutral trials. There was no difference in RT when comparing moderate values of reward (£0.25 and £0.50). The presence of reward thus appeared to be the important factor in driving an effect upon behaviour, with little to be gained from the manipulation of specific magnitude. This differed from the parametric effect of reward magnitude reported by Englemann and colleagues (Engelmann, et al., 2009; Engelmann & Pessoa, 2007). It was possible differences in the specific task parameters may have led to the discrepancies in the nature of the reward effects. The behavioural measure

upon which reward had an effect in the studies of Englemann and colleagues (Engelmann, et al., 2009; Engelmann & Pessoa, 2007) was d', rather than RT. Though both this task and those of Engelmann and colleagues required participants to discriminate visual stimuli, degraded or faint stimuli utilised in the two studies of Englemann et al. (Engelmann, et al., 2009; Engelmann & Pessoa, 2007) may have placed a greater emphasis on stimulus discrimination, while the emphasis was on speed of response in this task. Not only did these task differences lead to effects of reward upon different behaviour measures, but the nature of the effects differed. This would be consistent with the argument that reward targets the process(es) of greatest relevance to task performance. Furthermore, incentives in the tasks of Englemann et al. (Engelmann, et al., 2009; Engelmann & Pessoa, 2007) could be in the form of monetary wins or losses. Though absolute incentive value was used in the report of behavioural data, the brain processes wins and losses differently (Elliott, Friston, & Dolan, 2000). This may have led to a difference in the nature of effects upon behaviour, in addition to changes in underlying neural activity. Finally, the range of the potential magnitude of monetary gain was larger in the studies of Englemann and colleagues (from +$4.00 to -$2.50) than in this study (from £1 to £0). It is possible that larger differences in monetary value than were used in this task are necessary for a parametric modulation of behaviour by reward value.

Though reward did not modulate accuracy or d', spatial attention led to improvements in both measures, as well as speeding RTs. These effects replicated that of the prevailing literature (Corbetta, et al., 2002; Kim, et al., 1999; Mesulam, 1999; Nobre, et al., 2004; Nobre, et al., 1997; Nobre, et al., 2000b; Posner, 1980; Posner, et al., 1977; Yantis, 2008). Furthermore, these effects of spatial attention were observed in both experiments. Accurate spatial information thus improved performance irrespective of task conditions. It was possible that spatial attention effects were less sensitive to specific task parameters than reward.

The findings of this chapter suggested that the basic task structure, with grating tilt discrimination of peripherally-presented stimuli, was effective in eliciting reward effects, provided the judgements were performed under time pressure. The categorical effect of reward, however, suggested the parametric manipulation of reward magnitude might not be optimal in probing reward effects. In the next chapter, therefore, this will be reduced to a binary presence or absence of reward. This will allow the reduction of target locations to two and the maximisation of statistical power. Furthermore, though the results demonstrated an effect upon behaviour, the behavioural measures included a confluence of several successive stages of processing. It was impossible to ascertain the earliest point at which reward began to act upon information processing, nor did behavioural measures allow the illustration of the relationship between reward and attention at successive processing stages. Though the two factors interacted at the behavioural endpoint, it was possible earlier independent effects arose that were not visible with the measurement of behaviour alone. Electrophysiological methods will thus be used in the next study. ERPs will more clearly elucidate the time point(s) at which reward and attention modulate processing, as well as when and how they interact.

Chapter 4: Probabilistic manipulation of reward and spatial expectations

The experiments of Chapter 3 illustrated the ability of reward to influence behaviour in a cued attention task under conditions of RT pressure. The behavioural measures used, however, provided a relatively coarse view of the effects of experimental factors, providing results only at the endpoint of the summation of processing that ultimately resulted in response (Luck, 2005; Luck, et al., 2000). These measures did not allow the investigation of the effects of reward expectation and spatial attention upon each successive stage of processing. Furthermore, the relationship between these two factors may change across processing stages, with independence at some stages and interaction at others. To this end, ERPs were recorded in Chapter 4 to overcome the limitations of the purely behavioural measures of Chapter 3.

The allocation of spatial attention has been associated with benefits in performance (Posner, 1980; Posner, Snyder, & Davidson, 1980) and enhancement of neural activity at multiple stages of processing (Kastner & Ungerleider, 2000; Nobre, 2004). Effects of attention were evident early, with enhancement of the visual analysis of stimuli. This was evident in the increased amplitude of the P1 potential for stimuli presented at an attended location (Clark, et al., 1994; Di Russo, et al., 2002; Mangun & Hillyard, 1991). The effects of reward expectation upon such early stages of visual processing were less clear. The expectation of a reward, as well as violations of this expectation, was signalled by the phasic firing rates of neurons in the midbrain and PFC (Amiez, et al., 2005; Amiez, et al., 2006; Fiorillo, et al., 2003; Hollerman & Schultz, 1998). The existence of neural connections between these regions and visual processing areas, either directly or indirectly via multisensory areas that control the allocation of attention, suggested a potential for reward information to influence visual processing

(Alexander, Delong, & Strick, 1986). Such a proposition was further supported by observed increases in BOLD activation in visual processing regions as a function of reward expectation (Engelmann, et al., 2009; Mohanty, et al., 2008; Small, et al., 2005). The poor temporal resolution of fMRI, however, made it impossible to determine whether such effects of reward were due to modulation of early visual processing or a later feedback mechanism. ERPs were recorded in this chapter to elucidate the time point(s) at which reward expectation influenced information processing.

The probability with which a reward was expected influences choice behaviour and neural activity. Midbrain dopamine and ACC neurons exhibited higher firing rates for stimuli associated with lower probability of reward (Amiez, et al., 2005; Amiez, et al., 2006; Fiorillo, et al., 2003). The importance of probability may relate to the role of these regions in tracking expected reward (the reward prediction error) and updating the outcome of a current trial with respect to recent reinforcement history (Rushworth & Behrens, 2008; Schultz, et al., 1997). ACC damage or deactivation caused animals to cease using history of reward outcomes to guide their behaviour (Amiez, et al., 2006; Kennerley, et al., 2006). The ability to use prior history is vital in the optimisation of behaviour. This probabilistic tracking of potential outcome, however, was not restricted to the reward system. The P300 potential was also sensitive to stimulus probability, in terms of frequency of presentation or probability of a given stimulus type. A larger P300 potential was observed in response to less frequent, unexpected or novel stimuli (Donchin & Coles, 1988a; Johnson, 1986; Nieuwenhuis, et al., 2005a). The importance of task relevance upon P300 amplitude carried important reward implications, given the increased relevance of reward-associated stimuli. Probability-governed expectation may thus influence both reward and attention systems. To investigate whether this was the case, reward expectation and spatial location were manipulated probabilistically and

factorially in the experiments of this chapter. The effect of probability with respect to each factor was examined, as was the relationship between reward and spatial expectations.

Behaviour appeared insensitive to reward magnitude in the parametric manipulation utilised in Chapter 3. Instead, it appeared that behaviour was influenced categorically, by the potential availability of a reward, irrespective of its possible value. This was consistent with the suggestion that, at least in some brain regions, a coarse and discrete coding of reward value may occur in terms of a binary present/absent signal (Nieuwenhuis, et al., 2005b). For this reason, the parametric manipulation was removed in Chapter 4 in an attempt to maximise statistical power.

In the experiments of this chapter, probability of target location and reward availability were manipulated independently block by block. The main experimental aims were to determine the time point(s) at which spatial attention and reward expectation modulated information processing and the relationship between these two factors. ERPs were measured, as their high temporal resolution allows such a delineation of the information-processing time course. Two groups of participants performed two similar versions of the task. One version was purely behavioural (Experiment 4.1), with reward availability signalled by the colour of the target stimulus. The second (Experiment 4.2) used ERP methodology, with reward availability signalled by a visual stimulus (£ or X) presented after responses were made. It was hypothesised that both spatial attention and reward expectation would modulate information processing, and that there would be some degree of interaction between the two.

Experiment 4.1

4.1.1 Materials and Methods

4.1.1.1 Participants

Fifteen healthy young adults (mean age=27 years, range=19-44 years, 9 females) were recruited from the University of Oxford community. Verbal and written consent was obtained. Visual acuity was normal or corrected-to-normal. The experimental methods were non-invasive and had ethical approval from the University of Oxford Research Ethics Committee. Participant numbers were determined by counterbalancing considerations. All were right-handed volunteers, as determined by self-report, participating for monetary reward. One individual was removed from analysis for failure to perform the task at accuracy levels above chance.

4.1.1.2 Task Design and Stimuli

The task is illustrated in Figure 4.1. Trials began with the centrally presented fixation stimulus (black plus symbol subtending 0.57 degrees) turning red to signal trial onset (100ms duration). A short variable interval (400-800ms) was followed by the target grating stimulus (33ms, centred at 5.36 degrees to the left or right of fixation on the horizontal meridian, and subtending 0.89 degrees visual angle with spatial frequency of 0.11 cycles per degree). Participants were required to make a covert discrimination judgement about the tilt direction of the grating stimulus and to respond with a button press with the index finger of one hand for vertically tilted gratings and the other hand for horizontally tilted gratings. Hand

assignment to response was counterbalanced. Participants' responses were followed by a variable interval of 1000-2000ms before onset of the next trial.

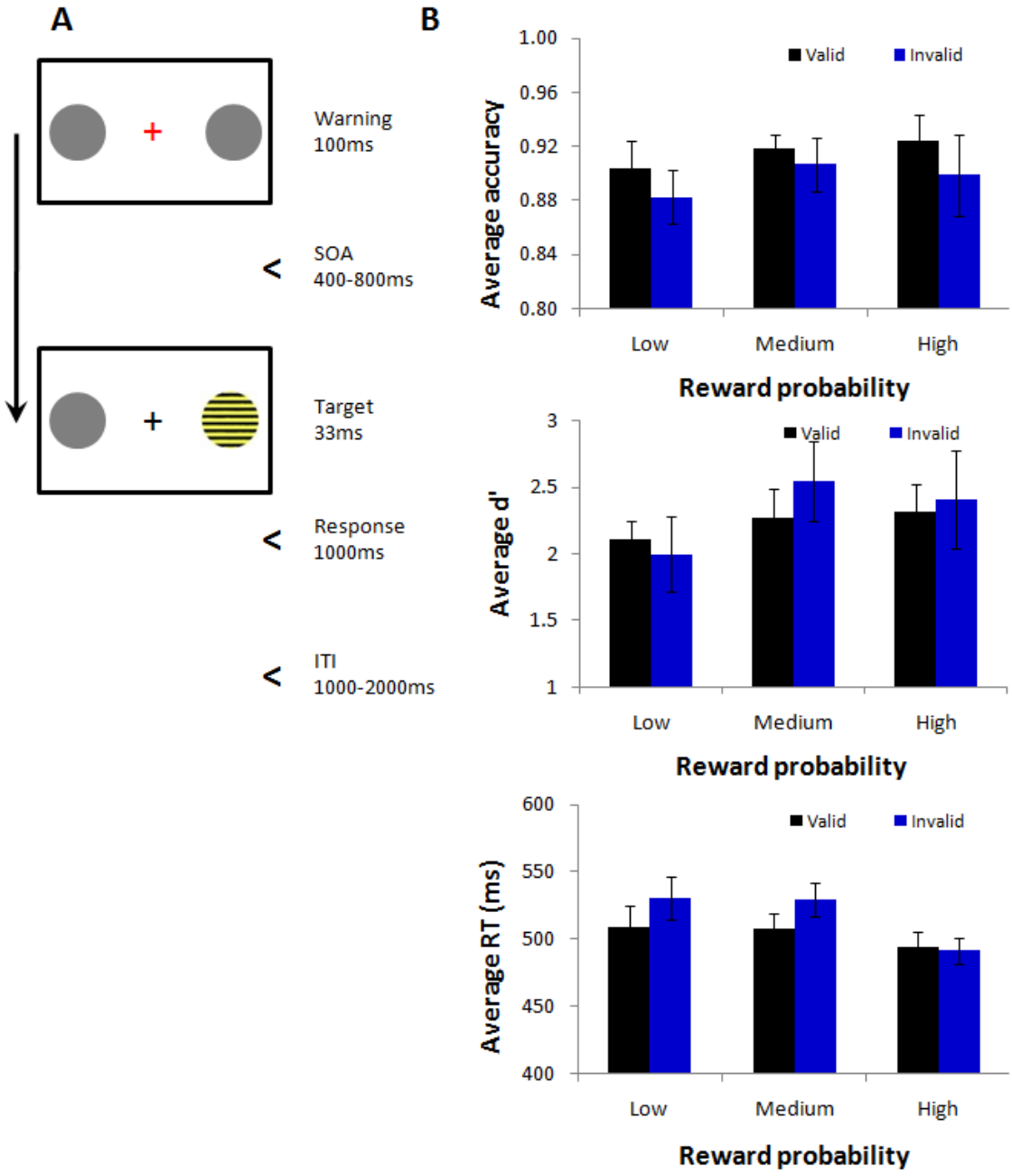

Figure 4.1: Task schematic and behavioural data for Experiment 4.1. (A) Trials began with a warning stimulus (100ms), followed by a variable SOA (400-800ms) before presentation of the target (33ms). Response was followed by a variable ITI (1000-2000ms) before the next trial began. (B) Graphs show the average accuracy (top panel), d' (middle panel) and RT (lower panel) for all participants in Experiment 4.1 as a function of reward probability. Valid trials are plotted with black bars, invalid trials with blue bars. Error bars use the standard error of the mean.

Spatial and reward expectation were manipulated independently, in blocked fashion. The target stimulus could be presented to the left or right of fixation with 0.8, 0.6, 0.4 or 0.2 likelihood. Trials could be rewarded or not as determined by an independently manipulated probability (target rewarded 0.8, 0.6, 0.4 or 0.2 likelihood). Probability manipulations of spatial location and reward expectation were not explicitly given to participants, but rather they were learned during the course of a block of trials. The four levels of spatial expectation and reward expectation were crossed factorially. Sixteen blocks, one for each combination of spatial and reward probability, were created, with order of presentation fully counterbalanced across participants.

Reward availability was indicated by the colour of the target, which could be a black-and-white or a black-and-yellow grating. Colour association was counterbalanced across participants. Stimuli were presented on a light grey background. Black location markers, with the same dimensions as targets, occupied potential target locations throughout each trial, as well as the unoccupied location during target presentation, to avoid visual afterimages. A centrally presented fixation stimulus (black plus symbol subtending 0.57 degrees) remained onscreen throughout the course of trials.

4.1.1.3. Procedure

Tasks were prepared using Presentation software (Neurobehavioural Systems, CA). Participants were seated comfortably in a dimly illuminated, electrically shielded chamber, 100cm in front of a computer monitor. They were given written and verbal task instructions. Head position was stabilised with use of a chin rest. Maintenance of visual fixation was

monitored using a video-based infrared RK-464 eye-tracker (ISCAN, Woburn, MA). Participants were required to make speeded discrimination responses to targets. An RT threshold was used, with participants instructed they would only receive any earned reward for trials in which correct responses were faster than or equal to their average RT in the preceding block.

4.1.2 Results

For both Experiments 4.1 and 4.2, the first ten trials in each block were removed from analysis to allow for learning of spatial and reward expectations (Walton, et al., 2004). Data were analysed in the high spatial prediction conditions (P(L)=0.2 and 0.8), due to the high between-subjects variability in low spatial prediction conditions. Data from the 0.6 and 0.4 reward probability conditions were combined to form a medium reward probability condition, as participants were not able to detect a difference from 0.5 reward likelihood in these two conditions. This resulted in three levels of reward probability; high (0.8 probability), medium (0.6 and 0.4 probability) and low (0.2 probability). Behavioural measures (accuracy, d' and RT) were analysed with repeated-measures ANOVAs testing the factors of spatial expectation (target location valid, invalid) and reward expectation (probability of reward 0.8, medium (0.6 and 0.4), 0.2). For each participant, RT outliers greater or less than 2.5 standard deviations from the mean were replaced by the mean of that condition.

The results of Experiment 4.1 are shown in Figure 4.1. There was no significant effect of attention on accuracy ($F(1,14)=2.59$, $p=.13$). There was also no significant effect of reward ($F(2,28)=1.49$, $p=.25$). The two factors did not interact ($F(2,28)=0.70$, $p=.47$). For d' there was no significant effect of attention ($F(1,14)=0.67$, $p=.43$). There was a marginally significant

effect of reward (F(2,28)=3.32, p=.05). Tests of within-subjects contrasts revealed a significant quadratic contrast (F(1,14)=4.96, p=.04). D' was greater for medium probability of reward (mean=2.56, SD=0.98) than either low (mean=2.02, SD=0.98) or high (mean=2.35, SD=1.15) reward probability. There was no interaction between attention and reward (F(2,28)=0.78, p=.46).

For RT, responses were faster in the valid (mean=504ms, SD=49ms) than invalid (mean=517ms, SD=53ms) attention condition [main effect of attention (F(1,14)=8.072, p=.01)]. There was also a significant main effect of reward (F(2,28)=4.652, p=.02). Tests of within-subjects contrast revealed a significant linear trend (F(1,14)=5.338, p=.04), with RTs faster with increasing probability of reward. There was no interaction between reward and attention (F(2,28)=3.20, p=.09).

4.1.3 Discussion

In contrast to previous experiments (Chapter 3), both RT and d' were sensitive to the reward manipulation. Data suggest the d' and RT effects resulted from different aspects of processing. RT displayed a linear relationship with reward probability, with responses fastest for high reward likelihood. D', alternatively, exhibited a quadratic reward relationship. Sensitivity was greatest at medium reward probability. These differences may underlie the proposed separate coding of reward probability and uncertainty (Behrens, Woolrich, Walton, & Rushworth, 2007; Fiorillo, et al., 2003; O'Doherty, 2004; Platt & Huettel, 2008; Robbins & Everitt, 1996; Rushworth, 2008; Rushworth & Behrens, 2008; Rushworth, Behrens, & Walton, 2007; Schultz, 2000; Schultz, et al., 1997; Walton & Mars, 2007; Walton, et al., 2007; Yang & Shadlen, 2007a).

It was possible that perceptual processing, indexed by d', was influenced by (un)certainty, while motor and/or cognitive processing, related to RT, were more subject to reward value. ERPs provide a valuable tool for elucidating this proposition. A further ERP study was therefore conducted.

In this experiment, spatial attention enhanced performance mainly by speeding responses. There was no attentional effect on accuracy or d'. This may have been due to the un-cued manipulation of spatial probability across blocks. The requirement to learn target location likelihood during blocks may have resulted in weaker attentional effects than those triggered by explicit cues, such as those used in Chapter 3.

It was possible that signalling reward availability by target colour may have led participants to exploit some form of feature-based attention (Blaser, Pylyshyn, & Holcombe, 2000; Rodríguez, Valdés-Sosa, & Freiwald, 2002). To avoid this possible confound, the reward signal was therefore altered in Experiment 4.2, with the use of a £ or X symbol after response to indicate whether reward was or was not available on the trial, respectively. This was not indicative as to whether the response had been fast enough or accurate, merely whether there was the potential to have earned reward. This stimulus was decoupled from performance-related feedback to avoid trial-by-trial fluctuations in cognitive state (such as arousal) in response to the reward signal, but rather to learn reward probability in a block-wise fashion.

Experiment 4.2

4.2.1 Materials and Methods

All methods were as per Experiment 4.1 unless specifically stated otherwise.

4.2.1.1 Participants

Twenty healthy young adults (mean age=23 years, range=19-50 years; 11 females) participated in the task. Data from 16 participants were analysed (mean age=24 years, range=19-49 years, 9 females), with four participants removed from analysis due to excessive eye movements, blinks or alpha activity in the EEG data. Fifteen participants were right-handed and one left-handed (average handedness 61.37) (Oldfield, 1971). Fourteen participants were undergraduate students in the Department of Experimental Psychology at the University of Oxford, who participated for course credit and monetary rewards earned during the experiment. Two were volunteers from the University of Oxford community, participating for monetary reward only.

4.2.1.2 Design and Stimuli

The task is illustrated in Figure 4.2. All target gratings were black and white. Stimuli presented 100ms after the response indicated whether reward had been available on that trial (£ symbol) or not (X symbol). Reward-indicator stimuli were presented centrally in black font, and subtended 1.32 degrees vertically and 0.77 degrees horizontally.

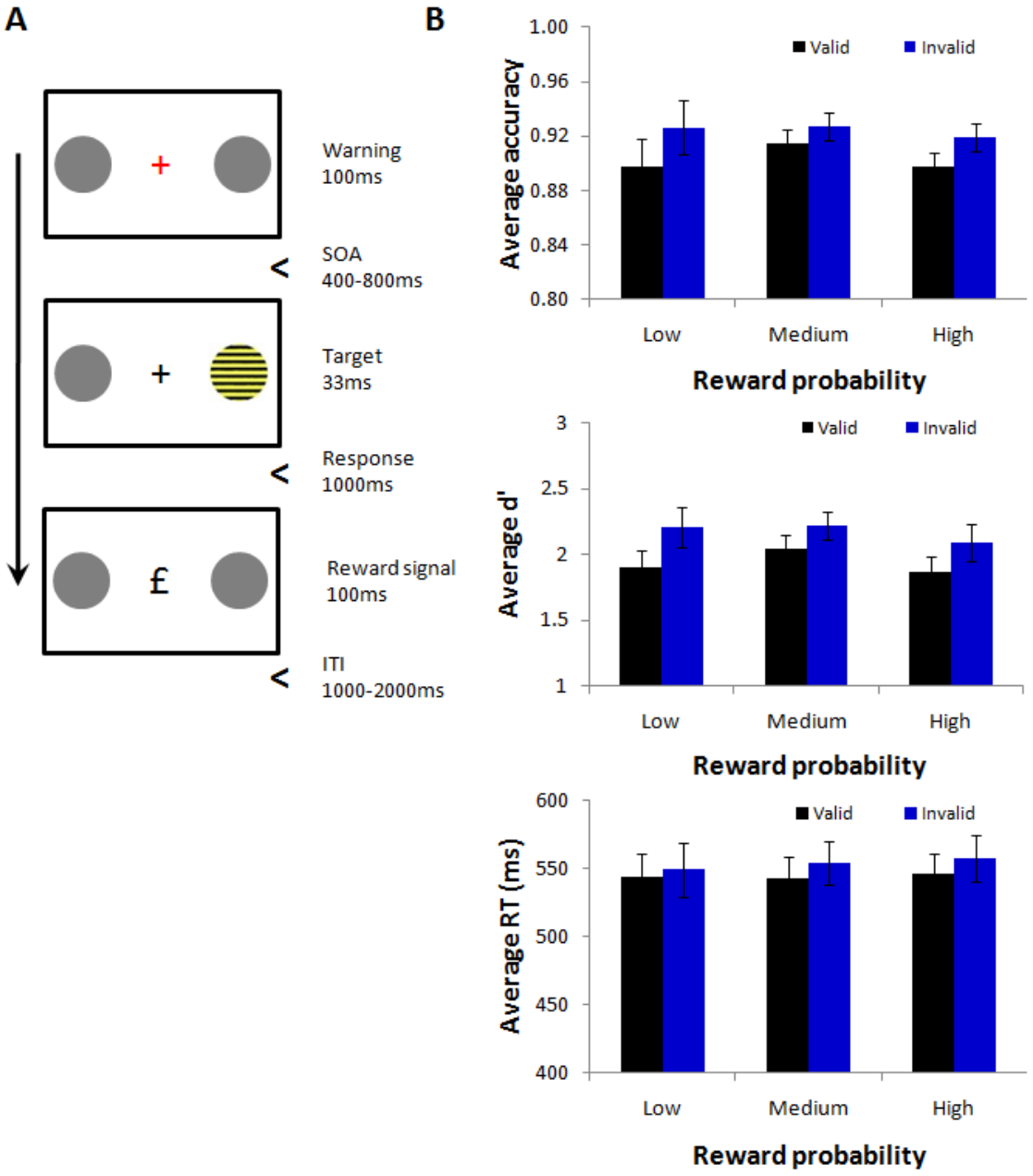

Figure 4.2: Task schematic and behavioural data for Experiment 4.2. (A) Trials began with a warning stimulus (100ms), followed by variable SOA (400-800ms) prior to target presentation (33ms). In this experiment, response was followed with presentation of a reward signal (100ms). A variable ITI (1000-2000ms) intervened before the next trial. (B) Graphs show the average accuracy (top panel), d' (middle panel) and RT (lower panel) for Experiment 4.2 as a function of reward probability. Valid trials are plotted with black bars, invalid trials with blue bars. Error bars use the standard error of the mean.

4.2.1.3 ERP Procedure

4.2.1.3.1 EEG recording

Continuous EEG was recorded using Neuroscan NuAmp amplifiers (Compumedics USA, Charlotte, NC) from 40 Ag/AgCl electrodes affixed to the head by means of elasticated cap (www.easycap.de). Electrodes were positioned according to the 10-20 system, with a montage that included six midline sites (Fz, FCz, Cz, CPz, Pz and Oz) and 14 sites over each hemisphere (FP1/FP2, F3/F4, F7/F8, FC3/FC4, FT7/FT8, C3/C4, T7/T8, CP3/CP4, TP7/TP8, P3/P4, P7/P8, PO3/PO4, PO7/PO8 and O1/O2). Electrodes were also placed above and below the eyes to monitor blinks and eye movements. Gaze was monitored using a video-based infrared RK-464 eye-tracker (ISCAN, Woburn, MA). Additional electrodes served as ground (AFz, positioned between FPz and Fz) and reference (A1 and A2 mastoid sites, with A2 serving as the online reference). Electrode impedances were maintained below 5kohm. Activity at each electrode site was sampled every 1ms (1000Hz analog-to-digital sampling rate). A 300Hz low-pass filter was used during continuous EEG recording. Digital stimulus-presentation codes were sent to the EEG acquisition computer via the parallel port from the stimulus presentation computer, indicating the exact time and type of each stimulus presentation.

4.2.1.3.2 EEG processing

EEG was re-referenced offline to the average of the left and right mastoid. Bipolar EOG signals were derived by computing the difference between the voltage at electrodes above and below the eye (vertical EOG) and at the side of each eye (horizontal EOG). Transformed re-referenced data were filtered by 40Hz low-pass filter to remove high-frequency noise. Epochs were

constructed commencing 800ms before target presentation and lasting until 800ms post-stimulus. The long pre-stimulus interval was used to monitor for possible anticipatory eye movements to the likely target location prior to its presentation. EEG epochs were normalised to the peri-stimulus period (-50 to 50ms). Data quality was initially inspected using automated algorithms. Trials containing drift, deflections exceeding +/- 150μV in any channel, were excluded. Trials containing blinks and eye movements were removed via a process of two iterations. Initially deflections greater than +/- 70μV in HEOG and VEOG were excluded automatically by computer algorithm. In addition, trials were visually inspected for the occurrence of saccades before or after target presentation. This procedure ensured that ocular artefacts or brain activity associated with systematic eye movements would not influence the results. Trials containing incorrect behavioural responses were removed also. A minimum of 20 trials per condition per participant was set to ensure a sufficient signal-to-noise ratio. ERPs were combined for targets appearing on the left and right side of the screen by averaging procedure that preserved the electrode position relative to target location (ipsilateral or contralateral). Six ERP averages were consequently constructed, differentiating trials by spatial expectation (valid, invalid) and reward probability (high, 0.8, medium, 0.6 and 0.4 or low, 0.2).

4.2.1.3.3 EEG analysis

Statistical analyses were performed using the mean voltage value (mean amplitude) around the peak of each potential of interest and the latency of the peak. Topographical segmentation of the data using CarTool software (http://brainmapping.unige.ch/cartool.htm) was used as an exploratory measure to guide ERP waveform analysis. The segmentation procedure identified periods of stable topography, which indicated the most appropriate time windows for ERP waveform analysis. This procedure was also useful in highlighting timing differences in the

onset of potentials across experimental conditions. This could be used to cross validate latency analysis, given the sensitivity of this form of analysis to noise. Furthermore, topographical analysis can be used to demonstrate whether the voltage signatures between two (or more) experimental conditions differ in strength (using the Global Field Power, the root mean square of voltage across electrodes at a given time point) or distribution (Murray, et al., 2008). A difference in strength suggests some form of enhancement, such as the amplitude enhancement of the P1 potential by attention prevalent in the literature (Hillyard, et al., 1998). A difference in distribution suggests a differentiation in the underlying neural source(s) of the signal under different experimental conditions, or a different relative weighting of the contribution of each neural source. It was of particular importance, given the limited number of ERP studies of reward expectation, to determine whether the effects of reward and attention produced potentials that differed in strength, topographical distribution, or both factors.

Furthermore, topographical analysis was useful in identifying the most appropriate electrodes for ERP analysis, by highlighting the spatial focus of a given potential. Topographic Atomize and Agglomerate Hierarchical Clustering was used. Clusters with a correlation above 96% were merged and segments less than 10 time frames were rejected. These small segments were unlikely to be true potentials, thus this procedure ensured the analysis was not confounded by noise, particularly prevalent in the peri-stimulus period. Segmentation was performed using an epoch that began at the time of stimulus presentation and endured until 600ms post stimulus. Minimisation of the Cross Validation criterion was used to determine the appropriate set of maps produced by the segmentation procedure. The same parameters were used in subsequent chapters unless specifically stated otherwise. Spatial attention and reward did not produce significant topographical differences.

ERP data were analysed by repeated-measures ANOVAs with factors of spatial attention (valid, invalid), reward probability (high 0.8, medium 0.6 and 0.4, low 0.2), hemisphere (ipsilateral, midline, contralateral) and electrode. The effects of interest were those pertaining to reward expectation, spatial attention, and the interaction between the two. As such, these were the only effects reported in the ERP results. The approach was maintained in subsequent chapters.

4.2.2 Results

4.2.2.1 Behavioural Results

The behavioural results are illustrated in Figure 4.2. Contrary to the usual pattern, accuracy was higher for invalid (mean=0.92, SD=0.05) than valid spatial expectation (mean=0.90, SD=0.05) [main effect of attention (F(1,15)=6.52, p=.02)]. There was no significant effect of reward (F(2,30)0.75, p=.45), nor an interaction between attention and reward (F(2,30)=0.23, p=.79). D' showed a similar pattern of results. D' was higher for invalid (mean=2.17, SD=0.46) than valid attention (mean=1.94, SD=0.53) [main effect of attention (F(1,15)=8.80, p=.01)]. There was no significant effect of reward (F(2,30)=0.81, p=.43). Attention and reward did not interact (F(2,30)=0.19, p=.83). RT was faster for valid (mean=544ms, SD=61ms) than invalid attention (mean=554ms, SD=69ms) [main effect of attention (F(1,15)=14.09, p<.01)]. There was no significant effect of reward (F(2,30)=0.21, p=.74). Attention and reward did not interact (F(2,30)=0.54, p=.59).

To determine whether changing the reward signal to post-response presentation shifted effects of reward to the next trial, an additional analysis was performed to examine trial context upon behaviour. Factors of current trial spatial expectation (valid, invalid), previous trial spatial expectation (valid, invalid), current trial reward expectation (reward, no reward) and previous trial reward expectation (reward, no reward) were used. Whether the previous trial was a reward or non-reward trial did not have any influence upon accuracy ($F(1,15)=0.78$, $p=.39$), d' ($F(1,15)=0.36$, $p=.56$) or RT ($F(1,15)=0.05$, $p=.83$). The only significant effects were those of spatial expectation for the current trial on d' ($F(1,15)=6.24$, $p=.03$) and RT ($F(1,15)=5.68$, $p=.03$). D' was higher for current-trial invalid (mean=2.29, SD=1.16) than valid (mean=2.06, SD=0.76) stimuli. RT was faster for current-trial valid (mean=543ms, SD=64ms) than invalid (mean=547ms, SD=63ms) trials. There were no other significant effects, nor were there any significant interactions (all p values>.05), thus the reward value on the previous trial and location of the previous stimulus did not influence any of the performance measures, nor did these expectancies interact.

To test whether a difference in task difficulty may have accounted for the differences in behaviour in Experiment 4.2, accuracy on this task was compared with that of Experiments 4.1 and 3.2 with repeated-measures ANOVAs with the additional factor of experiment (4.2 and 4.1; 4.2 and 3.2). In the comparison of Experiments 4.2 and 4.1 there was no effect of experiment upon accuracy ($F(1,15)=0.45$, $p=.52$). There was an interaction between experiment and attention ($F(1,15)=7.37$, $p=.02$). This was owing to the effect of attention in Experiment 4.2 ($F(1,15)=6.52$, $p=.02$) but not 4.1 ($F(1,18)=2.86$, $p=.12$). In the comparison of Experiments 4.2 and 3.2 there was no effect of experiment on accuracy ($FI1,11)=1.33$, $p=.27$). There was an interaction between experiment and attention ($F(1,11)=7.59$, $p=.02$). This was owing to opposite directions of the attention effects in the two tasks. For experiment 3.2

accuracy was higher for valid (mean accuracy=0.94, SD=0.05) than neutral (mean accuracy=0.92, SD=0.05) trials ($F(1,11)=7.52$, $p=.02$). In Experiment 4.2 the reverse was the case, accuracy was higher for invalid (mean accuracy=0.92, SD=0.05) compared with valid (mean accuracy=0.90, SD=0.05) trials ($F(1,15)=6.52$, $p=.02$). The across-experiment comparisons demonstrate there was not a difference in difficulty to account for the differences in behaviour in Experiment 4.2.

4.2.2.2 ERP Results

The results of the Cartool segmentation are illustrated in Figure 4.3. Presentation of the target stimulus elicited clear P1 and N1 potentials, as well as two late positive P300 peaks. The first clearly observable potential, the P1, had an onset of approximately 115-125ms post stimulus at parieto-occipital electrode sites, particularly in the ipsilateral hemisphere. Following this was the N1, commencing between 155 and 185ms post stimulus maximal at the same electrode sites as the P1, though with a focus in the contralateral hemisphere. There were two prominent late potentials, the $P3_1$ (320-380ms) and $P3_2$ (450-550ms). These late positive potentials had a more broad distribution, maximal from central to occipital electrode sites.

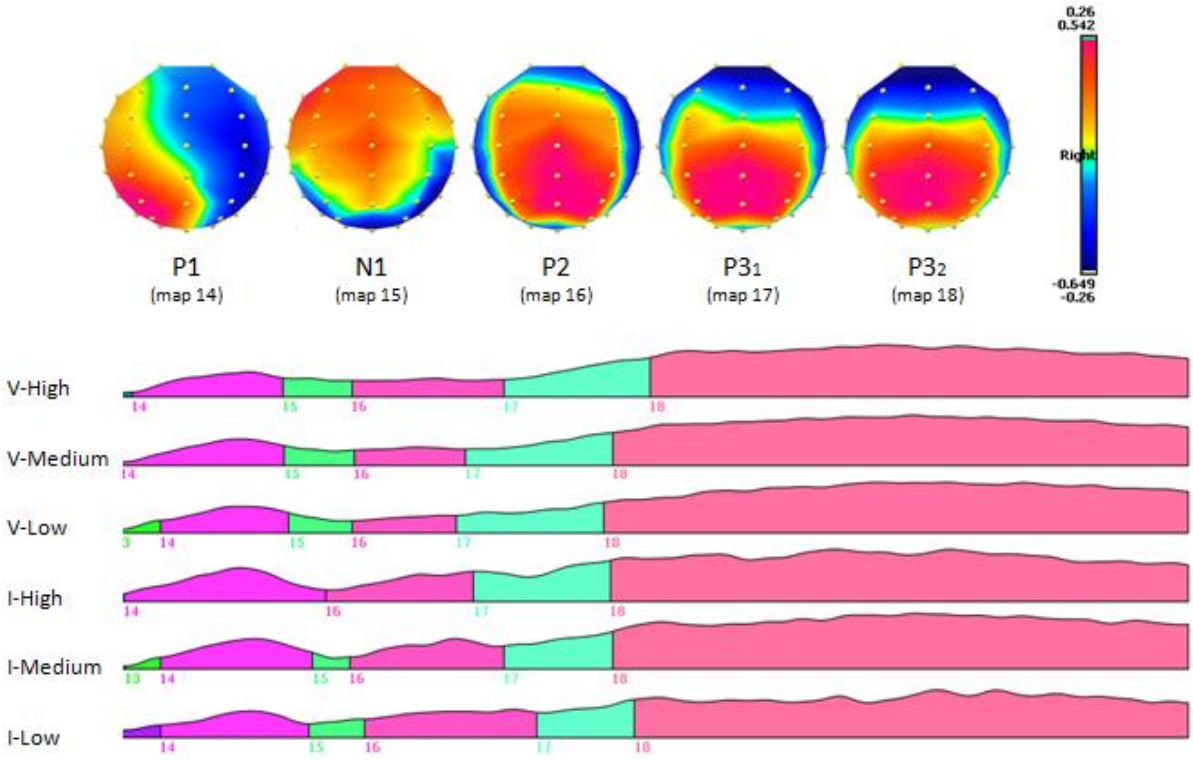

Figure 4.3: Cartool segmentation and topographical mapping from the onset of the P1 potential (approximately 100ms post stimulus) in response to the target stimulus for Experiment 4.2. The top panel shows the topographies identified for each period of topographical stability. Topographical maps show (from left) the P1 and N1 potentials, a P2 potential and two P300 subcomponents. The bottom panel shows the segmentation results for each condition, illustrating the topographical distribution of each potential were common to all conditions (with the exception of an absence of a clear N1 in the invalid-high reward condition). V refers to valid spatial location, I refers to invalid spatial location, high, medium and low refer to reward probability.

4.2.2.2.1 Early potentials

Mean amplitude analysis of visual potentials revealed no early effects of either factor (Figure 4.4). Early potentials were examined in time windows symmetrical around the peak of the potential. A prominent P1 was observed in the ipsilateral hemisphere at lateral occipital and parietal electrodes, with a peak at approximately 150ms. The P1 was analysed 115-165ms (contralateral) and 125-175ms (ipsilateral) at electrodes PO3/4, PO7/8, P7/8 and O1/2. There was no effect of attention ($F(1,15)=0.53$, $p=.48$) or reward ($F(2,30)=0.61$, $p=.50$). The two factors did not interact ($F(2,30)=0.27$, $p=.76$). There was a trend toward a linear effect of reward [linear contrast, reward-by-hemisphere interaction ($F(1,15)=3.54$, $p=.079$)] as well as a trend towards a reward-by- attention interaction [linear contrast, attention-by-reward-by-hemisphere interaction ($F(1,15)=3.45$, $p=.083$)]. However, subsidiary analyses within each hemisphere did not reveal any significant effects of reward in the ipsilateral hemisphere ($F(2,30)=1.39$, $p=.26$) or contralateral hemisphere ($F(2,30)=0.18$, $p=.76$). There were no effects of attention [ipsilateral hemisphere ($F(1,15)=0.69$, $p=.42$), contalateral hemisphere ($F(1,15)=0.34$, $p=.57$)] or interactions between reward and attention [ipsilateral hemisphere ($F(2,30)=0.92$, $p=.40$), contralateral hemisphere ($F(2,30)=0.04$, $p=.96$)].

Peak detection was performed using the same electrodes sites as employed for mean amplitude analysis. The peaks were identified within the time windows utilised in mean amplitude analysis, then confirmed and corrected, if necessary, through visual inspection. Peak latency of early visual processing was modulated by attention, but not reward. P1 latency was modulated by attention [attention-by-hemisphere interaction $F(1,15)=5.16$, $p=.04$)]. Subsidiary ANOVAs were performed to compare the effects of attention in each hemisphere. There was a trend towards an effect of attention in the ipsilateral hemisphere ($F(1,15)=3.27$,

p=.09), with P1 peaking earlier on valid (mean=152ms, standard error=3ms) compared with invalid (mean=155ms, standard error=3ms) trials. There was no effect of attention in the contralateral hemisphere (F(1,15)=2.03, p=.17).There was no effect of reward (F(2,30)=0.75, p=.46) nor did the two factors interact (F(2,30)=0.99, p=.37).

The N1 had a contralateral maximum at lateral occipital and parietal electrodes, reaching peak just before 200ms in the contralateral hemisphere and slightly later at ipsilateral electrodes. The N1 was analysed at 155-195ms (contralateral) and 185-225ms (ipsilateral) post-stimulus at electrodes PO3/4, PO7/8, P7/8 and O1/2. There was a trend toward an effect of attention (F(1,15)=3.83, p=.07), showing that the N1 potential tended to be larger in valid (mean=-0.80μV, standard error=0.53μV) compared to invalid (mean=-0.17μV, standard error=0.74μV) trials. There was no effect of reward (F(2,30)=1.40, p=.26). Attention and reward did not interact (F(2,30)=0.47, p=.62).

There were no effects upon N1 latency. N1 latency was not modulated by reward (F(2,30)=0.15, p=.86)]. There was no effect of attention (F(1,15)=0.42, p=.53). Attention and reward did not interact (F(2,30)=0.41, p=.60).

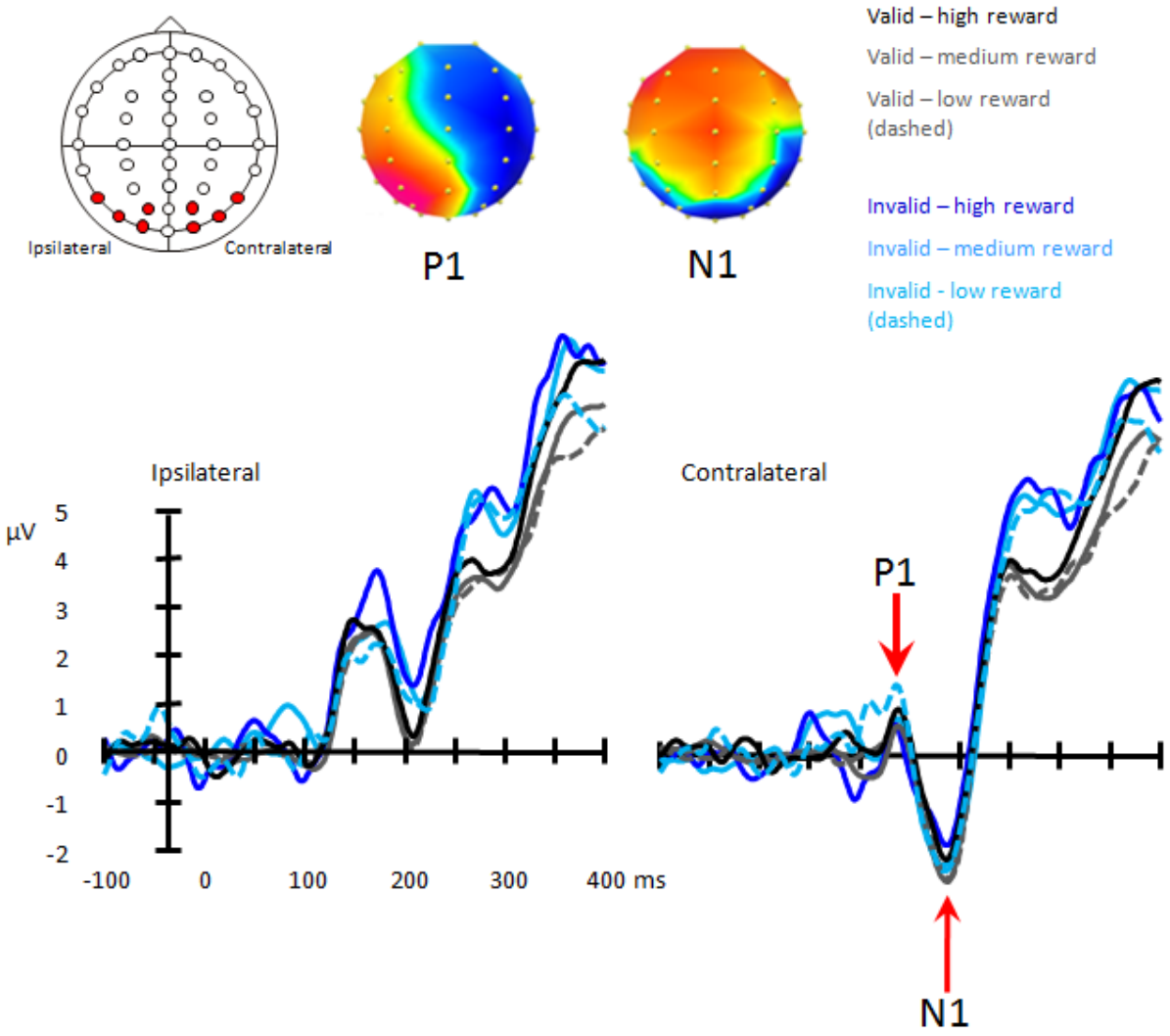

Figure 4.4: Grand average waveforms showing the early potentials produced in response to presentation of the target stimulus. Waveforms averaged across the electrodes used for analysis are shown, with ipsilateral shown on the left and contralateral on the right. Valid trials are plotted in shades of grey, invalid trials in shades of blue. The topographies for the P1 and N1 potential are shown. Electrodes used for analysis are indicated in red on the electrode montage. Positive voltage is plotted upwards.

4.2.2.2.2 Later potentials

Two distinct late positive peaks were observed after 300ms post stimulus (Figure 4.5). Both peaks showed a parietal distribution, maximal over central, parietal and occipital electrodes. It was therefore unlikely the earlier of the two peaks was the novelty-induced P3A, which is more frontal in distribution. The two peaks were therefore termed $P3_1$ and $P3_2$, respectively. The $P3_1$ peaked at approximately 360ms post-stimulus. The $P3_1$ was examined between 320 and 380ms post stimulus at electrodes C3/z/4, P3/z/4, O1/z/2. Attention and reward both modulated the amplitude of the $P3_1$. $P3_1$ amplitude was larger for invalid (mean amplitude=7.65μV, standard error=0.64μV) than valid attention (mean amplitude=6.48μV, standard error=0.72μV) ($F(1,15)=12.79$, $p<.01$). Reward increased $P3_1$ amplitude ($F(2,30)=5.10$, $p=.02$) with a linear increase in amplitude with increasing reward probability [linear contrast ($F(1,15)=8.82$, $p=.01$); high reward mean amplitude=7.70μV, standard error=0.81μV, medium reward mean amplitude=7.16μV, standard error=0.61μV, low reward mean amplitude=6.34μV, standard error=0.68μV]. There was no interaction between attention and reward ($F(2,30)=0.27$, $p=.76$).

Peak latency of later potentials was analysed in the same manner as for early potentials. Attention modulated latency of the $P3_1$ ($F(1,15)=9.13$, $p=.01$). The $P3_1$ peaked earlier for invalid (mean latency=354ms, standard error=2ms) than valid trials (mean latency=363ms, standard error=3ms). Reward did not modulate $P3_1$ latency ($F(2,30)=0.41$, $p=.66$). Reward and attention did not interact ($F(2,30)=0.95$, $p=.40$).

The second late positive component, the $P3_2$, peaked at approximately 500ms, with a distributed topography, maximal over central and posterior electrode sites, similar to that of the $P3_1$. The $P3_2$ was examined between 450 and 550ms post stimulus at electrode sites C3/z/4, P3/z/4 and O1/z/2. Reward did not modulate the amplitude of the $P3_2$ ($F(2,30)=1.64$, $p=.22$). Attention also did not modulate $P3_2$ amplitude ($F(1,15)=0.10$, $p=.76$). Reward and attention did not interact ($F(2,30)=0.90$, $p=.41$).

Attention and reward both modulated the latency of the $P3_2$ potential. This was achieved via an attention-by-reward interaction ($F(2,30)=3.61$, $p=.04$). There were no independent main effects of reward ($F(2,30)=2.46$, $p=.10$) or attention ($F(1,15)=1.72$, $p=.21$). Subsidiary analyses were used to clarify the relationship between attention and reward with respect to $P3_2$ latency. There was an effect of reward on invalid ($F(2,30)=3.46$, $p<.05$) but not valid ($F(2,30)=1.81$, $p=.19$) trials. This was a quadratic relationship ($F(1,15)=5.18$, $p=.04$), with earlier peak latency for medium reward probability (mean peak latency=486ms, standard error=8ms) than with high (mean peak latency=503ms, standard error=7ms) or low (mean peak latency=510ms, standard error=7ms) reward probability.

There was an effect of attention upon $P3_2$ latency with high reward probability ($F(1,15)=5.34$, $p=.04$). The $P3_2$ peaked earlier on valid (mean peak latency=486ms, standard error=7ms) than invalid (mean peak latency=503ms, standard error=7ms) trials. There was no effect of attention with medium ($F(1,15)=1.02$, $p=.33$) or low ($F(1,15)=2.15$, $p=.16$) reward probability.

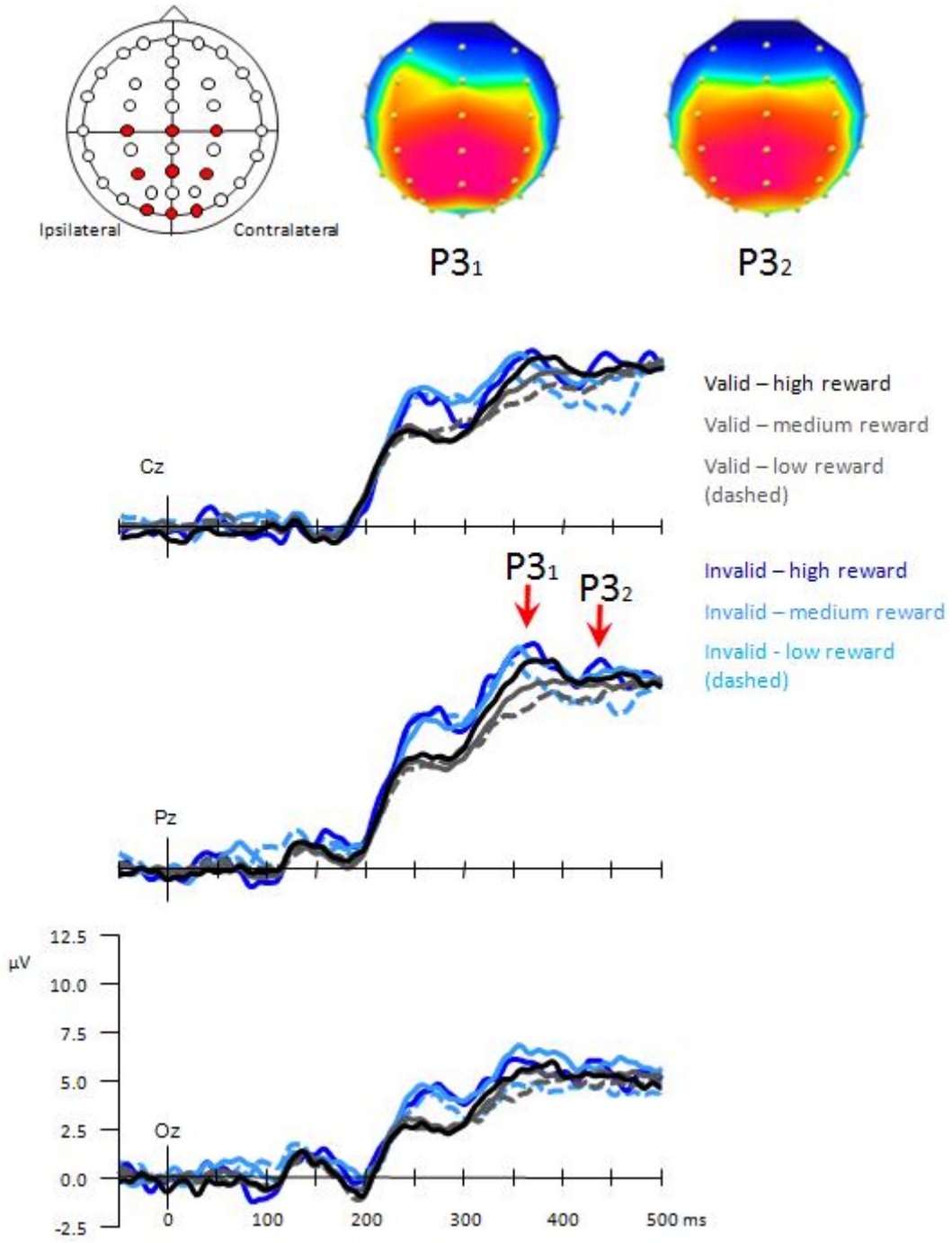

Figure 4.5: Grand average waveforms illustrating the two P300 subcomponents observed in Experiment 4.2. Waveforms at the three midline electrode sites used for analysis are shown. The topographies of the $P3_1$ and $P3_2$ are shown in the top panel. Valid trials are plotted in shades of grey, invalid trials in shades of blue. Electrodes used for analysis are indicated in red on the electrode montage. Positive voltage is plotted upwards.

4.2.3 Discussion

The behavioural effects in Experiment 4.2 differed from the previous experiments for both reward and attention. In Experiment 4.2 spatial attention was associated with behavioural improvement in the form of increased response speed for stimuli presented at the valid (expected) spatial location. This was consistent with the prevailing literature (Posner, 1980; Posner, et al., 1980), as well as with the experiments of Chapter 3. Whilst spatial attention also influenced stimulus discrimination, the effects were somewhat contrary to the initial hypothesis. Accuracy and d' were greater for stimuli presented to the invalid location. The task parameters may have been partially responsible for such an effect. In this task, high-contrast stimuli were presented at the target location, with no comparable stimulus presented to the other potential location. This may have induced a bottom-up capture of attention that was greater for stimuli presented to the unexpected location. These stimuli may have been more salient than those presented to the attended location (Hickey, et al., 2006; Luck, 1994; Luck & Hillyard, 1994b; Theeuwes, 1991). Alternatively, the location to which stimuli were more frequently presented may have been associated with degraded visual input resulting from afterimages, some form of adaptation of visual processing or inhibition of return, resulting in superior processing of stimuli presented at the less frequent location (Boynton & Whitten, 1970; Klein, 2000; Posner, Rafal, Choate, & Vaughan, 1985; Rushton, 1977).

At the behavioural level, reward did not influence any of the performance measures in Experiment 4.2, nor did it interact with attention. It is possible that reward expectation can influence behaviour when able to work through feature-based attention (as in Experiment 4.1), but not influence behaviour of its own accord. In Experiment 4.1, reward may have worked by inducing allocation of attention to the colour feature of the stimulus to boost d'

through the attention system (Blaser, et al., 2000; Rodríguez, et al., 2002). Single-unit, ERP and fMRI studies have suggested that feature-based attention may enhance responses to the attended feature dimension and suppress responding related to the ignored dimension, increasing stimulus discriminability for the attended feature (Liu, Larsson, & Carrasco, 2007; Nobre, Rao, & Chelazzi, 2006; Serences & Boynton, 2007; Treue & Martinez Trujillo, 1999; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998). Furthermore, a recent study has suggested that a colour associated with reward influences behaviour and neural activity on the subsequent trial (Hickey, Chelazzi, & Theeuwes, 2010a). Though target status was defined by shape, a colour associated with high reward on the previous trial captured attention, such that participants were faster at responding if the target was of the highly-rewarded colour, and slower to respond if the distractor was of the reward-associated colour. An N2pc potential was elicited to the stimulus baring the high-reward colour, regardless of whether this stimulus was the target or distractor. This suggested a capture of attentional resources by the feature associated with reward (Hickey, et al., 2010a). There may have been increased attention to the reward-associated colour in Experiment 4.1, leading to a selective enhancement of d' for these stimuli, particularly under conditions of reward uncertainty. Indeed some studies have demonstrated that association of non-target stimuli with task relevant features could override top-down task set, such that non-targets capture resources away from target processing (Brignani, et al., 2010; Hickey, et al., 2010a; Seiss, Kiss, & Eimer, 2009). Some degree of interaction between reward and attention systems was consistent both with the observation that the activity of certain brain regions was modulated by both reward and attention, as well as by the interactive effects of reward and attention upon behaviour reported in previous studies (Bendiksby & Platt, 2006; Della Libera & Chelazzi, 2006; Engelmann, et al., 2009; Engelmann & Pessoa, 2007; Mohanty, et al., 2008; Raymond & O'Brien, 2009; Small, et al., 2005). It was noteworthy that in Chapter 3, effects of reward were apparent in the speeding of

RT in the absence of any ability to tap into feature-based attention. It was possible, however, that the blocked association of reward magnitudes with spatial locations allowed reward to work through the attention system in Chapter 3 also, albeit through spatial rather than feature-based attention. Furthermore, reward and attention interacted to modulate RT in Chapter 3, which was further evidence for some degree of overlap between the two systems. It must be noted, however, that behavioural effects showed the concatenation of the output of several successive stages of processing, thus an interaction at the behavioural level cannot be used to argue there was no independent action of reward and attention systems within the information-processing stream. The co-opting of the attention system by reward may also account for the absence of spatial attention effects in Experiment 4.1. Removing the ability to combine reward expectation and feature-based attention in Experiment 4.2 may consequently have weakened the effects of reward upon behaviour, whilst allowing attention effects to become evident.

Alternatively, the lack of explicit reward information at the time of target presentation, rather than a feature-based attention mechanism, may explain the lack of reward effects upon behaviour in Experiment 4.2. Removal of explicit reward information has been shown to eliminate the activity observed in reward processing regions such as the ventral striatum (Huettel, Song, & McCarthy, 2005). In Experiments 3.1, 3.2 and 4.1 the reward availability or magnitude was known at the time of target presentation. This may have been necessary for reward to influence behaviour. Furthermore, the reward system is highly sensitive to timing information. Manipulation of reward delivery timing leads to considerable alterations in neuronal firing. Omission of an expected reward suppressed firing of midbrain dopamine neurons at the time of anticipated delivery. Early or late reward presentation elicited increased firing in response to delivery (Hollerman & Schultz, 1998). For this reason, changing

the indication of potential reward from the time of the target stimulus to post response may have influenced behaviour. Reward information was not available on the current trial, but effects of reward expectation may have been observed instead on the following trial. The results of Hickey et al. demonstrated the ability of reward to influence performance on the subsequent trial. In this task, however, there were no such effects, as illustrated by the lack of significant behavioural differences following a rewarded or non-rewarded trial. Participants did appear to be using the reward information in a more block-wise fashion, as intended. It was therefore likely that a feature-based attention mechanism exploited by reward, rather than the timing of reward signal, was a greater influence on behaviour in this task.

Task difficulty was unlikely to be responsible for the differences in effects across experiments. Average accuracy did not differ between Experiments 4.1 and 4.2. In addition, there was no difference in accuracy from Experiment 3.2, where robust effects of both attention and reward upon behaviour were observed.

Whereas reward had no effects on behavioural performance in Experiment 4.2, it did influence neural measures of information processing. Effects of reward were not evident upon visual analysis, but began at later stages associated with cognitive processing. Early visual processing was modulated by attention alone, with the ipsilateral P1 peaking earlier for stimuli presented at the expected location. This suggested if attention had been deployed to the location at which the target was presented, visual analysis could begin immediately. For stimuli presented at the unexpected location, attention must be disengaged and reoriented to the target location (Corbetta & Shulman, 2002; Posner, 1980; Posner, et al., 1977). Attention effects on P1 usually arise in the form of a boosting of amplitude by attention, with latency effects

commonly absent (Clark & Hillyard, 1996; Eimer, 1998; Hillyard & Anllo-Vento, 1998; Hillyard, et al., 1998; Mangun, 1995). Even when behavioural responses on a temporal order judgement task showed participants perceived two stimuli as having been presented with temporal separation, latency effects usually failed to arise (McDonald, Teder-Salejarvi, Di Russo, & Hillyard, 2005). One study, however, has reported a speeding of P1 latency by attention in a multi-sensory temporal order judgement task (Vibell, Klinge, Zampini, Spence, & Nobre, 2007). The P1 elicited in response to visual stimuli was observed to peak earlier when vision, rather than touch, was the attended modality. Vibell and colleagues (2007) suggested the temporal demands may have been at least partially responsible for the observation of latency differences in their task compared with the comparative absence in the literature at large (Clark & Hillyard, 1996; Eimer, 1998; Hillyard & Anllo-Vento, 1998; Hillyard, et al., 1998; Mangun, 1995; McDonald, et al., 2005). It was possible that the stressing of response speed in this task similarly induced a speeding of not just behavioural measures, but also information processing from the earliest stages of visual analysis.

Furthermore, consistent with this task, spatial attention was blocked in the task of Vibell et al. (2007). It was possible that using blocked attentional expectancies was an optimal parameter for the inducement of latency changes. Such small effects may not have been observable in tasks with a trial-by-trial manipulation of attention. Not only do blocked manipulations typically result in stronger modulation of perceptual potentials (Eimer, 1998), but they avoid the potential conflation of multiple successive effects that may occur in response to trial-by-trial manipulations of stimuli presented in close temporal proximity (Vibell, et al., 2007). Additionally, sampling rate may have been an important contributing factor. The higher sampling rate utilised in this task (1000Hz) and that of Vibell et al. (2007) (500Hz) in

comparison with that of Hickey and colleagues (2005) (250Hz) may have provided the additional temporal sensitivity necessary to observe the small differences in latency.

It was possible that attention optimised processing to such a degree that any effects of reward upon early processing were not observable. Alternatively, reward simply may not be able to influence visual analysis of stimuli, at least not through any direct, independent means. Though previous neuroimaging studies had demonstrated the ability of reward to increase BOLD signal in visual processing regions (Engelmann, et al., 2009; Mohanty, et al., 2008; Small, et al., 2005), the results of this task suggested this may have been via re-entrant feedback rather than direct modulation of early visual processing. Though Hickey and colleagues (2010) demonstrated a modulation of the P1 potential by reward, this was achieved through a colour-attention mechanism with a highly-salient stimulus feature. Endogenous reward expectation, of the nature manipulated in this task, did not appear to induce P1 modulation.

Effects of reward expectation emerged at later stages of processing, with modulation of the $P3_1$ and $P3_2$ potentials. Effects of reward were independent from spatial attention with respect to the earlier potential, with a shift to an interaction upon $P3_2$ latency. Reward expectation modulated both the amplitude and latency of the $P3_1$. The $P3_1$ was largest in amplitude and peaked earlier with increasing probability of reward. The posterior P300 has been hypothesised to reflect contextual updating (Donchin & Coles, 1988a; Johnson, 1986; Nieuwenhuis, et al., 2005a). The amplitude enhancement suggested a more in-depth contextual updating procedure was undertaken when reward was more likely to result from the processing of and interaction with a stimulus. This was reminiscent of the probability-scaled phasic signals of the midbrain dopamine and ACC neurons, where increased probability

of reward resulted in a greater magnitude of firing in response to reward-predicting stimuli (Amiez, et al., 2005; Fiorillo, et al., 2003). This probability-determined $P3_1$ potential may therefore reflect the reward prediction signal, which should have been largest for stimuli most highly predictive of reward (Fiorillo, et al., 2003). This was consistent with the interpretation of the P300 as indexing construction and maintenance of stimulus representations, as the midbrain-ACC reward prediction signals were integrated with reinforcement history, behavioural goals and attentional biases in the updating of stimulus-outcome representations (Rushworth & Behrens, 2008; Walton, et al., 2007; Walton, et al., 2004).

Attention also modulated $P3_1$ amplitude, and did so independently from reward. Amplitude was larger for targets presented to the low probability location. This was consistent with previous reports of the posterior P300, where amplitude was larger in response to infrequent or unexpected task-relevant stimuli (Donchin & Coles, 1988a; Johnson, 1986; Nieuwenhuis, et al., 2005a). The $P3_1$ also peaked earlier on invalid trials. The earlier peak and larger amplitude may have resulted from a more short-lived process when spatial expectations were violated, or an earlier, more intensive process. This may reflect the updating of stimulus representations to accommodate the new spatial information (Donchin & Coles, 1988a; Johnson, 1986; Nieuwenhuis, et al., 2005a).

A different mechanism appeared to underlie the modulation of the $P3_2$ potential. There were no independent effects of either factor, but rather an interactive effect of reward and attention on peak latency. Effects of reward were evident on invalid trials, with an earlier peak with medium reward probability. This suggested an earlier peak under conditions of greatest uncertainty with respect to either reward or spatial expectation, consistent with the effects of

reward upon behaviour in Experiment 4.1. New information is most informative when uncertainty is higher (Behrens, et al., 2007; Huettel, et al., 2005; Rushworth & Behrens, 2008). It was therefore likely that contextual updating was more necessary in medium reward probability blocks, or when spatial expectations were violated, resulting an in earlier peak of the $P3_2$. With respect to reward, this may reflect the activity of the striatal-OFC reward pathway. Activity in the ventral striatum in response to reward-predicting stimuli was maximal under greatest reward uncertainty (Fiorillo, et al., 2003). Furthermore, the OFC appeared active in the construction of stimulus-outcome representations, having been particularly active when the outcome of a stimulus-guided action must be monitored to determine appropriateness (Walton, et al., 2004). It was possible that in this task, the $P3_2$ modulation by reward reflected a greater necessity for contextual updating when the likelihood of reward was uncertain.

The nature of the effect was different for targets presented to the expected location. On these valid trials, the $P3_2$ peaked earlier with a high probability of reward. This suggested that separate mechanisms may take effect under conditions in which both reward and spatial expectation were highly predictable or when both factors were unpredictable. $P3_2$ peaked earlier under both greatest uncertainty and maximal certainty of a positive outcome.

The results suggested that the reward and attention systems may have prioritised different information in construction and maintenance of stimulus representations. For the attention system, importance was placed upon updating representations when spatial predictions were violated. The reward system, however, placed priority on stimuli highly likely to result in reward or when reward probability was maximally uncertain. The differences may also have

resulted from the timing of spatial versus reward information. At the time of target presentation, to which the $P3_1$ and $P3_2$ were elicited, spatial expectations had already been confirmed or violated. Reward signals, however, were not presented until after responses were made, thus still unknown at the time of stimulus presentation. The reward system, therefore, may have been intensively updating the representation of a stimulus expected to be rewarded ($P3_1$) or where reward likelihood was unclear ($P3_2$), under conditions in which reward predictions were yet to be tested and verified or violated. The interaction of reward and attention with respect to $P3_2$ latency may reflect a late-stage integration of the top-down signals of the two systems. It was possible that this late-stage integration was responsible for the interaction evident in the RT data of Chapter 3.

Overall, the pattern of effects suggested that there may have been multiple points at which reward and spatial expectations operated. The predominant effects of reward appeared relatively late in the information processing time course, upon those potentials reflecting cognitive processing. The lack of strong behavioural effects of reward suggested some aspects of the experimental design were not optimised for this line of investigation. This may have resulted from the lack of performance-related feedback. The rationale for not including this was to decouple the effects of reward expectation from feedback-induced changes in arousal or processing. Performance-related feedback may, however, be important for the integration of reward information into prediction estimates. Huettel and colleagues (2005) suggested lack of explicit feedback may have been responsible for the absence of observed striatal activation in conditions usually associated with activity in this region. Trial-by-trial performance-based feedback will thus be introduced in the next chapter. In addition, trial numbers were problematic with the probabilistic manipulation. This induced an uneven number of trials, with small numbers for some conditions (such as 0.2 reward probability). To reduce ERP noise,

more trials are desirable. Finally, the blocked probability manipulations may have introduced different subjective states across experimental blocks. To minimise the contribution of any spurious set-related effects, it would be advantageous to manipulate reward expectation dynamically, in a trial-by-trial fashion.

Chapter 5: Modulation of neural activity with trial-by-trial fluctuations in reward expectation and spatial attention.

The experiments of Chapter 4 illustrated the ability of reward expectation to modulate behaviour under time pressure and neural activity at later stages of processing. Reward did not influence early visual analysis. This suggested that reward may not exert a direct effect upon visual processing. Alternatively, it was possible that the task parameters were not optimised in Chapter 4. The lack of performance-based feedback and the non-explicit manipulation of reward and spatial expectations may have diluted the effectiveness of reward to influence behaviour and neural activity. Furthermore, the lack of outcome feedback may have been partly responsible. Some regions of the reward system, such as the striatum, showed no BOLD activation in the absence of performance-related feedback (Huettel, et al., 2005). In addition, activation of the ACC and OFC has been demonstrated to depend upon the necessity to monitor the outcome of a motor response to determine which of a set of action alternatives was the correct option. When the requirement to monitor outcomes was removed there was no observable BOLD activity in these regions (Walton, et al., 2004). For this reason, performance-related feedback was included in this experiment. Though the non-cued reward manipulation was useful in studying the learning process, the initial learning stage may have weakened statistical power by necessitating removal of early trials from analysis. Given the emphasis on the influence of learned expectations upon perceptual and later processing, the non-cued manipulation was not necessary. Explicit reward and spatial cues were therefore employed in the experiment of Chapter 5. Furthermore, the blocked manipulation of reward may have instigated changes in subjective state, such as arousal, across experimental blocks. In this experiment, reward and spatial attention were manipulated independently, on a trial-by-trial basis, to investigate the effects of each factor upon information processing under dynamically changing expectation.

This new experiment used a modified Posner cueing paradigm with explicit reward and spatial cues to examine the effects of trial-by-trial manipulation of reward expectation and spatial attention. As in the previous chapters, the two factors were manipulated independently in a factorial design. Each trial commenced with a cue that signalled both the availability of reward and the likely spatial location of the target stimulus. Performance-related feedback was also provided on a trial-by-trial basis. Independent and interactive effects of reward expectation and spatial attention were measured on potentials reflecting successive stages of information processing between perception and action. Perceptual effects were examined on the visual P1 and N1 potentials. Intermediate cognitive processing was examined with respect to the P300 potential. Given that RT was the behavioural measure most sensitive to reward, it was also of importance to examine how reward modulated motor-related activity across the time-course of a trial, and how this pattern of modulation related to that of attention. For this reason, effects of reward and attention upon the LRP were also examined in this chapter. If effects of reward are mediated through the attention system, interactions in the modulation of potentials by reward expectation and spatial attention would be expected. Independent modulation of potentials by each factor would suggest independent influences of reward expectation and attention at a given stage of processing.

5.1 Materials and Methods

5.1.1 Participants

Fourteen healthy, right-handed individuals participated in the task (mean age=23 years, range=19-31 years, five females). Participants were recruited from the University of Oxford community. Individuals participated as paid volunteers, with verbal and written consent obtained. Visual acuity was normal or corrected-to-normal. The experimental methods had ethical approval from the University of Oxford Research Ethics Committee.

5.1.2 Task Design and stimuli

Participants were required to discriminate the direction of tilt of a target grating stimulus in a Posner-style cueing task (Posner, 1980). Cues independently predicted the likely location of the upcoming target stimuli and the reward availability for correct performance. The task is illustrated in Figure 5.1.

Stimuli appeared on a grey background with a white fixation dot at the centre. Each trial began with central presentation of a symbolic compound cue (100ms, 1.25 degrees in width). Cue stimuli indicated whether the upcoming trial was rewarded or non-rewarded (100% valid; 50% of trials rewarded), and predicted the likely spatial location of the target stimulus (75% valid). The colour (red or green) and shape (plus or cross) of the cue were used for these instructions. The assignment of dimension (shape or colour) and its features to the cue meanings were counterbalanced across participants. After a variable SOA (800-1200ms), the target stimulus

was presented to the left or right of fixation (3.58 degrees from screen centre to stimulus centre, upon the horizontal meridian). Targets were black and white gratings (subtending 1.79 degrees, spatial frequency of 0.22 cycles per degree) tilted 12 degrees to the left or right of vertical, presented for two refreshes of the monitor (33 ms). Black circles with the same dimensions as gratings were used as placeholders for target presentation, and remained on the screen while no target was presented and at the unoccupied location during target presentation. Participants were required to discriminate the direction of the grating tilt using covert attention only and to respond as quickly and accurately as possible. Responses were a button-press with the index finger of the left or right hand to indicate a leftward or rightward tilt respectively. Average RT was calculated after each block and set as an RT threshold. Only correct responses that were faster than the RT threshold added money to the total earnings. Feedback was provided (100ms) by centrally presented compound symbolic stimuli (subtending 1.25 degrees). Feedback indicated whether the response was accurate and within the RT threshold. It also indicated whether the trial had been a rewarded or non-rewarded trial. This allowed the provision of information pertaining to both performance speed and accuracy and whether or not reward had been earned with the response. Stimulus shape (triangle or square) and colour (black filled or empty) were used to provide this information, with dimension meaning counterbalanced across participants. The white fixation dot remained at the centre of the screen throughout the course of trials. A variable ITI (1800-2800ms) intervened before the next trial.

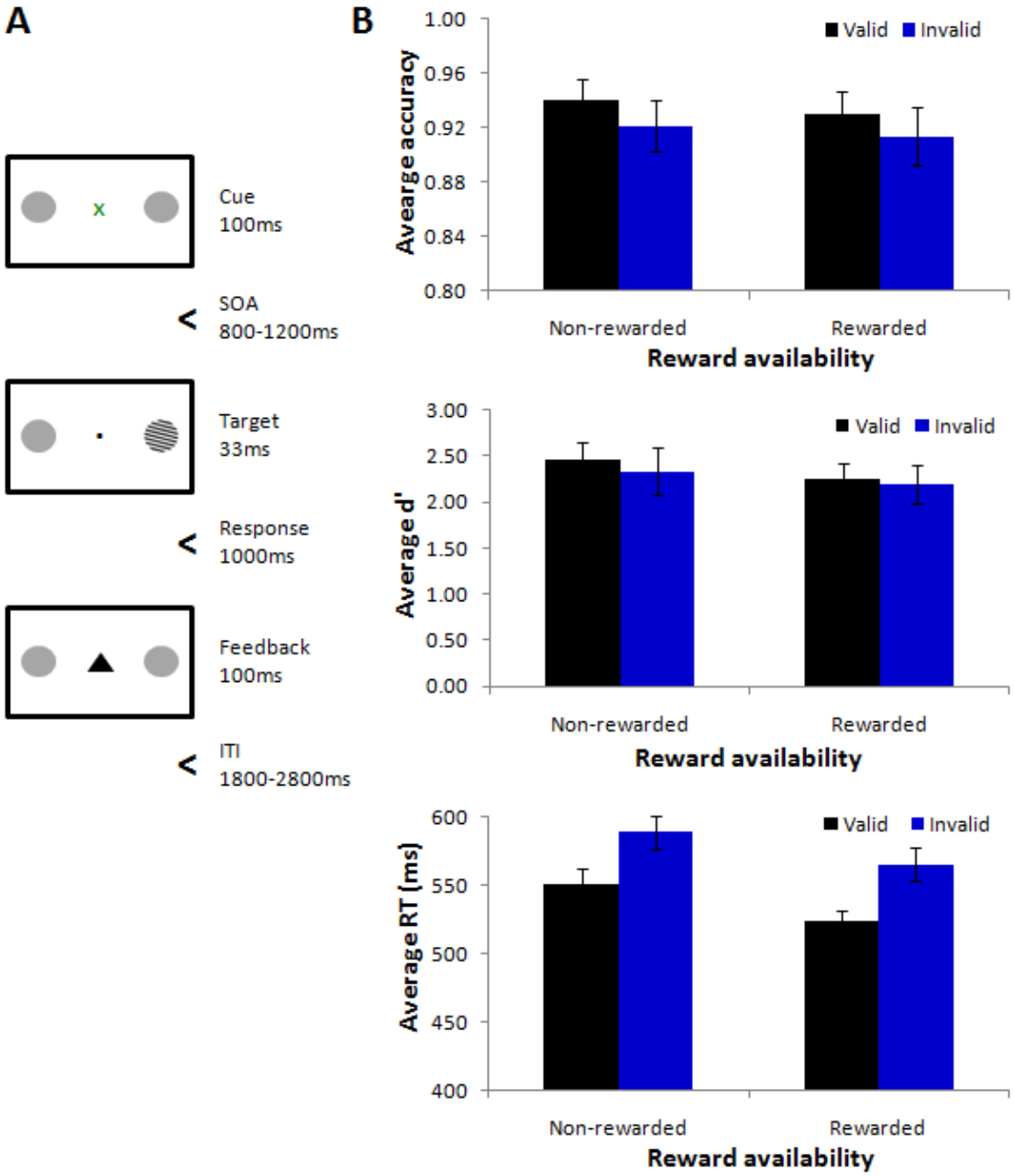

Figure 5.1: Task schematic and behavioural results for the experiment of Chapter 5. (A) Trials began with presentation of the cue (100ms). A variable SOA (800-1200ms) was followed by presentation of the target stimulus (33ms). After response, feedback was presented (100ms), followed by a variable ITI (1800-2800ms) before the next trial. (B) Graphs show the average accuracy (top panel), d' (middle panel) and RT (bottom panel) for all participants as a function of reward availability. Valid trials are plotted in black, invalid trials in blue. Error bars use the standard error of the mean.

5.1.3 Procedure

"Presentation" software (Neurobehavioural Systems, CA) was used for programming and controlling the experimental task. Participants were seated comfortably in a dimly illuminated, electrically shielded chamber, 100cm in front of a computer monitor. They were given written instructions, followed by an oral synopsis. Maintenance of visual fixation was required throughout the active phase of the task. In order to ensure this, head position was stabilised using a chin rest and gaze was monitored using a video-based infrared RK-464 eye-tracker (ISCAN, Woburn, MA). Total experimental duration, including EEG setup, was approximately three hours.

Participants completed two blocks of 20 practise trials, one before and one after EEG setup. This was followed by five experimental blocks of 160 trials. The second of the practise blocks was used to calculate the RT threshold for the first block of experimental trials. Feedback on accuracy and earnings was presented on screen at the end of each block. Participants were informed they would receive the earnings from their two best blocks. This was done to ensure motivation remained high throughout the duration of the experiment, with a maximum of £32 earnings available.

5.1.4 Behavioural analyses

The effects of reward expectation and spatial attention were tested using a repeated-measures ANOVA with two within-subjects factors: reward (rewarded, non-rewarded) and

spatial attention (valid, invalid). Accuracy, d' and RT were analysed. Only correct responses were included in the RT analysis.

5.1.5 ERP procedure

5.1.5.1 EEG recording

A high-density 128 Ag/AgCl electrode array was fixed to the head by means of an elasticated cap (www.easycap.de). Electrodes were placed at standard locations, according to the 10-5 electrode system (Oostenveld & Praamstra, 2001). Six additional electrodes were affixed to the face. HEOG was recorded from electrodes at the external canthus of the left and right eye; VEOG was recorded from electrodes placed above and below the right eye. In addition, electrodes were placed at the left and right mastoids for later offline re-referencing. Data were amplified by the Biosemi Active-Two amplifier (www.biosemi.com) and digitised at 512Hz sampling rate with 100Hz low-pass filter and 0.16Hz high-pass filter.

5.1.5.2 ERP processing

Data were processed and analysed using Neuroscan Software (Compumedics USA, Charlotte, NC). Data were re-referenced to the average of the two mastoids. Epochs were constructed commencing 1200ms before stimulus presentation and ending 600ms post-stimulus. The pre-stimulus period was set to the maximum cue-target interval, allowing examination of data for eye movements in anticipation of the target. HEOG and VEOG were derived by taking the difference between pairs of EOG electrodes by offline bipolar derivation. Trials containing

drift, deflections exceeding +/- 150μV in any channel, were excluded. Trials containing blinks, deflections greater than +/- 70μV in the eye channels, were excluded automatically by computer algorithm. Waveforms were also visually inspected, with trials containing saccades and residual blinks removed. Incorrect behavioural responses were removed also. A minimum of 30 trials per condition was set to ensure a sufficient signal-to-noise ratio. ERPs were constructed for each of the four possible combinations of attention and reward – valid rewarded, valid non-rewarded, invalid rewarded, invalid non-rewarded.

5.1.6 Statistical analysis

The effects of reward expectation and spatial attention upon information processing were subjected to repeated-measures ANOVA with factors of reward expectation (rewarded, non-rewarded), spatial attention (valid, invalid), hemisphere (ipsilateral, contralateral) and electrode. Topographical segmentation of the data using CarTool software (http://brainmapping.unige.ch/cartool.htm) was used to guide the identification of the appropriate time windows and electrodes for ERP analysis. The same parameters were used as in Experiment 4.2, except that segments less than 20 time frames were rejected. ERPs were analysed within periods of stable topographies, using the electrodes where the potentials were maximally distributed. CarTool was also used to compare the topographies of electrical activity in a given time period for different experimental conditions. The effect of experimental factors upon early perceptual stages of processing was investigated by examination of the P1 and N1 potentials at lateral occipital and parietal electrode sites. The effects of reward expectation and spatial attention on later stages of information processing focused on analysis of the P300 potential, over central electrodes. Effects on motor preparation and execution

were analysed around electrode position C3/C4 using the lateralized readiness potential (LRP), calculated using the following formula (Coles, 1989):

$$LRP = [mean(C4\text{-}C3)_{\text{left-hand movement}} + mean(C3\text{-}C4)_{\text{right-hand movement}}]/2$$

5.2 Results

5.2.1 Behavioural Results

Results are shown in Figure 5.1. Performance in the task was highly accurate, not showing much differentiation across conditions. Accuracy tended to be higher for valid (mean=0.94, SD=0.06) than invalid trials (mean=0.92, SD=0.07) ($F(1,13)=4.54$, $p=.05$). There was no significant effect of reward upon accuracy ($F(1,13)=2.52$, $p=.14$) and no interaction between the two factors ($F(1,13)<1$, $p=.87$). There was no effect on d' for attention ($F(1,13)=0.56$, $p=.47$), reward ($F(1,13)=1.86$, $p=.20$), or their interaction ($F(1,13)=0.05$, $p=.84$). RT was sensitive to both reward and attention. Responses were significantly faster for rewarded (mean=545ms, SD=44ms) than non-rewarded (mean=570ms, SD=45ms) trials ($F(1,13)=21.20$, $p<.01$). RTs were also faster for valid (mean=537ms, SD=37ms) than invalid (mean=577ms, SD=46ms) trials ($F(1,13)=30.54$, $p<.01$). The effects of the two factors upon RT were independent, with no significant interaction between attention and reward ($F(1,13)=1.43$, $p=.25$).

5.2.2 ERP results

The results of the Cartool segmentation are shown in Figure 5.2. Presentation of the target stimulus elicited P1 and N1 potentials at lateral occipital and parietal electrode sites consistent with extrastriate visual processing. The P1 reached a peak at around 140ms post stimulus. The N1 extended slightly more posteriorly in topographical distribution than the P1 and peaked at approximately 190ms post stimulus. Two late positive peaks were observed, both maximal over central electrode sites. As in Chapter 4, the distribution of the P300 potentials made it unlikely that the first peak was a novelty-induced P3A. The potentials were therefore termed $P3_1$ and $P3_2$. The $P3_1$ extended slightly more anteriorly than the $P3_2$ and peaked around 330ms post stimulus. The $P3_2$ reached a peak at approximately 515ms post stimulus. The LRP was concentrated over electrode sites C3/C4. This was a slowly-developing negative potential, maximal between 350 and 500ms post stimulus.

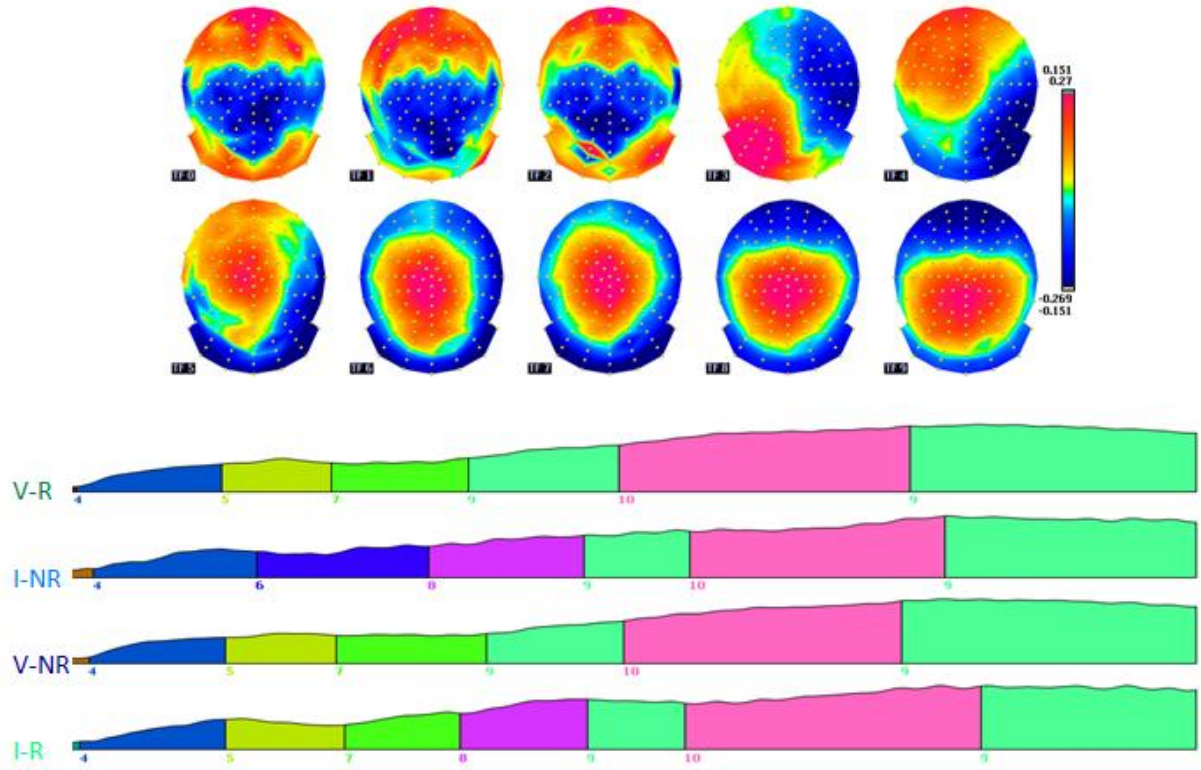

Figure 5.2: Cartool segmentation and topographical maps from the onset of the P1 potential (approximately 100ms post stimulus) for the experiment of Chapter 5. The top panel shows the topographies identified for each period of topographical stability. Topographical maps show (from left) the P1 and N1 potentials, a P2 potential and two P300 subcomponents. The bottom panel shows the segmentation results for each condition, illustrating the topographical distribution of each potential were common to all conditions. V refers to valid spatial location, I refers to invalid spatial location, R to rewarded trial, NR to non-rewarded trial.

5.2.2.1 Early potentials

The early potentials are illustrated in Figure 5.3. The first potential of interest was the P1, peaking between 130 and 140ms (depending upon hemisphere) at lateral parieto-occipital electrode sites. The P1 was analysed 20ms around the average peak latency at each hemisphere (between 120 and 140 ms contralaterally and 130 to 150ms ipsilaterally). Nine occipito-parietal electrode sites in each hemisphere corresponding to the cluster around PO7/8, PO3/4 and O1/2 were used for analysis. There was no main effect of attention ($F(1,13)=<1$, $p=.97$) or reward ($F(1,13)<1$, $p=.80$), nor did the two interact ($F(1,13)<1$, $p=.85$).

Peak detection was performed using the same electrodes as employed for mean amplitude analysis. Given the high variability of data between subjects, the peaks were identified within the time windows utilised in the mean amplitude analysis, then correct peak detection confirmed (and adjusted if necessary) through visual inspection. The peak latency of the P1 potential was not modulated by reward ($F(1,13)=2.21$, $p=.16$). Attention also did not modulate P1 peak latency ($F(1,13)=0.38$, $p=.61$). There was no interaction between reward and attention ($F(1,13)=0.20$, $p=.66$).

N1 was examined 40ms around the average peak latency for each hemisphere (160 to 200ms contralaterally and 180 to 220ms ipsilaterally). A slightly more lateral set of nine electrodes in each hemisphere than examined for P1 was used for analysis, corresponding to a cluster around PO7/8, P7/8 and O1/2. There was a significant main effect of attention ($F(1,13)=9.11$, $p=.01$). N1 amplitude was larger for valid (mean amplitude=-1.16μV, standard error=0.55μV) than invalid (mean amplitude=-0.46μV, standard error=0.59μV) trials. Though expected, there

was no interaction between attention and hemisphere ($F(1,13)=0.03$, $p=.87$). This was probably due to the time windows for analysis having been tailored to the peak in each hemisphere. There was no effect of reward ($F(1,13)=0.15$, $p=.71$). Reward and attention did not interact ($F(1,13)=2.71$, $p=.12$).

N1 peak latency was modulated by reward ($F(1,13)=5.09$, $p=.04$). The N1 peaked earlier for rewarded (mean latency=188ms, standard error=3ms) than non-rewarded (mean latency=193ms, standard error=2ms) trials. There was no effect of attention ($F(1,13)=1.93$, $p=.19$). There was no interaction between the factors ($F(1,13)<1$, $p=.45$).

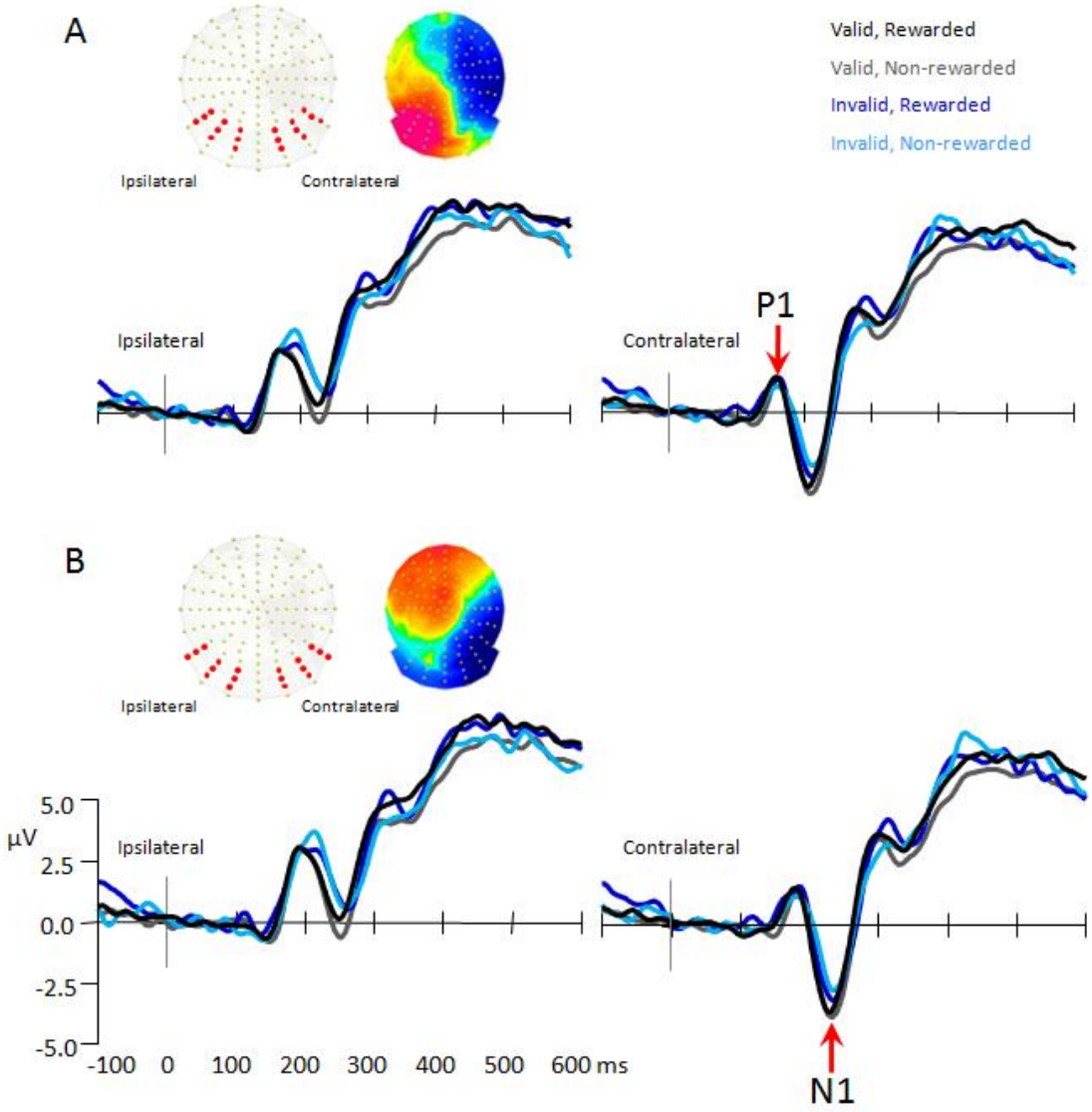

Figure 5.3: Grand average waveforms showing the early potentials produced in response to presentation of the target stimulus. Waveforms averaged across the electrodes used for analysis are shown, with ipsilateral shown on the left and contralateral on the right. The top panel shows the P1 potential, with the topography of the P1 shown above the waveforms. The bottom panel shows the N1, with topographical map above the waveforms. Valid trials are plotted in shades of grey, invalid trials in shades of blue, rewarded trials are represented by dark lines, non-rewarded trials with pale lines. Electrodes used for analysis are indicated in red on the electrode montage. Positive voltage is plotted upwards.

5.2.2.2 Later potentials

Two distinct late positive peaks were observed during the time period of the P300 potential (Figure 5.4). The first P300-like potential ($P3_1$) was prominent over central electrode sites, peaking at approximately 330ms post stimulus. It was analysed between 300 and 350ms post stimulus at four electrode sites in each hemisphere and at the midline, surrounding Cz. Reward and attention both modulated the amplitude of $P3_1$, and did so independently from one another. There was a main effect of reward ($F(1,13)=14.17$, $p<.01$). $P3_1$ amplitude was larger for rewarded (mean amplitude=9.85μV, standard error=1.06μV) than non-rewarded (mean amplitude=8.45μV, standard error=1.16μV) trials. There was also a significant effect of attention ($F(1,13)=6.83$, $p=.02$). $P3_1$ amplitude was larger for invalid (mean amplitude=10.20μV, standard error=1.32μV) than valid (mean amplitude=8.12μV, standard error =0.99μV) trials. The two factors did not interact ($F(1,13)=0.60$, $p=.45$).

Peak latency was examined in the same way as for visual potentials. Reward did not influence the peak latency of the $P3_1$ ($F(1,13)=0.38$, $p=.55$). Attention also did not modulate $P3_1$ latency ($F(1,13)=0.06$, $p=.82$). Reward and attention did not interact ($F(1,13)=0.70$, $p=.42$).

A second P300-like component ($P3_2$) occurred between 450 and 550ms post stimulus. This potential was maximal over Cz, though did differ slightly from the topography of the $P3_1$ and was identified as a separate potential by Cartool segmentation. The $P3_2$ was analysed at four electrode sites in each hemisphere and at the midline around Cz. There was a significant interaction between reward and attention on $P3_2$ amplitude ($F(1,13)=5.30$, $p=.04$). Subsidiary analyses were used to clarify the interaction. There was an effect of reward on valid

(FI1,13)=6.56, p=.02) but not invalid (F(1,13)=0.07, p=.79) trials. The $P3_2$ was larger for rewarded (mean amplitude=12.60μV, standard error=1.06μV) than non-rewarded (mean amplitude=11.31μV, standard error=1.32μV) valid trials. There was an effect of attention on rewarded (F(1,13)=7.71, p=.02) but not non-rewarded trials (F(1,13)<0.01, p=.96). $P3_2$ amplitude was larger for valid (mean amplitude=12.60μV, standard error=1.06μV) than invalid (mean amplitude=11.09μV, standard error=1.06μV) rewarded trials.

It was not possible to analyse the effects of reward and attention on $P3_2$ latency. This potential did not always reach a clear peak within the time period of analysis.

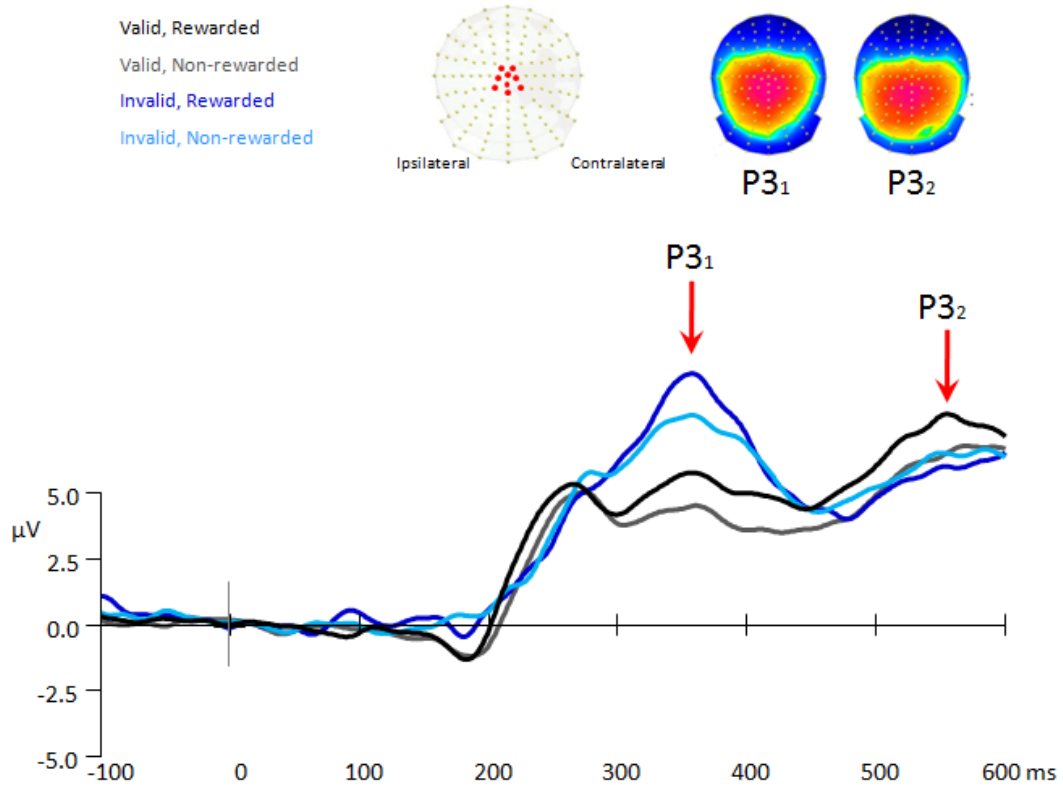

Figure 5.4: Grand average waveforms illustrating the two P300 subcomponents observed in the experiment of Chapter 5. Waveforms averaged across the electrode sites used for analysis are shown. The topographies of the $P3_1$ and $P3_2$ are shown in the top panel. Valid trials are plotted in shades of grey, invalid trials in shades of blue, rewarded trials are plotted in dark lines, non-rewarded trials in pale lines. Electrodes used for analysis are indicated in red on the electrode montage. Positive voltage is plotted upwards.

5.2.2.3 LRP

Topographical maps confirmed the LRP was concentrated over central electrode sites analogous to C3/C4 contralateral to the response hand, consistent with activation of the primary motor cortex (Figure 5.5). This was a slowly-developing negative potential, evolving from around 250ms post stimulus and peaking around 400ms post stimulus. Since RT was the behavioural measure most sensitive to the reward manipulation, the effects of reward and attention, and the relationship between the two, upon the LRP was examined. An important function of the LRP is its use as an index of where differences in processing across conditions that manifest themselves in RT differences arise. A difference in LRP onset latency suggests processing differences occur prior to response preparation commencement, whilst no difference in LRP onset latency implies divergence after response preparation begins (Miller, Patterson, & Ulrich, 1998). An onset latency analysis was thus performed, using the jack-knife procedure. This method sets an amplitude criterion value greater than amplitude would be expected to exceed by chance, with LRP onset determined as the time at which amplitude exceeds this conservative criterion (Miller, et al., 1998). Due to the high degree of noise, to which latency measures are so sensitive, no criterion value was discovered with which effects of any experimental factors or interactions between factors reached significance after corrections for multiple comparisons (all p values>.05). A less noise-sensitive method of analysis was therefore employed in this and the subsequent chapter. Sliding time windows of 50ms were used to determine the first time period during which each experimental factor modulated LRP amplitude. This also allowed examination of the relationship between reward and attention. Mean amplitude was analysed in 50ms time windows between 250 and 500ms post stimulus at four electrode sites in each hemisphere analogous to the C3/C4 position. In the 300-350ms time window reward modulated LRP amplitude ($F(1,13)=5.00$, $p=.04$). The LRP

was larger on rewarded (mean=-1.35μV, standard error=0.26μV) than non-rewarded (mean=-0.82μV, standard error=0.19μV) trials. Attention also modulated the LRP ($F(1,13)=7.02$, $p=.02$). The LRP was larger on valid (mean=-1.33μV, standard error=0.22μV) than invalid (mean=-0.84μV, standard error=0.22μV) trials. Reward and attention did not interact ($F(1,13)=0.15$, $p=.70$).

In the 400-450ms time window reward and attention interacted to modulate LRP amplitude ($F(1,13)=5.04$, $p=.04$). There was no main effect of reward ($F(1,13)=2.50$, $p=.14$) or attention ($F(1,13)=0.48$, $p=.50$). Subsidiary ANOVAs were used to clarify the interaction. There was an effect of reward on valid ($F(1,13)=14.18$, $p<.05$) but not invalid ($F(1,13)=0.17$, $p=.69$) trials. The LRP was larger for rewarded (mean=-1.72μV, standard error=0.28μV) than non-rewarded (mean=-0.84mV, standard error=0.25mV) trials. There was an effect of attention on non-rewarded ($F(1,13)=4.85$, $p=.05$) but not rewarded ($F(1,13)=1.89$, $p=.19$) trials. Contrary to the validity effect in the early time window, the LRP was larger for invalid (mean=-1.48μV, standard error=0.32μV) compared with valid (mean=-0.84μV, standard error=0.25μV) trials.

Due to the slowly-evolving nature of this potential, the peak latency of the LRP could not be analysed.

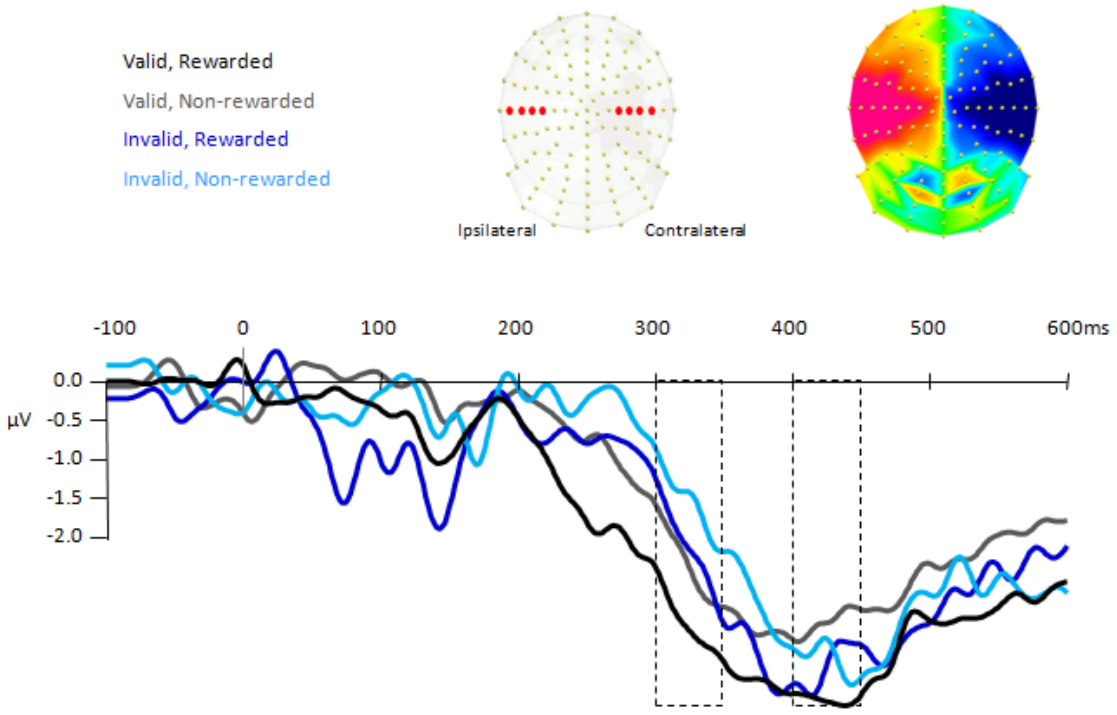

Figure 5.5: Grand average waveforms illustrating the derived LRP potential. Waveforms averaged across the electrodes used for analysis are shown. Dashed boxes illustrate the time periods during which significant modulation of LRP amplitude occurred. Valid trials are plotted in shades of grey, invalid trials in shades of blue. The topography for the valid rewarded condition is shown in the top panel. Electrodes used for analysis are indicated in red on the electrode montage. Positive voltage is plotted upwards.

5.3 Discussion

The results of this task extended those of the previous chapter by demonstrating clear effects of reward expectation and spatial attention upon behaviour and at multiple stages of information processing. In this experiment, effects of reward were evident from the early visual analysis of stimuli. Effects of reward were primarily independent from those of attention until late cognitive processing ($P3_2$, 450-550ms post stimulus) and motor preparation (the LRP). This suggested that the two systems may have operated in parallel until late stages of processing, where information with respect to reward and spatial expectations was integrated for the construction of accurate representations of the current environment and the production of responses.

The behavioural results were consistent for the most part with those of Experiment 3.2. As with Experiments 3.2 and 4.1, RT was the behavioural measure that was most sensitive to the reward manipulation. This may have been due to the emphasis on time pressure in these tasks. In all three experiments, reward and attention both reduced response speed, and did so independently from one another. As noted in chapters 3 and 4, reward information may have led to effects upon those processes most relevant to task performance, in this case RT. It must be noted, however, that the results were not entirely consistent with Experiment 3.2, where there was an interactive effect of reward and attention on RT. Task parameters, in particular the difference in cue type in this task and that of Experiment 3.2, might have been responsible for this difference. In this chapter the cue was a compound symbolic cue, so in decoding the complex cue is was more difficult or impossible to process one dimension (reward) and not the other (attention). In chapter 3 the reward was fixed for a block and associated with the peripheral spatial location, whilst attention cues were central trial-by-trial indicators of likely

target location. The attention cue could be ignored when reward was not available. The differential influence of blocked compared with trial-by-trial manipulation of reward information might also explain the difference in results from the experiments of Chapter 4. The behavioural results of this chapter suggested that when reward and attention were explicitly cued on each trial, both were able to enhance response speed and they did so independently from one another. In addition to the effects on RT, there was a clear effect of attention but not reward on accuracy, with performance higher when stimuli were presented to the cued location. This was consistent with the prevailing literature (Posner, 1980; Posner, et al., 1977) and with the experiments of Chapter 3.

The consistency of the reward effect on RT with explicit reward cues (this chapter and Experiment 3.2) was strongly indicative that the absence of robust behavioural effects in Chapter 4 was indeed the result of the non-cued manipulation of reward and spatial probabilities. It was possible that under greater reward uncertainty, d' was the more sensitive behavioural measure (Experiment 4.1), whilst with explicit cues it was RT on which the greatest effects were manifest. A recent study by Padmala and Pessoa (2010) suggested the relationship between attention and motivation may be greatly dependent upon task parameters. In their task, participants were rewarded only for correct performance on go trials of a stop-signal RT task. Behavioural data and the interaction between inhibition and motivation on BOLD activation in several brain regions, including inferior frontal gyrus, inferior parietal lobe, IPS and the putamen, suggested that in this paradigm, participants found it more difficult to withhold a response during rewarded trial blocks compared with those in which no reward was available. Thus rather than reward expectation improving performance, as in other studies (Della Libera & Chelazzi, 2006; Engelmann, et al., 2009; Engelmann & Pessoa, 2007; Raymond & O'Brien, 2009), in this case it was detrimental to never-rewarded stop

performance. The inclusion of trial-by-trial feedback in this task may also have strengthened the behavioural effects. Brain activity has been demonstrated to differ depending upon whether or not feedback was included to guide behaviour (Huettel, et al., 2005). The exact pattern of effects upon behaviour may therefore depend upon task parameters, with stronger effects apparent with the use of explicit cues, and greater independence of the two systems when both reward and attention were manipulated trial by trial.

In this chapter, reward was demonstrated to influence neural activity at multiple stages from perception to action, beginning with early visual analysis of stimuli. Reward modulated the latency of the N1 potential, such that peak was reached earlier for rewarded stimuli. The N1 is thought to index discriminative processing of visual stimuli (Hopf, et al., 2002). The results thus indicated discriminative processing may have been more rapidly instigated when reward was anticipated. This was consistent with the argument that reward targeted processes most pertinent to optimal task performance, given the necessity to correctly and rapidly discriminate the tilt of the target grating in order to maximise earnings on this task. This early effect of reward demonstrated the ability of the reward system to modulate visual processing on a trial-by-trial basis.

At the early visual analysis stages of processing, the effects of reward and attention were independent. Whilst both reward and attention modulated the N1 potential, the modulation by each factor was achieved through different means. Reward modulated peak latency whilst attention modulated the amplitude of the N1. This amplitude enhancement with attention suggested more in-depth processing for stimuli presented to the expected location. This was

consistent with the enhancement of visual processing typically observed with attentional cues of this nature (Posner, 1980; Posner, et al., 1977).

A potential pathway by which modulation of visual processing by reward may have occurred was via the striatal-OFC circuit. Several aspects of striatal and OFC activity implicated these regions with a potential role in the sensory-related N1 latency modulations. The OFC receives sensory input and is a site of integration of sensory and motivational information (Kringelbach, 2005; O'Doherty, 2004; Rushworth & Behrens, 2008). Thus whilst some prefrontal cortical regions appear to code reward value in relation to stimulus-response requirements, reward value in OFC appears to be linked to stimulus-reward associations (O'Doherty, 2004; Rushworth & Behrens, 2008). The OFC and striatal dopaminergic neurons code and dynamically track the current relative value of a stimulus, in terms of context-dependent representations (Kringelbach, 2005; O'Doherty, 2004; Robbins & Everitt, 1996; Rushworth & Behrens, 2008; Schultz, et al., 1998; Tobler, et al., 2005). These regions displayed high activation when a stimulus reward value was high, such as a food item under conditions of hunger. When individuals were fed to satiety with that item, however, activation in this reward circuit diminished (Kringelbach, 2005; Mohanty, et al., 2008; O'Doherty, 2004). It was possible that this value-dependent activity was also able to track the trial-by-trial variations in reward expectation in this task, and use this expectancy information to modulate activity in extrastriate visual cortex. These regions also appeared to encode reward expectation. Reward prediction error signals were encoded by the ventral striatum (Hollerman & Schultz, 1998; Hollerman, et al., 1998; Schultz, et al., 1998; Tremblay, et al., 1998). An unexpected reward elicited an increase in firing, whilst the absence of an expected reward induced firing suppression. These factors suggested that the striatal-OFC pathway may have been able to

track fluctuations in expected reward dynamically and to use this information to influence visual processing, evident in the N1 latency modulation (Hopf, et al., 2002).

Reward expectation continued to influence neural activity at later stages of processing. The amplitude of both late positive P300-like potentials was enhanced for rewarded relative to non-rewarded trials. For the earlier $P3_1$ potential, this was independent from the action of the attention system, consistent with the independent enhancement of this potential observed in Experiment 4.2. With the proposed role of the P300 in contextual updating, this suggested stimuli associated with reward received priority for encoding into working memory, or were valued more highly in the construction and updating of stimulus representations (Donchin & Coles, 1988a; Johnson, 1986; Nieuwenhuis, et al., 2005a; Yeung & Sanfey, 2004). Attention also modulated the $P3_1$, with amplitude larger for invalid spatial cues. This was consistent with the observed attentional modulation of the $P3_1$ in Experiment 4.2. Increased P300 amplitude has been observed for less probable, infrequent or novel stimuli (Donchin & Coles, 1988a; Johnson, 1986; Nieuwenhuis, et al., 2005a). Presentation to the invalid location comprised only 25% of trials in this task, which may have induced this effect. As with earlier processing stages, the effects of reward and attention modulated $P3_1$ independently. This suggested stimulus-outcome representations may be constructed and updated independently by each system. This may allow for the independent biasing of early visual analysis observable in the independent effects of reward and attention on the N1 potential, by means of separate top-down pathways from PFC. The consistency of the independent effects of reward and attention on $P3_1$ amplitude in this task and Experiment 4.2 suggested a robust effect that was not as susceptible to paradigm changes as behavioural measures and visual processing. This further demonstrated that reward was able to influence contextual updating with dynamically-changing reward expectation, not just with the blocked probability of Chapter 4. This

suggested reward history was updated on a trial-by-trial basis, at least when a target was associated with reward.

In the later $P3_2$ time window, the effects shifted from independence to interaction. As with $P3_1$, reward boosted amplitude, however at this stage of processing it did so in interaction with spatial attention. Amplitude of this late positivity was largest in the valid rewarded condition. This suggested a further boosting of activity resulted from the combined enhancement of the two systems on valid rewarded trials. It was noteworthy that whilst the reward effects remained consistent with the enhancement by reward of $P3_1$ amplitude, the attention effect shifted from greater amplitude of $P3_1$ for invalid trials to greater $P3_2$ amplitude for valid trials, when the valid spatial cue was coupled with expectation of reward. It was possible that early contextual updating was influenced by stimulus location invalidity, with priority granted to those stimuli violating spatial expectations. This may have been a more rapid process than the updating of representations with respect to those stimuli that conformed to spatial expectations, thus this later effect was observed on the $P3_2$ amplitude. Given the greater need to update expectations when predictions were violated, the earlier influence of invalid stimuli was understandable. This late interaction between reward and attention systems was consistent with an interactive effect on $P3_2$ latency in Chapter 4, though the nature of the relationship differed on this task. The interaction in Experiment 4.2 appeared to prioritise updating under greater conditions of uncertainty, whereas in this task validation of reward and spatial expectations led to amplitude enhancement. This may have been induced by task differences, or it might be that the $P3_2$ amplitude is influenced by certainty and the latency by uncertainty. In this task, it appeared that at this late processing stage the reward and attention systems acted to construct a coherent stimulus-outcome representation that encompassed both reward expectation and spatial location information, with the greatest

emphasis on rewarded stimuli appearing at the expected location. It was these stimuli that were most likely to result in reward, given the ability of both reward and attention to speed RT, thus these stimuli may have been most greatly favoured in the contextual updating process at this late time period.

Despite grand-average waveforms indicating a potential difference in LRP onset latency as a function of reward, no effects reached significance. This was likely due to the combination of small differences in onset and high noise in the waveforms. The lack of onset differences was perhaps surprising, given the faster RTs observed with reward available. LRP onset latency is an important index of the time at which such differences between conditions may evolve. The lack of onset latency differences may be interpreted as processing divergences resulting from differences that began after response preparation began (Miller, et al., 1998). Such an interpretation must be made with caution, however. It is possible that earlier differences did arise, but were not evident in the data due to the high degree of noise around the time of LRP onset.

LRP amplitude was, however, influenced by both reward and attention. Initially, the effects of reward and attention were independent. Reward enhanced LRP amplitude, suggesting that a greater degree of motor preparation occurred when reward was expected. This was consistent with the speeding of RTs on rewarded trials. Attention also enhanced LRP amplitude, such that targets occurring at the expected location were associated with greater motor preparation. As with the reward effect, this was consistent with the behavioural results. Later motor preparation, however, was modulated by reward and attention in an interactive manner. Reward was observed to boost motor preparation for targets occurring at the expected

location. This was consistent with the ability of both reward and attention to speed responses, suggesting that perhaps at late stages of motor preparation the reward and attention systems interact to induce the greatest enhancement of processing on those trials on which reward is most likely to result, or when both reward and spatial expectations are confirmed. Interestingly, the effects of attention presented an alternative pattern. There was an increase in LRP with invalid targets on non-rewarded trials. This may be the result of some attempts by the reward and/or attention systems to compensate for the violations of reward and spatial expectations. This would be consistent with the observation of a more rapid resetting of the attention system following low reward (Della Libera & Chelazzi, 2006).

The results of this chapter demonstrated the ability of reward to modulate multiple stages of information processing under dynamically changing expectations. Reward expectation was able to influence early visual processing in a manner independent from the effects of attention. The effects of reward expectation and spatial attention remained relatively independent until late in the information processing time course. It was possible that the two systems worked primarily in parallel to boost those stages of processing deemed most necessary for optimal task performance. At a late stage of processing, an interaction between the two systems occurred, where a cohesive representation of the current stimulus and outcome environment was constructed, inclusive of both reward and attentional biases. The differences between this task and the effects observed in chapters 3 and 4 suggested that the exact pattern of modulation may have depended upon task requirements and stimulus parameters (Della Libera & Chelazzi, 2006; Engelmann, et al., 2009; Engelmann & Pessoa, 2007; Mohanty, et al., 2008; Padmala & Pessoa, 2010; Small, et al., 2005). Whilst the dynamic cueing paradigm employed in this chapter was more reminiscent of an actual environment than the previous chapters, stimuli are unlikely to be presented in isolation often. In the next

chapter, the ability of reward expectation to influence neural activity during the search for a target stimulus amongst multiple distractor items will be examined.

Chapter 6 – Reward expectation as a modulator of visual search

The experiments in chapters 3 to 5 demonstrated the ability of reward expectation to influence behaviour as well as multiple stages of neural processing, with effects beginning during early visual analysis of target stimuli. Reward appeared to modulate information processing primarily independently from the effects of the attention system. The two factors modulated separate aspects of the N1 potential in Chapter 5 and exerted independent effects on the $P3_1$ in the experiments of chapters 4 and 5. There appeared to be some degree of interaction between reward and attention during late cognitive processing, however, as evident in interactive effects upon $P3_2$ amplitude (Chapter 5) or latency (Chapter 4). It was possible that the two systems were primarily independent, but information regarding reward and attention was integrated at a late processing stage to create and maintain a cohesive stimulus representation that included both reward and attentional information. Whilst chapters 3 to 5 demonstrated the ability of reward to influence behaviour and information processing, as well as the relationship between reward and attention, stimuli are unlikely to appear in isolation often. Rather, multiple stimuli are usually present in a visual scene. Stimuli are therefore in competition for processing resources. This necessitates the prioritisation for processing of those stimuli currently of greater task relevance. This chapter therefore manipulated reward association of target and distractor items in a multi-stimulus array to examine the effects of motivational factors upon information processing during visual search.

The allocation of attention was one way in which competition for resources could be biased towards a stimulus. This could be achieved by bottom-up capture of attentional resources by stimuli of greater salience than the others in a multi-stimulus array (Hickey, et al., 2008; Hickey, et al., 2006; Kiss, et al., 2008a; Theeuwes, 1991). Salient stimuli may even capture

attention away from a less salient but task-relevant target stimulus. The introduction of more salient non-targets into an array containing a target stimulus delayed responses (Theeuwes, 1991). The N2pc, a lateralised component thought to index visual search, produced in response to a more salient non-target stimulus preceded that elicited by a target stimulus (Hickey, et al., 2006). This suggested that attention could be captured in a stimulus-driven manner by the more salient stimulus, even when that item was not the task-relevant target at that time.

It was unlikely, however, that only bottom-up factors could drive attentional capture. Attentional capture has also been shown to be contingent upon the degree to which a distractor matches the current task set (Folk, Leber, & Egeth, 2002; Folk & Remington, 1998; Folk, Remington, & Johnston, 1992; Yantis, 1993). Attentional allocation appeared to be scaled to the degree of similarity between a stimulus and top-down task set. Distractor singletons presented concurrently with targets elicited an N2pc, albeit smaller than that elicited by the target, when distractor and target were of the same stimulus dimension (Luck & Hillyard, 1994a, 1994b). These dimension-matched non-targets also reduced the N2pc produced to target singletons, and thus appeared to have captured some of the processing resources that may otherwise have been allocated to the target (Luck & Hillyard, 1994a, 1994b; Telling, Kumar, Meyer, & Humphreys, 2010). Amplitude of the distractor-elicited N2pc was more greatly attenuated or absent with increasing discrepancy between distractor and target stimuli (Kiss, et al., 2008a). Spatially non-predictive yet salient singletons presented prior to a target stimulus in spatial cueing paradigms also attracted attention, but did so only if they matched the target dimension. This was evident in faster RTs and lower error rates for targets presented to the distractor location in spite of the fact that non-targets were not predictive of target location. Attending to them may in fact be detrimental to task performance (Eimer, Kiss,

Press, & Sauter, 2009). Cueing effects were absent for singletons of task-irrelevant dimensions (Eimer, et al., 2009). Peripheral, non-salient, task-irrelevant items also captured attention when they matched task-defining target attributes. Furthermore, these items elicited an N2pc indistinguishable from that elicited by target items (Brignani, et al., 2010). The results suggested attentional capture could be modified by top-down task set, with more resources being allocated to those stimuli that most closely matched the current target stimulus (Kiss, et al., 2008a).

The ability of top-down task set to modulate attentional capture suggests that stimulus information, such as salience, is not the only factor by which stimuli in an array may be prioritised for processing. Indeed, distractor stimuli sharing completely abstract semantic associations with target stimuli have been shown to receive priority over non-associated stimuli. Such stimuli disrupted target selection and were recalled more frequently than non-associated items (Moores, Laiti, & Chelazzi, 2003; Telling, et al., 2010). Target stimuli defined in purely abstract terms, such as word stimuli, also produced an N2pc (Eimer, 1996). It is therefore possible that motivational factors, such as the reward associations carried by stimuli, may influence visual search. Two recent studies in which singleton targets were associated with high or low reward demonstrated this to be the case (Hickey, et al., 2010a; Kiss, Driver, & Eimer, 2009). Responses were faster for high- than low-reward stimuli. In addition, the N2pc began earlier and was larger in amplitude for high-reward stimuli (Kiss, et al., 2009) or was elicited in response to the stimulus baring a colour associated with reward on the previous trial. The experiment in this chapter builds on these findings by investigating the ability of reward associations to influence neural processing during visual search in the absence of any other, additional bottom-up factors to drive capture. The design systematically manipulated the reward association of both target and distractor stimuli that were matched for salience.

Rather than using pop-out targets in a homogenous stimulus array (or an array containing a highly salient distractor in the case of Hickey et al., 2010), this experiment employed a more difficult feature-search task based on stimulus shape.

The aim of this experiment was to chart the time course of reward-association effects on processing during visual search. A primary objective was to examine the way in which associating a target stimulus with reward influenced behavioural performance and processing of that stimulus. In addition, the effects of associating task-irrelevant distractor stimuli with reward were examined. Independent manipulation of both target and distractor reward association allowed examination of reward-association effects when identical stimuli were relevant or irrelevant for task performance. It also allowed examination of the relationship between the effects of target and distractor reward association. The task required participants to detect the presence or absence of an abstract sample shape in an array of similar items. The presence or absence of the target in the array as well as the reward association of the target and/or one of the three distractors varied on a trial-by-trial basis. By using stimuli that differed only in shape, any differences in low-level visual qualities were controlled. Visual search should thus be guided by the top-down representation of the target stimulus. The N2pc was utilised as an index of visual search. To study the effects of reward association on later processing the P300 was also examined. The LRP was inspected to test the effects of reward on motor processing. The P1 and N1 potentials were also examined to test for differences in early perceptual processing with changing reward expectation. ERPs evoked by both the sample stimulus and array presentation were examined.

6.1 Materials and Methods

6.1.1 Participants

Fourteen healthy, right-handed (mean handedness = 74.79, (Oldfield, 1971)) individuals participated in the task (mean age = 25 years, range=17-33 years, 10 females). Participants were recruited from the University of Oxford community. Individuals participated as paid volunteers, with verbal and written consent obtained. Visual acuity was normal or corrected-to-normal. Experimental methods were non-invasive and had ethical approval from the University of Oxford Research Ethics Committee.

6.1.2 Task Design and Stimuli

The task is depicted in Figure 6.1. Participants were required to search a visual array of four stimuli covertly for a previously presented sample item, whilst maintaining central fixation. A target that matched the sample stimulus was present on 50% of trials. In target-present trials, the target was rewarded on half of the trials (reward target) and had no reward association on the remaining trials (non-reward target). On target-absent trials, a correct response of absent for a reward target would still add to participants' earnings. In both target-present and target-absent arrays, one of the distractors could be a stimulus that acted as the relevant sample in other trials. These possible sample stimuli carried reward association on one third of the trials (reward distractor), had no reward association on one third (non-reward distractor) and were all foil stimuli never acting as the sample on the remaining one third of trials (foils only distractors). When the sample was present in the array, the distractor was always in the other visual hemifield. The remaining two or three stimuli in the array never acted as samples and

carried no reward association (foils). The design was fully factorial, and manipulated target reward type (reward, non-reward), distractor type (foils only, reward, non-reward), and target presence (target-present, target-absent).

A trial began with a centrally-presented asterisk (500-1000ms) to indicate trial onset. This was followed by the central presentation of a sample stimulus (200ms, subtending 1.72 degrees visual angle), which was a white closed-contour non-verbalisable shape (Endo, Saiki, Nakao, & Saito, 2003). Following a variable SOA (500-1000ms), a 2 x 2 array of peripherally-presented items was displayed (200ms). All shape stimuli had the same dimensions as the sample, with array stimuli presented at 2.58 degrees eccentricity and 2 degrees elevation. Participants were required to make a speeded button press, using the index finger of one hand to indicate if the sample item was present in the array and the index finger of the other hand if the sample was absent. Hand response assignment was counterbalanced across participants. A variable ITI (500-1500ms) intervened before commencement of the next trial. Trial types were presented in randomised fashion. Participants were required to make speeded discrimination responses to the presence or absence of the sample within the array and were instructed to respond as quickly and accurately as possible. Participants were shown the two sample stimuli for which correct responses would earn reward and instructed to learn these shapes prior to commencement of the experiment. The stimuli used as rewarded samples, non-rewarded samples and foils were counterbalanced across participants. Participants completed a practise block of 64 trials to familiarise themselves with the task and to solidify their learning of the possible sample-reward associations. Following practise, eight blocks of 96 trials each were presented. Each block was initiated by the participant, allowing for breaks between blocks to avoid fatigue and rest the eyes. Since in previous experiments of this thesis it was found that reward-related effects became more pronounced under time pressure, an RT threshold was

set for correct responses. The average RT during the practise trials was calculated and set as a threshold, with participants instructed their responses on reward trials would have to be faster than this value, in addition to correct, in order to add money to their earnings. Participants were informed that reward would be calculated on the basis of their fast correct responses, with total potential earnings of £32. Feedback as to accuracy was provided at the end of the practise block.

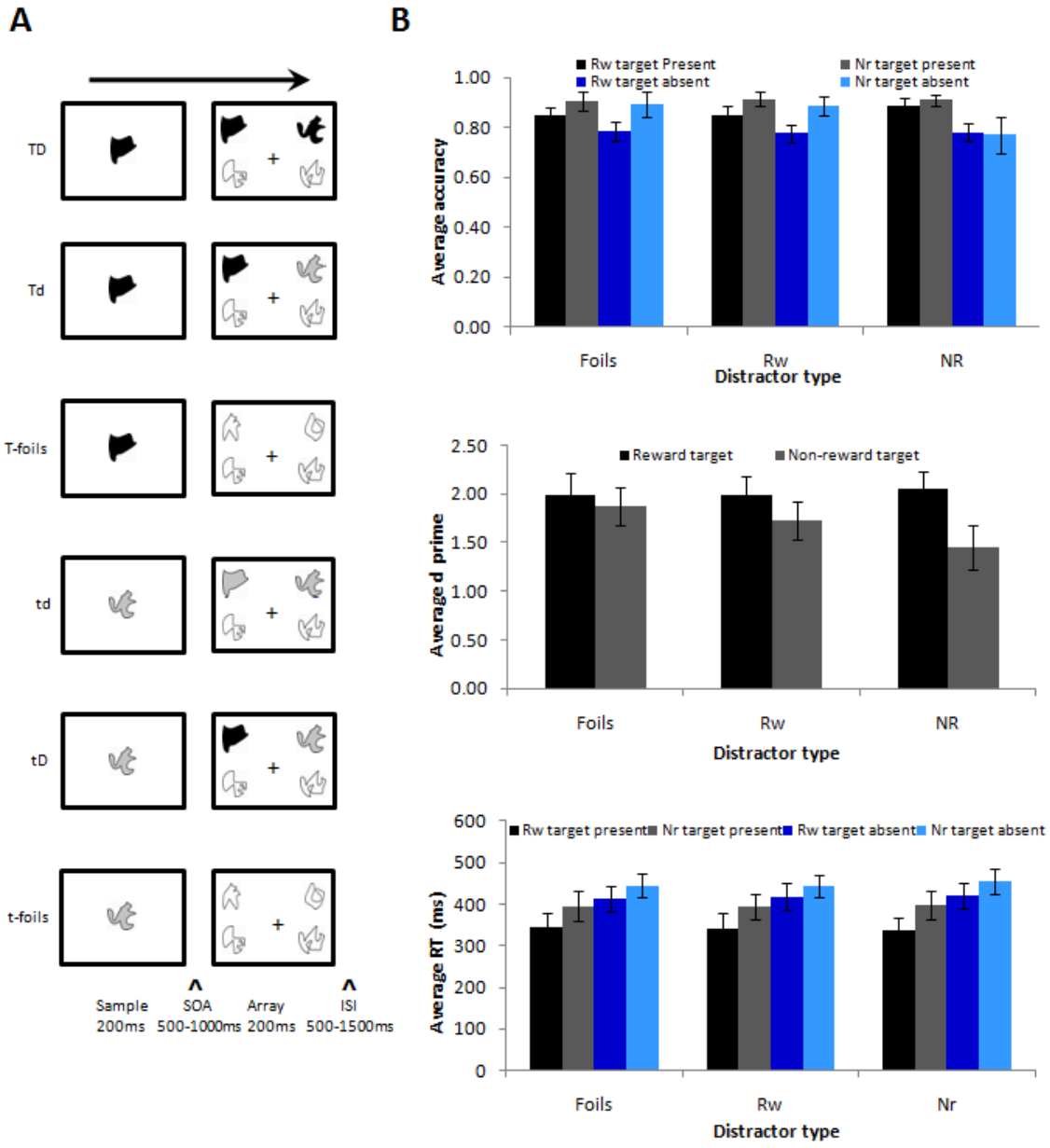

Figure 6.1: Task schematic and behavioural results for the experiment of Chapter 6. (A) The panels from left to right illustrate the time course of a trial. Each trial began with presentation of the sample stimulus (200ms). After a variable SOA (500-1000ms) the multi-stimulus array (200ms) was presented. A variable ITI (500-1500ms) intervened before the next trial. The panels from top to bottom depict the different possible combinations of target and distractor reward association. T denotes target, D denotes distractor, upper-case letters denote rewarded, lower-case letters denote non-rewarded. Note that stimuli were not coloured during the actual experiment, colour is used here for illustrative purposes only. (B) Graphs show the average accuracy (top panel), d' (middle panel) and RT (bottom panel) for all participants as a function of distractor type. Present trials are plotted in shades of grey, absent trials in blue, rewarded target trials are plotted with dark bars, non-rewarded target trials with pale bars (Rw indicates rewarded, Nr indicates non-rewarded). Error bars use the standard error of the mean.

6.1.3 Procedure

"Presentation" software (Neurobehavioural Systems, CA) was used for task preparation and presentation. Participants were seated comfortably in a dimly illuminated, electrically shielded chamber, 100cm in front of a computer monitor. They were given written instructions, followed by an oral synopsis. Maintenance of visual fixation was required throughout the active phase of the task. In order to ensure this, head position was stabilised with use of a chin rest, and gaze was monitored using a video-based infrared RK-464 eye-tracker (ISCAN, Woburn, MA). Participants were instructed to refrain from blinking and moving their eyes during the active phase of the experiment.

6.1.4 Behavioural analyses

The effects of reward association were tested using a repeated-measures ANOVA. A two (target presence: present, absent) by two (target reward type: reward, non-reward) by three (distractor type: foils, reward, non-reward) factorial design was used for the analysis of accuracy and RT, and a two (target reward type: reward, non-reward) by three (distractor type: foils, reward, non-reward) factorial design for d'. To calculate d', the hit rate was defined as the probability the participant responded "target-present" given the target was present. The false-alarm rate was the probability participants responded "target-present" given the target was absent (Green & Swets, 1966). D' was calculated using hit and false alarm rate by the equation:

$$d' = \frac{1}{\sqrt{2}}[z(H) - z(F)]$$

(Engelmann & Pessoa, 2007).

Only correct responses were included in RT analysis.

6.1.5 ERP Procedure

6.1.5.1 EEG recording

Continuous EEG was recorded using NuAmp amplifiers (Compumedics USA, Charlotte, NC) from 40 Ag/AgCl electrodes affixed to the head by means of elasticated cap (www.easycap.de). Electrodes were positioned according to the 10-20 system, with a montage that included seven midline sites (Fz, FCz, Cz, CPz, Pz, POz and Oz) and 13 sites over each hemisphere (F3/F4, F7/F8, FC3/FC4, FT7/FT8, C3/C4, T7/T8, CP3/CP4, TP7/TP8, P3/P4, P7/P8, PO3/PO4, PO7/PO8, and O1/O2). Electrodes were placed lateral and horizontal to the eyes to monitor blinks and eye movements. Additional electrodes served as ground (AFz, positioned between FPz and Fz) and reference (A1 and A2 mastoid sites, with A2 serving as the active online reference). Electrode impedances were maintained below 5kΩ. Activity at each electrode site was sampled every 1ms (1000Hz analog-to-digital sampling rate). A 300Hz low-pass filter was used during continuous EEG recording. Digital stimulus presentation codes were sent to the EEG acquisition computer via parallel port from the stimulus presentation computer, indicating the type and exact time of presentation for each stimulus.

6.1.5.2 EEG processing

EEG was re-referenced offline to the average of the left and right mastoids. Bipolar EOG signals were derived by computing the difference between the voltage at electrodes above and below the eye (VEOG) and at either side of the eye (HEOG). Transformed re-referenced data were filtered using a 40Hz low-pass filter to remove high-frequency noise.

Epochs were constructed commencing 100ms before sample stimulus or array presentation and lasting until 700ms post sample or 500ms post array. Trials containing drift, deflections exceeding +/- 150μV in any channel, were excluded. Trials containing blinks and eye movements were removed via a process of two iterations. Initially deflections greater than +/- 70μV in HEOG and VEOG were excluded automatically by computer algorithm. In addition, trials were visually inspected for the occurrence of saccades before or after target presentation. This procedure ensured that systematic eye movements did not influence the results. Trials containing incorrect behavioural responses were removed also. A minimum of 30 trials per condition per participant was set to ensure a sufficient signal-to-noise ratio.

6.1.6 ERP analysis

Topographical segmentation of the data using CarTool software (http://brainmapping.unige.ch/cartool.htm) was used to guide the identification of the appropriate time windows and electrodes for ERP analysis. ERPs were analysed within periods of stable topographies, using the electrodes where the potentials were maximally distributed. CarTool was also used to compare the topographies of electrical activity in a given time period

for different experimental conditions. The same parameters as used in Chapter 5 were employed. Statistical analyses were performed using the mean voltage value surrounding the peak of the potentials of interest as well as the mean peak latency. The effects of reward association and attention upon visual search were tested using repeated-measures ANOVAs.

For sample-related potentials, stimuli were presented at the centre of the screen, thus the original left and right hemisphere locations were retained. Since target presence was determined only at the time of array presentation, target present and absent trials were collapsed for sample-elicited potentials. ERPs were constructed by averaging for each target type (rewarded, non-rewarded). For array-elicited potentials, ERPs were combined for targets appearing on the left and right side of the screen by an averaging procedure that preserved the electrode position relative to target location (ipsilateral or contralateral). ERPs were constructed by averaging for each target presence (present, absent), target reward type (rewarded, non-rewarded) and distractor type (foils only, rewarded, non-rewarded). Six ERPs were consequently constructed, present-rewarded target with foils only, present-rewarded target with rewarded distractor, present-rewarded target with non-rewarded distractor, absent-rewarded target with foils only, absent-rewarded target with rewarded distractor, absent-rewarded target with non-rewarded distractor.

The N2pc potential at lateral occipital electrode sites contralateral to the stimulus of interest was the potential of primary interest. The analyses tested whether the reward association of a target modulated the amplitude of the target-elicited N2pc following presentation of the stimulus array. Furthermore this experiment aimed to examine whether and how having a reward-associated but task-irrelevant distractor in the opposite hemifield to the target

modulated the target-elicited N2pc. It was hypothesised that a distractor associated with reward might capture some attention away from the target stimulus, thus attenuating the amplitude of the target-elicited N2pc. The effects of target and distractor reward association upon early perceptual stages of processing were investigated by examination of the sample- and array-elicited P1 and N1 components at occipital electrode sites. This allowed the examination of visual processing of the sample in anticipation of reward, as well as the initial processing of the array stimuli. The effects of reward association on later stages of information processing focused on analysis of the P300 component elicited to sample and array presentation, observed over frontal and central electrodes. An additional late potential, the CNV, was analysed in response to the sample stimulus. This slow ramp-like negative potential is typically observed in anticipation of a task-relevant stimulus, in this case the array. The fronto-central CNV was examined to determine if a sample associated with reward would elicit differences in anticipatory activity to that produced by non-rewarded sample stimuli. Effects on motor preparation and execution following presentation of the array were analysed using the LRP, calculated using the following formula (Coles, 1989):

$$LRP = [mean(C4\text{-}C3)_{\text{left-hand movement}} + mean(C3\text{-}C4)_{\text{right-hand movement}}]/2$$

6.2 Results

6.2.1 Behavioural results

The behavioural results are illustrated in Figure 6.1.

6.2.1.1 Accuracy

There were no main effects of the experimental factors upon accuracy (all p values>.05). There was, however, a significant interaction between target presence and distractor type ($F(1,13)=6.76$, $p=.01$). There was also a significant interaction between target reward and distractor type ($F(2,26)=4.98$, $p=.03$). Subsidiary ANOVAs were used to clarify these interactions. These showed that both interactions were driven by an effect of distractor type when the target was absent and non-rewarded ($F(2,26)=4.62$, $p=.04$). Paired-samples t tests were used for further clarification, and showed that this effect was due to significantly lower accuracy when a non-rewarded distractor (mean=0.78, SD=0.25) was present in the array, compared with the foils-only condition (mean=0.90, SD=0.17) ($t(13)=2.32$, $p=.04$). There was no difference in accuracy with foils only or a rewarded distractor (mean=0.89, SD=0.13) ($t(13)=0.40$, $p=.07$). There was a trend towards significantly lower accuracy with a non-rewarded than rewarded distractor ($t(13)=2.10$, $p=.06$).

6.2.1.2 d'

As with accuracy, there was not a main effect of target reward type ($F(1,13)=2.02$, $p=.18$) or distractor type ($F(2,26)=1.44$, $p=.26$) on d'. Modulation occurred in the form of a significant

interaction between target reward type and distractor type (F(2,26)=6.90, p=.01). Subsidary ANOVAs showed this was due to an effect of distractor type for non-rewarded targets (F(2,26)=3.86, p=.03). There was no such effect for rewarded targets (F(2,26)=0.3, p=.75). Paired-samples t tests were used for further clarification. These showed that, consistent with the accuracy data, the effect was driven by significantly lower d' with a non-rewarded distractor (mean=1.46, SD=0.85), compared with the foils-only (mean=1.88, SD=0.75) condition (t(13)=2.28, p=.04). D' did not differ between the foils-only and rewarded distractor (mean=1.72, SD=0.74) (t(13)=1.81, p=.09) or rewarded and non-rewarded distractor (t(13)=1,56, p=.14) conditions.

6.2.1.3 RT

There was a significant main effect of target presence (F(1,13)=18.94, p<.01). RTs were faster in trials where targets were present (mean=365ms, SD=122ms) compared with absent (mean=444ms, SD=181ms). There was also a significant main effect of target reward type (F(1,13)=4.90, p<.05). RTs were faster for rewarded (mean=372ms, SD=122ms) than for non-rewarded (mean=437ms, SD=183ms) trials. There were no other significant effects or interactions (all p values>.05).

6.2.2 ERP results

6.2.2.1 Sample-related potentials

The Cartool segmentation is illustrated in Figure 6.2. Presentation of the sample stimulus elicited prominent P1 and N1 potentials at lateral occipito-parietal electrode sites. The P1 peaked at approximately 100ms post stimulus, with the N1 peaking around 150ms post stimulus. The P300 evolved from around 300ms post stimulus, with a late peak at approximately 450ms post stimulus. Following this, a late frontal negativity was observed from approximately 650ms. This was the CNV, maximal over fronto-central scalp, continuing until the end of the epoch. This was the only sample-elicited potential to produce different topographies for the rewarded compared with non-rewarded sample stimuli.

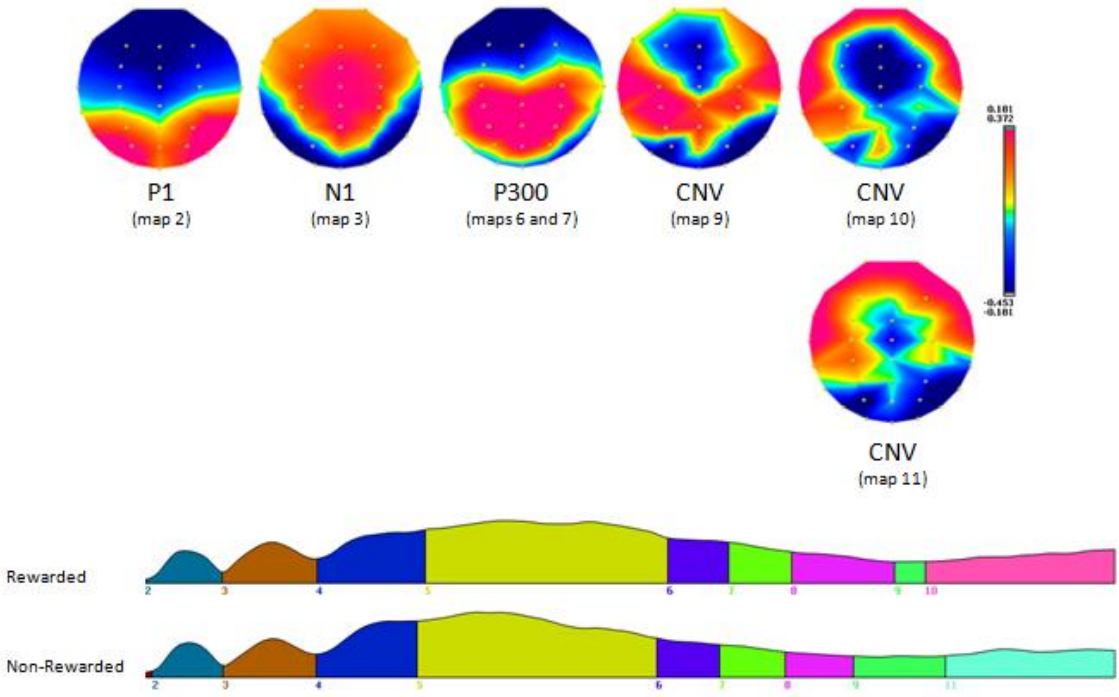

Figure 6.2: Cartool segmentation and topographical mapping for the sample-related potentials from the onset of the P1 potential (approximately 80ms post stimulus) for the experiment of Chapter 6. The top panel shows the topographies identified for each period of topographical stability. Topographical maps show (from left) the P1 and N1 potentials, the P300 potential and two successive CNV topographies. The CNV was the only potential for which a difference in topography was observed for rewarded and non-rewarded samples. The upper CNV (map 10) was observed with respect to rewarded samples, the lower topography (map 11) for non-rewarded samples. The bottom panel shows the segmentation results for each sample reward association, illustrating that the topographical distribution of each potential, other than the late CNV, was common to both conditions. The different topographies produced for rewarded and non-rewarded sample stimuli are evident in the different coloured segments at the late stage of the segmentation, pink for the rewarded sample (corresponding with map 10) and turquoise for non-rewarded samples (corresponding with map 11).

6.2.2.1.1 Early potentials

A P1 elicited to the sample stimulus was observed over lateral occipital and parietal electrode sites. The P1 was more prominent over the contralateral hemisphere, reaching a peak at approximately 100ms post stimulus. The P1 elicited to the sample stimulus was examined between 80 and 120ms at electrodes PO3/4, P3/4, PO7/8, P7/8, O1/2. Reward did not modulate the amplitude of the P1 ($F(1,13)=2.73$, $p=.12$). Following the P1, the N1 potential was observed, with a slightly more lateral topography than the P1. The N1 peaked at approximately 150ms. N1 mean amplitude was analysed at electrodes PO3/4, P3/4, PO7/8, P7/8, O1/2 between 120 and 180ms. Reward did not modulate the amplitude of the N1 ($F(1,13)=0.76$, $p=.40$).

Peak detection was performed using the same electrodes sites as employed for mean amplitude analysis. The peaks were identified within the time windows utilised in mean amplitude analysis, then correct peak detection confirmed (and adjusted if necessary) through visual inspection. There was no modulation of P1 latency by reward ($F(1,13)=0.37$, $p=.56$). N1 latency was also not modulated by reward ($F(1,13)=1.57$, $p=.23$). There were no other effects or interactions for the latency of either potential (all p values>.05).

6.2.2.1.2 Later potentials

The P300 was apparent at central, posterior and occipital electrode sites, peaking at approximately 450ms post stimulus (Figure 6.3). The P300 was examined between 420 and 520ms post-stimulus at electrode sites C3/z/4, P3/z/4, O1/z/2. Reward modulated P300

amplitude ($F(1,13)=5.88$, $p=.03$). The P300 was larger for rewarded (mean amplitude=5.10μV, standard error=0.99μV) than non-rewarded trials (mean amplitude=4.32μV, standard error=0.79μV).

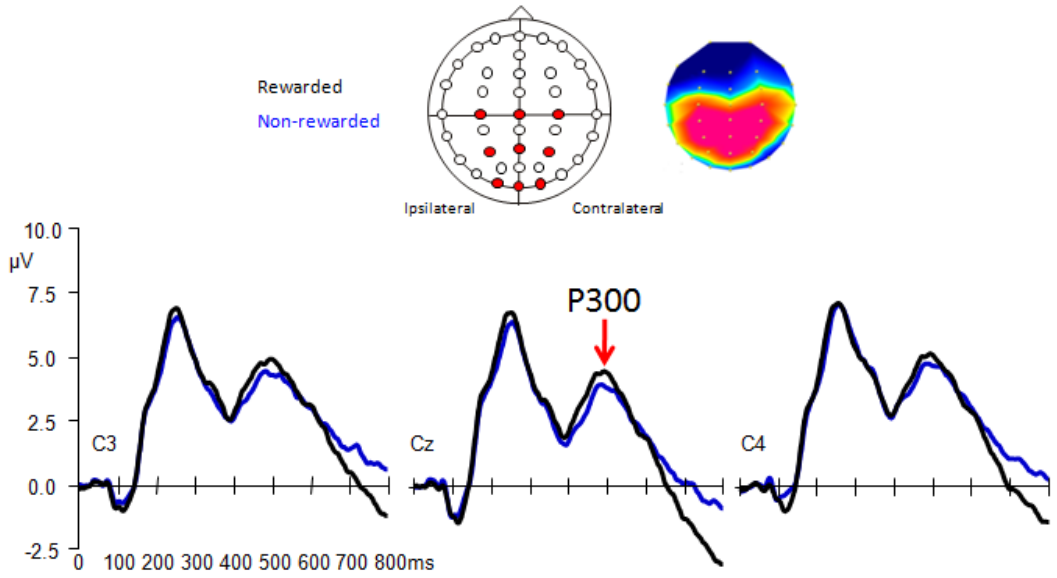

Figure 6.3: Grand average waveforms illustrating the P300 observed in the experiment of Chapter 6. Waveforms at the C3/z/4 electrode positions are shown. The topography of the P300 is shown in the top panel. Rewarded trials are plotted in black, non-rewarded trials in blue. Electrodes used for analysis are indicated in red on the electrode montage. Positive voltage is plotted upwards.

The CNV was most prominent over frontal and central scalp sites from around 650ms post stimulus (Figure 6.4). The CNV was examined between 650 and 800ms post stimulus at electrode sites F3/z/4, FC3/z/4 and C3/z/4. Reward modulated CNV amplitude ($F(1,13)=10.18$, $p=.01$). The CNV was larger for rewarded (mean amplitude=-0.73μV, standard error=0.61μV) than non-rewarded trials (mean amplitude=0.81μV, standard error=0.65μV).

The P300 and CNV were both slow-wave potentials. As such, peak latency analysis was not performed.

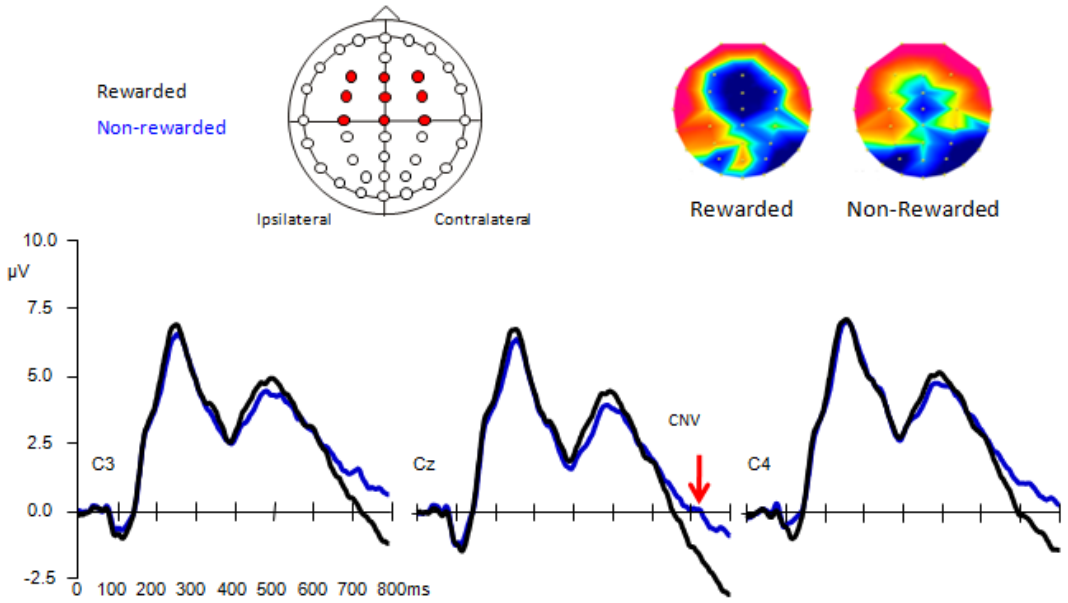

Figure 6.3: Grand average waveforms illustrating the CNV observed in the experiment of Chapter 6. Waveforms at the C3/z/4 electrode positions are shown. The topographies of the CNV are shown in the top panel. Rewarded trials are plotted in black, non-rewarded trials in blue. Electrodes used for analysis are indicated in red on the electrode montage. Positive voltage is plotted upwards.

6.2.2.2 Array-related potentials

The Cartool segmentation of the array-related activity for target-present trials is illustrated in Figure 6.5. As with sample-elicited potentials, prominent P1 and N1 potentials were observed at lateral occipital-parietal electrodes. The P1 peaked just after 100ms post-stimulus and the N1 at approximately 150ms post stimulus. The P300 evolved from around 350ms post stimulus, peaking at approximately 450ms post stimulus. Unlike previous experiments, only one P300 peak was evident in response to array presentation.

The N2pc was evident when directly comparing waveforms that were contralateral verus ipsilateral to the target location in target-present trials. It was largest between 230 and 250ms post stimulus at lateral posterior electrodes.

Motor preparation was studied by analysing the LRP. The LRP was concentrated over electrode sites C3/C4. This was a slowly-developing negative potential, beginning approximately 250ms post stimulus and maximal between 300 and 500ms post stimulus.

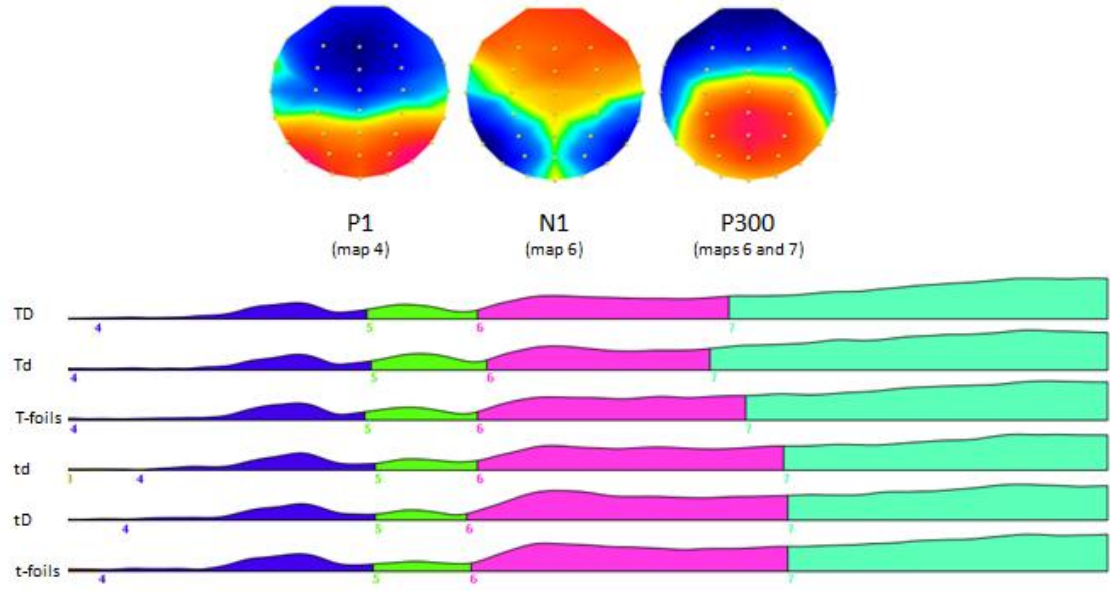

Figure 6.3: Cartool segmentation for the array-related potentials for target-present trials from the onset of the P1 potential (approximately 80ms post stimulus) for the experiment of Chapter 6. The top panel shows the topographies identified for each period of topographical stability. Topographical maps show (from left) the P1, N1 and P300 potentials. The bottom panel shows the segmentation results for each condition, illustrating that the topographical distribution of each potential was common to all conditions. T denotes target, D denotes distractor, upper-case letters denote rewarded, lower-case letters denote non-rewarded.

6.2.2.2.1 Early potentials

The P1 was observed over lateral occipito-parietal electrode sites, peaking at approximately 100ms post stimulus. The P1 potential was examined between 80 and 120msec post stimulus at electrodes P3/4, PO7/8, P7/8 and O1/2. There was no modulation of P1 amplitude by target presence ($F(1,13)=3.65$, $p=.08$), target reward type ($F(1,13)=1.06$, $p=.32$) or distractor type ($F(2,26)=1.15$), $p=.33$). There were no interactions between the three factors (all p values>.05).

The N1 potential was observed at lateral occipital and parietal electrodes, with a slightly more lateral distribution than P1. The N1 peaked at approximately 150ms post stimulus. N1 mean amplitude was analysed at electrodes P3/4, PO7/8, P7/8 and O1/2 between 120 and 180msec post stimulus. As with P1 amplitude, N1 amplitude was not modulated by target presence ($F(1,13)=2.64$, $p=.13$), target reward value ($F(1,13)=3.24$, $p=.10$) or distractor type ($F(2,26)=0.90$, $p=.39$). There were no interactions between the three factors (all p values >.05).

Peak detection was performed using the same electrodes sites as employed for mean amplitude analysis. The peaks were identified within the time windows utilised in mean amplitude analysis, then correct peak detection confirmed (and adjusted if necessary) through visual inspection. P1 latency was modulated by target presence and target reward type in an interactive manner [presence-by-target reward-by-hemisphere interaction ($F(1,13)=5.00$, $p=.04$); presence-by target-by electrode interaction ($F(3,39)=3.33$, $p=.04$)]. Subsidiary ANOVAs were performed to compare the effects of target presence and target reward in each hemisphere. There were no significant effects of either factor, nor an interaction between factors, in either hemisphere (all p values>.05)

There was a marginally-significant effect of target reward type on N1 latency ($F(1,13)=4.13$, $p=.06$). The N1 peaked earlier for rewarded (mean peak latency=153ms, standard error=2ms) than non-rewarded (mean peak latency=154ms, standard error=3ms) targets. There were no other effects on N1 latency (all p values>.05).

6.2.2.2.2 Lateralised potential – the N2pc

Cartool topographies and visual inspection of waveforms showed the N2pc to be prominent at lateral posterior electrodes contralateral to the target stimulus between 230 and 250ms post stimulus (Figure 6.6). The N2pc was therefore examined from 230 to 250msec post stimulus at posterior electrode sites PO3/4, P3/4, PO7/8 and P7/8. The effects of reward association were examined for target-present trials only. Distractor type significantly modulated amplitude of the target-elicited N2pc [distractor type-by-hemisphere interaction ($F(2,26)=5.00$, $p=.02$)]. Subsidiary t-tests performed by averaging together the differential voltage (ipsilateral minus contralateral) for rewarded and non-rewarded targets across the four electrode pairs used for analysis showed this was driven by a significant attenuation of target-elicited N2pc with a rewarded distractor (mean=-0.83μV, standard error=0.26μV) relative to the foils-only condition (mean=-1.48μV, standard error=0.27μV) ($t(13)=3.52$, $p<.01$). The target-elicited N2pc produced with a non-rewarded distractor (mean=-1.38μV, standard error=0.27μV) did not differ from that of the foils-only condition ($t(13)=0.50$, $p=.63$). There was a trend towards a significantly smaller N2pc with rewarded compared with non-rewarded distractors ($t(13)=2.10$, $p=.06$).

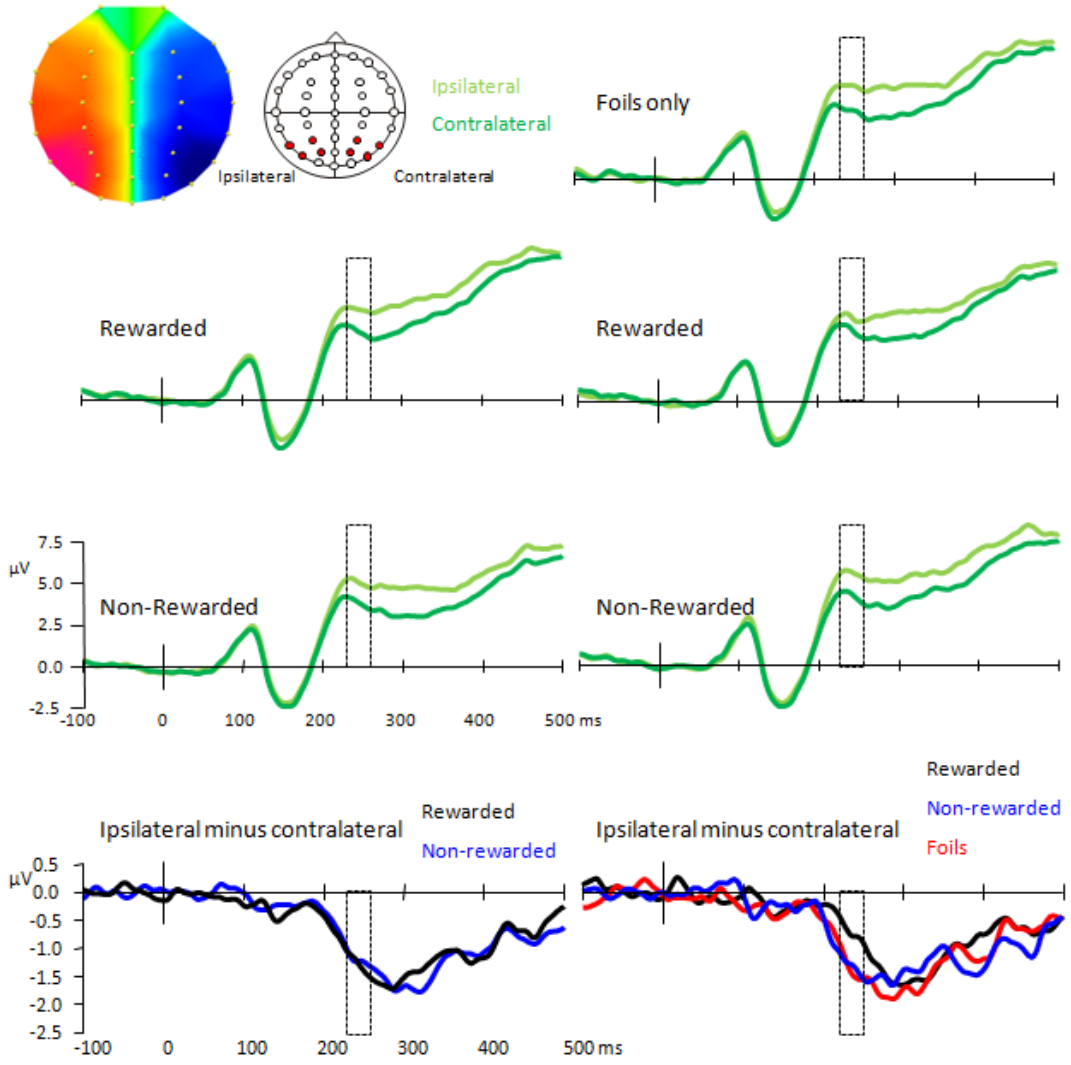

Figure 6.6: Grand average waveforms illustrating the target-elicited N2pc observed in the experiment of Chapter 6. Waveforms averaged across the electrodes used for analysis are shown. The dashed boxes show the time window used for analysis. The panels on the left show the target-elicited N2pc for the two different target reward types. The upper two panels show ipsilateral (light green) and contralateral (dark green) waveforms. The lower panel shows the ipsilateral minus contralateral subtraction. Rewarded targets are plotted in black, non-rewarded targets in blue. The panels on the right show the target-elicited N2pc for the differenct distractor reward associations. The upper three panels show ipsilateral (light green) and contralateral (dark green) waveforms. The lower panel shows the ipsilateral minus contralateral subtraction. Rewarded distractors are plotted in black, non-rewarded distractors in blue and foils in red. The topography of the N2pc in the rewarded target-foils distractor condition is shown (top left). The electrodes used for analysis are shown in red on the electrode montage. Positive voltage is plotted upwards.

6.2.2.2.3 Later processing – The P300

Unlike the P300 of chapters 4 and 5, there were not two distinct peaks in the P300 elicited to the target array, but rather a slow positive component emerging 350ms post array to reach a peak at approximately 450ms (Figure 6.7). The P300 component was therefore examined in 50ms time windows between 350 and 500ms post array. There were no differences across time windows, thus analysis was collapsed across the 350-500ms time window. The P300 had a broad topographical distribution across most of the scalp, from frontal to occipital electrodes. P300 mean amplitude was thus examined from frontal to occipital sites, using matched electrode sites F3/z/4, C3/z/4, P3/z/4, O1/z/2. Target presence modulated P300 amplitude ($F(1,13)=44.97$, $p<.01$). The P300 was larger for present (mean amplitude=5.41μV, standard error=1.30μV) than absent (mean amplitude=3.22μV, standard error=1.22μV) trials. Target reward type also modulated P300 amplitude ($F(1,13)=8.02$, $p=.01$). P300 amplitude was greater for rewarded (mean amplitude=5.27μV, standard error=1.44μV) than non-rewarded (mean amplitude=3.36μV, standard error=1.14μV) targets. There was no effect of distractor type ($F(2,26)=0.85$, $p=.41$). There were no interactions between factors (all p values>.05). The P300 continued to rise through the analysis time window, therefore peak latency analysis was not performed.

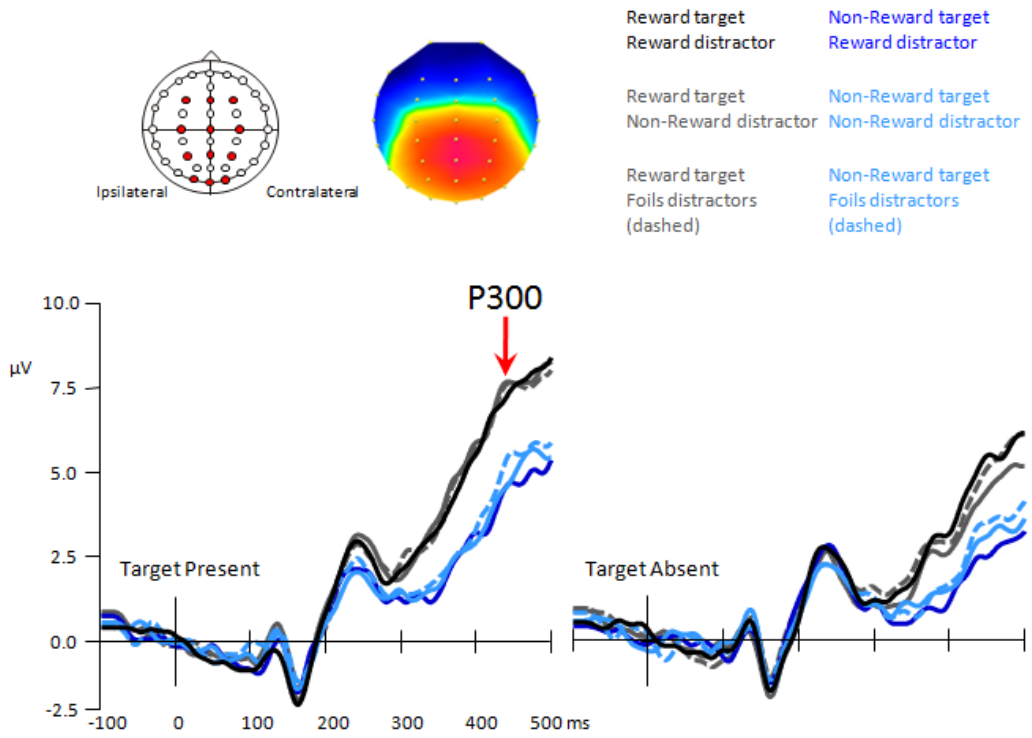

Figure 6.7: Grand average waveforms illustrating the P300 observed in the experiment of Chapter 6. Waveforms at the Fz electrode site are shown, with target-present trials on the left and target-absent trials on the right. The topography of the P300 is shown in the top panel. Rewarded targets are plotted in shades of grey, non-rewarded targets are plotted in shades of blue, rewarded distracters are plotted with dark lines, non-rewarded distracters with pale lines and foils with pale dashed lines. Electrodes used for analysis are indicated in red on the electrode montage. Positive voltage is plotted upwards.

6.2.2.2.4 Motor preparation – The LRP

To examine the effects of target and distractor reward association with respect to the presence or absence of a target in the search array upon motor preparation, the mean amplitude of the LRP was examined (Figure 6.8). Cartool topographies confirmed the LRP to be maximal over electrode pair C3/C4 contralateral to the hand of response, consistent with activation of the primary motor cortex. The LRP was a slowly-evolving negative potential, beginning around 150ms post stimulus and peaking around 250ms post stimulus. In order to capture these evolving preparatory effects, the LRP was examined from 150 to 500ms post stimulus in 50ms time windows. Analysis began early due to the rapid RTs produced on this task.

Early in the LRP time window (150 to 200msec post stimulus) all three factors modulated its amplitude. There was a main effect of target presence ($F(1,13)=5.71$, $p=.03$). LRP amplitude was larger (more negative) for target-present (mean amplitude=-0.52μV, standard error=0.26μV) than target-absent (mean amplitude=0.58μV, standard error=0.21μV) trials. There was also a main effect of target reward type ($F(1,13)=5.49$, $p=.04$). LRP amplitude was greater for rewarded (mean amplitude=-0.08μV, standard error=0.07μV) compared with non-rewarded (mean amplitude=0.14μV, standard error=0.06μV) trials. In addition, there was a three-way interaction between target presence, target reward type and distractor reward type ($F(2,26)=3.57$, $p<.05$). Subsidiary ANOVAs showed there was an effect of target reward association on present-reward distractor trials ($F(1,13)=4.86$, $p<.05$). The LRP was larger with a rewarded (mean amplitude=-0.60μV, standard error=0.27μV) than non-rewarded (mean amplitude=-0.02μV, standard error=0.23μV) ($t(13)=2.21$, $p<.05$) target. There were no effects of target type for any other presence-distractor type combinations (all p values>.05).

The effects of target presence continued in the next time window (200-250msec post stimulus). There was a main effect of target presence ($F(1,13)=5.41$, $p=.04$). The LRP was larger for target present (mean amplitude=-0.09μV, standard error=0.43μV) than target absent trials (mean amplitude=0.83μV, p=.033μV). There were no other effects, nor any interactions in this time window (all p values>.05).

Effects of target reward type were evident later in the LRP analysis time window. There was a main effect of target reward type 300 to 350msec post stimulus ($F(1,13)=8.98$, $p=.01$). As with the early target reward type effect, LRP amplitude was greater for rewarded (mean amplitude=-0.59μV, standard error=0.20μV) compared with non-rewarded (mean amplitude=-0.14μV, standard error=0.13μV) trials. There were no other effects, nor any interactions in this time window (all p values>.05).

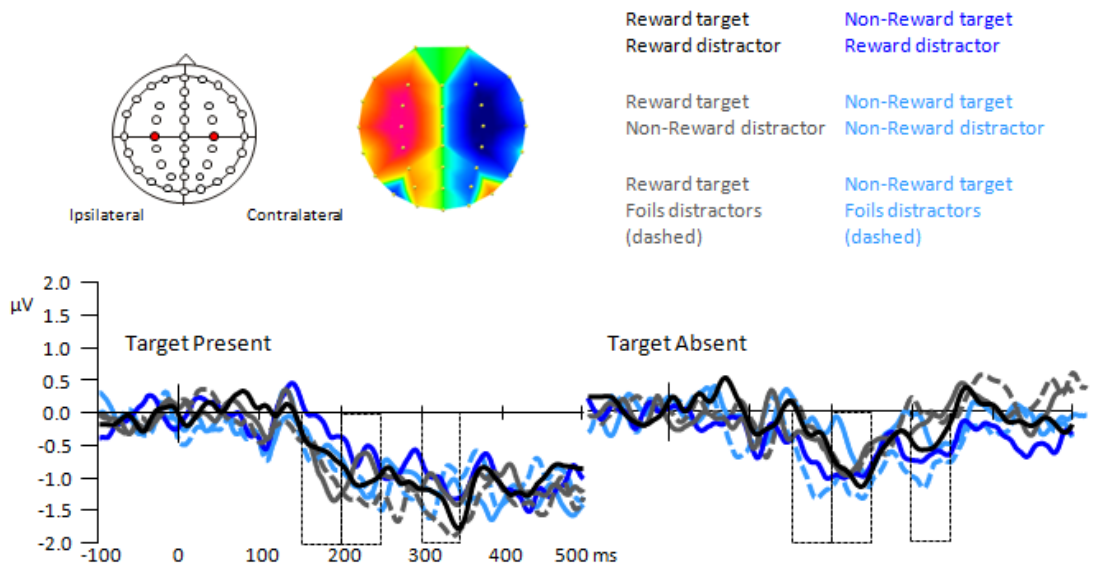

Figure 6.8: Grand average waveforms illustrating the derived LRP potential. Waveforms from the C3/C4 electrode pair are shown. Dashed boxes illustrate the time periods during which significant modulation of LRP amplitude occurred. Rewarded-target trials are plotted in shades of grey, non-rewarded-target trials in shades of blue, rewarded distracters are plotted with dark lines, non-rewarded distracters with pale lines and foils with pale dashed lines. The topography for the LRP in the rewarded-target, foils only condition is shown in the top panel. Electrodes used for analysis are indicated in red on the electrode montage. Positive voltage is plotted upwards.

6.3 Discussion

This experiment aimed to delineate the effects of reward expectation during visual search, where multiple stimuli must compete for processing resources. The independent manipulation of target and distractor reward association allowed examination of the effects of purely endogenous motivational factors upon processing, both when a stimulus was relevant on the current trial, and when it was not. As in the previous chapters, reward was demonstrated to influence behaviour. Responses were faster when the target stimulus was associated with reward. Reward associations of the distractor stimuli did not exert significant effects on response times. The findings were consistent with those of previous chapters and with the interpretation of reward speeding responses when speed was prioritised. In contrast with the other experimental chapters, reward information appeared to have a more extensive influence upon behaviour, with effects evident in accuracy and d' measures in addition to RT. The inclusion of a non-rewarded distractor appeared to disrupt performance, such that accuracy and d' were both lower when a non-rewarded distractor was presented. For accuracy, this disruptive effect occurred when the sample had not been associated with reward and the array subsequently contained no target. In the d' results, the non-rewarded distractor effect was evident only when the target was not associated with reward. It was possible that when the target was associated with reward, performance was boosted to overcome distractor interference, but this did not occur with non-rewarded targets. The more extensive effects of reward information in this compared with previous experiments suggested the greater competition instigated by the presentation of multiple stimuli may have increased the influence of reward information upon behaviour.

6.4.1 Sample-related potentials

The sample stimuli differed only in terms of reward association. They were matched for low-level features and were equal in terms of having been previously used as the sample. Examination of sample-related ERPs therefore allowed the tracking of the earliest time at which reward value was first retrieved and how it was subsequently able to influence the biasing of processing with respect to a future, upcoming perceptual array in the absence of any spatial information. Presentation of the sample stimulus likely necessitated uploading the representation of the item that was task relevant on a given trial into working memory, as well as any reward association that may have been carried by that item. Consistent with predictions, therefore, reward association did not bias early visual potentials. Reward association seems to have been retrieved after this early perceptual processing, strongly affecting the P300-updating related effect and the expectation-related CNV potential. This was evident in the enhancement of both P300 and CNV amplitude by reward association.

6.4.2 Array-related potentials

Of primary importance in this experiment was the N2pc potential. This marked the point at which target and distractor stimuli were identified in the array. Target and distractor reward association would therefore not have been expected to influence activity prior to this point. Consistent with this, target and distractor reward association did not modulate the amplitude of early visual potentials. Though a recent study has demonstrated the ability of reward to enhance the amplitude of the P1 potential, this was due to the use of a highly-salient colour to signal reward. This effect may therefore have been induced by the fast bottom-up capture of attention by physical salience (Hickey, et al., 2010a). The observed trend toward earlier N1

peak latency with rewarded targets suggests that when reward was available on a given trial, discrimination of the array may have begun earlier in an attempt to more quickly discriminate array stimuli and subsequently identify the target (or its absence) (Hopf, et al., 2002).

The prioritisation of processing of elements within a multi-stimulus array can be influenced by bottom-up, physical salience. Highly-salient stimuli capture processing resources away from a target stimulus, leading to the slowing of responses when a task-irrelevant yet highly salient stimulus was included in the search array (Theeuwes, 1991, 1994). Stimuli need not be highly salient in order to capture processing resources, however. Task-irrelevant stimuli that share top-down task-set features with the target can also capture attentional resources (Folk, et al., 2002; Folk & Remington, 1998; Folk, et al., 1992; Yantis, 1993). The N2pc potential can be used as an electrophysiological correlate to chart this capture process, as it is thought to reflect the allocation of attentional resources to a given stimulus within the array, for the suppression of distractor items and/or selection of the target stimulus (Eimer, 1996; Hickey, et al., 2009; Hickey, et al., 2006; Luck & Hillyard, 1994b; Mazza, et al., 2009a, 2009b). Task-irrelevant but salient singleton items elicit an N2pc or attenuate the amplitude of target-elicited N2pcs (Hickey, et al., 2008, 2009; Hickey, et al., 2006; Kiss, et al., 2008a; Luck & Hillyard, 1994b). Furthermore the N2pc amplitude is influenced by the degree of similarity between a singleton and the target item. A larger N2pc is evoked by a singleton that more closely resembles the target (Eimer & Kiss, 2008; Kiss, et al., 2008a; Telling, et al., 2010). Recent studies have also demonstrated the ability of task-irrelevant items to capture resources away from the current focus of spatial attention, independently from any bottom-up effects (Brignani, et al., 2010). This task was designed to investigate whether motivational factors, such as the reward association of a given item, could lead to the prioritisation of processing and selection of an item within an array, even when this item was not the target. Previous studies have examined

the capture of resources by reward association with the use of highly salient singleton targets (Hickey, et al., 2010a; Kiss, et al., 2009). These studies demonstrated the ability of singleton stimuli baring a colour associated with high reward to attract attentional resources, thus eliciting an N2pc potential (Hickey, et al., 2010a; Kiss, et al., 2009). This experiment aimed to extend these findings by attaching motivational associations in a purely endogenous manner, with stimuli matched for low-level salience, in order to isolate the effects of reward association. The results of this experiment suggested that reward association was able to induce the capture of attention. In this case it was motivational value of the distractor, rather than the target, that captured attentional resources. The amplitude of the target-elicited N2pc was attenuated when a reward-associated distractor was present in the opposite hemifield. This suggested the reward association of the task-irrelevant item was able to capture some of the processing resources away from the task-relevant target item, on the basis of its endogenous association with reward alone. This was consistent with the ability of distractor items baring the high reward colour to elicit an N2pc in the study of Hickey et al. (2010), and demonstrated that such attentional capture by motivational information could occur on the basis of endogenous reward association alone. Analysis would have been strengthened with a complementary analysis of the distractor-elicited N2pc on target-absent trials. A larger N2pc elicited to rewarded compared with non-rewarded or foil distracters would support the argument that rewarded distracters captured attention. Unfortunately the coding in the stimulus presentation programme did not allow the identification of the spatial location of distractor items, other than in reference to the target. When no target was presented it was therefore not possible to localise the rewarded (or other) distractor stimulus.

The observation of a distractor effect upon N2pc amplitude in the absence of any modulation by target reward value differed from other recent studies manipulating reward during visual search. Kiss and colleagues (2009) observed an N2pc that was larger in amplitude and peaked earlier for singletons of a colour associated with high reward. In the study of Hickey and colleagues (2010), an N2pc was produced to a singleton baring the colour associated with high reward, regardless of whether that stimulus was the target or distractor. Consistent with the observation in this and previous chapters, paradigm disparities such as the means of signalling reward may also have accounted for the differences in N2pc modulation across studies. Kiss and colleagues (2009) used a simple feature pop-out search. Targets differed in low-level visual qualities (colour) from distractors, thus were highly salient against the homogenous, unchanging array. In the case of Hickey et al. (2010) reward was also signified by a salient colour assigned to the target or distractor on a given trial. This form of manipulation may have allowed an integrative enhancement of reward through the attention system via bottom-up capture of attention. As noted in Chapter 4, reward effects may be greater when able to work through feature-based attention. In this study non-verbalisable complex shape stimuli necessitated a more difficult non pop-out, or 'inefficient' feature search (Luck & Hillyard, 1995; Treisman & Gelade, 1980). Target shapes differed from one another and foils only in terms of learned, endogenous associations with reward or no reward. Pop-out search differs phenomenologically from the 'inefficient' search employed in this task. Pop-out search is easier, placing less demand on processing resources. Detection of a pop-out item is not influenced by the number of items in an array, whereas RT increases with each additional item during inefficient search (Luck & Hillyard, 1995; Treisman & Gelade, 1980). This has been used to argue that pop-out detection does not utilise attention, but rather targets are identified by the use of preattentive feature information (Treisman & Gelade, 1980). Luck and Hillyard (1995) have argued additional processes are necessary for inefficient search. Though their

argument was based on the observation of P1 modulation during inefficient but not pop-out search, this reasoning could also be applied to additional or different processes necessary at the N2pc processing stage (Luck & Hillyard, 1995).

Later stages of processing were influenced by target, but not distractor, reward association. The P300 was enhanced for rewarded, relative to non-rewarded, targets. This was consistent with the reward enhancement observed in chapters 4 and 5, as well as the proposal that stimuli of greater motivational value enhance P300 amplitude (Donchin & Coles, 1988a; Johnson, 1986; Nieuwenhuis, et al., 2005a). Reward thus appeared to induce greater updating of stimulus representations, likely due to the greater necessity of remembering and processing those stimuli on subsequent trials to optimise performance and, ultimately, reward outcome. Target presence also modulated P300 amplitude, with a larger P300 on target-present trials. Greater contextual updating thus appeared to occur if the target was present in the array. This was consistent with the observation of the P300 being elicited in response to task relevant stimuli (Donchin & Coles, 1988a; Johnson, 1986; Nieuwenhuis, et al., 2005a). The observation of target but not distractor effects upon P300 amplitude was consistent with the proposal that distractor stimuli induced an early capture of attention, evident in the modulation of N2pc amplitude, but were then suppressed, allowing for later processing to be driven by the task-relevant target stimuli alone.

The effects upon motor preparation were consistent with a process whereby distractors influenced processing early, were suppressed, after which the target stimulus drove processing effects. Early motor preparation was modulated by all three factors, with target reward enhancing LRP amplitude on target present-reward distractor trials. Thus association

of both target and distractor stimuli with reward enhanced motor preparation in its early stages. At this early stage of motor preparation, the attention and reward systems appeared to interact. Mirroring the effects observed with respect to visual potentials, distractor effects did not endure past the early stages of motor preparation. Target presence and target reward both influenced LRP amplitude in later time windows in an independent manner. Reward enhanced motor preparation, suggesting a prioritisation of motor preparation on trials in which reward was expected. This was consistent with the faster RTs for rewarded targets and provided support for the argument that when reward outcome was dependent upon response speed, motor behaviour was particularly sensitive to reward expectation. Motor behaviour has been demonstrated to be particularly receptive to reward manipulation. Rewarding "go" responses on a stop-signal RT task, for example, led to greater difficulty inhibiting a response than during a control, non-rewarded condition (Padmala & Pessoa, 2010). This suggested not only was motor behaviour sensitive to reward association, but that the manner of reward influence may depend on the specific manipulation. In this task, where response speed was accentuated, reward enhanced LRP amplitude and produced faster RTs, whereas stop behaviour was impaired in the study of Padmala and Pessoa (2010). This was consistent with the dependence upon task parameters already discussed in this and previous chapters, and may account for the different pattern of LRP modulation in the experiments of chapters 5 and 6.

Target presence also enhanced LRP amplitude independently from the effects of reward. Greater motor preparation was observed when target stimuli were present in the array. This effect occurred earlier than the LRP enhancement by reward. In this task, the presence or absence of the target was the factor that determined the response. This would therefore be

expected to drive motor activity. This is likely to account for the effects of target presence from early preparatory stages, followed by a later effect of reward.

The results of this chapter extended the findings of experiments in chapters 3 to 5 that illustrated the ability of reward expectation to influence behaviour and multiple stages of information processing. The results of this experiment demonstrated that associating a stimulus with reward in a purely endogenous manner was able to prioritise stimuli for processing. Motivational association was even able to capture attentional resources away from target stimuli to reward-associated but task-irrelevant distractor items. This was evident in the attenuation of the target-elicited N2pc in the presence of a rewarded distractor item. The results further indicated that although distractor items may have influenced the initial allocation of attentional resources, these items were suppressed following their identification within the array. The later P300 potential was influenced by target reward association alone. Target items enhanced the amplitude of the P300 potential, suggestive of a greater emphasis on the contextual updating of stimulus representations with respect to items associated with reward. Motor activity was consistent with the observed pattern of modulation on the visual ERPs. Early motor preparatory activity was influenced by distractor and target reward association. In later stages, presumably following suppression of distractor items, the LRP was enhanced for reward-associated targets. This was consistent with the speeding of responses on rewarded-target trials. The results of this experiment demonstrated that prioritisation of processing could be driven by endogenous motivational associations between stimuli, and that motivational value could override top-down task set, at least at initial stages of processing.

Chapter 7: General Discussion

The primary aim of this thesis was to examine whether reward expectation was able to influence behaviour and information processing, as well as to chart the effects of reward expectation across the time course of information processing. The relationship between reward expectation and attention at successive stages of processing was also examined. The results demonstrated that not only was reward effective in modulating behaviour on classical attention tasks, but also that expectation of a reward modulated information processing at multiple stages from perception to action.

7.1 Behaviour

The results demonstrated that reward expectation was able to influence behavioural measures. As established in Chapter 3, the behavioural measure most sensitive to the manipulation of reward was RT. This was predominantly the case under conditions of accentuated response speed. Furthermore, cueing the likely spatial location of a target stimulus provided strong behavioural benefits. It was possible that these attentional gains optimised performance to such a degree that additional pressure, in this case the addition of an RT threshold, was required in order for reward effects to be observed. The results of Chapter 3 suggested that reward increased speed of response in a categorical way, with faster responses when reward was available, rather than a parametric modulation of RT with differing magnitude of reward available. Decreasing RT with reward expectation was consistently observed when reward information was explicitly available at the time of target presentation (Chapters 3, 5 and 6), suggesting a robust effect under this task paradigm.

The relationship between reward and attention was also examined in terms of behavioural measures. With the parametric manipulation of reward magnitude (Chapter 3) an interaction was observed between reward and attention. This appeared to be driven by a modulation of the effect of spatial attention according to the categorical difference between reward versus no-reward expectation. Whilst validity effects were apparent at any level of expected reward, there were no such effects of attention in the absence of reward expectation. However, the interaction between reward expectation and spatial attention at the behavioural level was not a robust, reliable effect. When the parametric manipulation was simplified to a binary present-absent reward manipulation, reward and attention independently enhanced RT (chapters 5 and 6).

Overall, the effect of reward expectation upon RTs was reproducible across the great majority of speed-response experiments in the thesis. However, it was noteworthy that there was not such a straightforward effect of reward upon RT in Chapter 4. Reward did speed responses when able to work through feature-based attention (Experiment 4.1) but failed to do so in Experiment 4.2. This may have related to the timing of the reward information, as reward availability was known at the time of response for Experiment 4.1 but not Experiment 4.2. Given the sensitivity of the reward system to timing factors, the pattern of behavioural modulation may have been highly dependent upon when reward was signalled. An interesting direction for future research would be to examine the effects upon behaviour and neural activity as the timing of reward signal was systematically manipulated. Altering the time of reward delivery in single-unit studies has demonstrated the ability of such a manipulation to alter greatly the neuronal firing patterns (Hollerman, et al., 1998). It would be of interest to

examine the way in which ERPs and behaviour were influenced by signalling reward availability or likelihood at different time points during a trial. Alternatively, the non-explicit, block-wise manipulation of reward may not have been optimal in examining effects upon behaviour, especially in Experiment 4.2. Given the ability of reward expectation to influence neural activity in this task, it was possible that the behavioural effects were simply too weak to be observed, due to higher within- and between-subjects variability. It would be interesting in future research to examine the parameters under which behavioural effects may emerge in such a task. It is possible that a greater degree of pre-task training or longer trial blocks might be necessary.

Reward tended not to influence accuracy or d' in the simple Posner-style paradigm with explicit cues (Chapters 3 and 5). It did, however, influence d' under conditions of uncertainty in Chapter 4 when it was able to work through feature-based attention (Experiment 4.1). Reward also influenced accuracy and d' when coupled with rewarded distractors in the multi-stimulus array in Chapter 6. Indeed, the effects of reward information on behaviour were more extensive in Chapter 6, when there was increasing competition for processing by addition of multiple stimuli. It is possible that when the perceptual tasks were performed under time pressure, RT was the primary measure to be influenced as the behavioural priority. As increasing demands were placed upon processing resources, as with the environmental uncertainty in Chapter 4 and the increasing number of stimuli in Chapter 6, reward information was used to enhance processing in increasingly pervasive ways. In particular, the greater stimulus uncertainty in the manipulation of Chapter 4 and the introduction of stimulus competition in Chapter 6 placed additional demands upon perceptual resources. This increase in perceptual processing requirements may therefore have resulted in a targeting of d' by reward, for similar reasons that motor demands with the RT threshold induce reward priority

upon RT modulation. This would be consistent with the reports of reward effects upon d' when degraded visual stimuli or stimuli close to detection threshold were utilised (Engelmann, et al., 2009; Engelmann & Pessoa, 2007).

7.2 ERPs

The ERP results of chapters 4 to 6 illustrated the ability of reward expectation to modulate multiple stages of information processing. Effects could begin early, with modulation of potentials indexing visual analysis of stimuli. Reward exerted a particularly robust effect upon later stages related to cognitive processing. Effects upon motor preparation were also observed in chapters 5 and 6.

7.2.1 Early potentials

Previous studies had suggested the possibility of reward to exert modulatory effects upon visual processing. Increased BOLD activity was observed in extrastriate visual cortical regions, as well as primary visual cortex itself, in response to stimuli associated with reward (Engelmann, et al., 2009; Mohanty, et al., 2008; Small, et al., 2005). The poor temporal resolution of the fMRI method, however, makes it impossible to determine whether the observed reward-related changes in BOLD activity were due to effects upon the early stages of visual processing. It was equally likely that such effects could have occurred late during stimulus processing and have been driven by late, re-entrant feedback. One of the primary aims of this thesis, therefore, was to chart the dynamics of the modulatory effects of reward across the information processing time course with the high temporal resolution provided by

the ERP method. This allowed the experiments to identify the earliest occurrence of modulation by reward factors. The results of chapters 5 and 6 demonstrated the ability of reward to modulate early perceptual processing. The exact nature of modulation was highly dependent upon task parameters and demands. It appeared that reward targeted the stages of processing most relevant to optimisation of task performance, in a manner consistent with that observed in behavioural measures. In Chapter 5, the latency of the N1 potential was modulated by reward, such that the N1 peaked earlier for rewarded stimuli. The N1 was thought to reflect discriminative processing (Eimer, 1998; Hopf, et al., 2002). Modulation of the N1 thus suggested anticipation of reward led to a more rapid induction of the discriminative processing necessary to make the required tilt judgement. The emphasis on speed as well as the necessity to correctly discriminate the grating tilt direction may have therefore led to a speeding of discriminative processing on this task (Eimer, 1998; Hopf, et al., 2002). It was possible that the task parameters employed in Chapter 5, with the explicit cueing procedure, single high-contrast grating stimuli, trial-by-trial manipulation and provision of outcome feedback were optimal in driving the effects of reward upon visual analysis of target stimuli. The observation of reward effects upon the N1 but not P1 potential were consistent with the behavioural data, whereby the processes most relevant to the current task, in this case speed of response and discriminative processing, were the processes upon which reward acted. In the other chapters, other stages of processing might have been more relevant for optimising task performance, such as the identification of the target stimulus and/or suppression of distractors in Chapter 6 and tracking reward and spatial probabilities and subsequently updating of stimulus representations in Chapter 4.

7.2.2 Prioritisation of stimulus processing – the N2pc

In Chapter 6, association of a stimulus with reward was demonstrated to influence the prioritisation of stimuli for processing, when several competing items were presented in a multi-stimulus array. The attenuation of a target-elicited N2pc with a reward-associated distractor in the opposite hemi-field suggested motivational information was able to induce the capture of attentional resources in a purely endogenous manner, even when a reward-associated item was not currently task relevant. This suggested endogenous reward signals were able to override top-down task set, consistent with previous reports of capture of attention by non-target stimuli sharing features with the currently active task set (Brignani, et al., 2010; Eimer & Kiss, 2008; Folk, et al., 2002; Folk, et al., 1992; Telling, et al., 2010; Theeuwes, 1994). This also extended previous reports of reward having been able to influence attentional capture during visual search when attached to a highly-salient stimulus feature such as colour (Hickey, et al., 2010a; Kiss, et al., 2009). An important direction for future research would be to examine the relationship between physical and motivational salience, by means of systematic manipulation of the two factors. It would be of great interest to manipulate independently reward association and bottom-up properties such as colour or shape of target and distractor items and examine the influence such a manipulation would have on N2pc amplitude.

7.2.3 Contextual updating – the P300

Effects of reward were particularly robust with respect to the P300 potential. Reward enhanced the amplitude of early and later P300 subcomponents (and the single potential in the case of the sample- and array-elicited P300 in Chapter 6), as well as speeding peak latency.

This was interpreted as suggesting that there was greater contextual updating for target stimuli associated with reward (Donchin & Coles, 1988a; Johnson, 1986; Nieuwenhuis, et al., 2005a; Yeung & Sanfey, 2004). The effects of reward upon $P3_1$ amplitude were typically independent from effects of attention. The $P3_1$ was typically larger and peaked earlier for invalid than valid trials. The results indicated the reward and attention systems may have undertaken independent contextual updating processes. The pattern of $P3_1$ modulation by the two systems also suggested that each might have prioritised different information with respect to contextual updating. For the reward system, the updating of stimulus representations was of greater import when reward was expected or the probability of reward greater. This may relate to the greater relevance of such stimuli to optimising earnings. The attention system, conversely, demonstrated an increased level of updating when spatial expectations were violated. Stimulus representations in such a case may have necessitated updating with the new information provided by the invalidly-presented stimulus.

It was possible that at a late stage of cognitive processing, information from the two systems was integrated to produce a comprehensive stimulus representation that included information pertaining to both reward and attention expectancies. This would account for the interactive effect of reward and attention upon latency or amplitude of the later $P3_2$ component in Chapters 4 and 5 respectively. Given the role of working memory in the process of contextual updating (Donchin & Coles, 1988a), systematic manipulation of the working memory demands in future studies would be useful in examining the nature of the relationship between reward expectation, stimulus prioritisation and working memory.

Reward also modulated the degree of expectation-related activity prior to presentation of the array in Chapter 5. The CNV was larger when the sample stimulus was rewarded, and thus expectation of a reward was greater. This suggested reward altered the state of expectation with respect to an impending stimulus requiring an imperative response. Rather than a broad increase in general arousal with reward as a task factor, motivation was able to increase expectation systematically on a trial-by-trial basis.

7.2.4 Motor preparation

In addition to the observed effects on visual and cognitive processing, reward also modulated motor preparation. There were both independent and interactive effects of reward and attention upon the LRP. The pattern of independence and interaction appeared to depend upon the task parameters. In Chapter 5, the earlier modulation (300-350ms post stimulus) of LRP amplitude by attention was independent from reward. This shifted to an interaction, with reward boosting LRP amplitude on valid but not invalid trials, between 400 and 450ms post stimulus. This was consistent with the early independence of the systems with respect to the N1 and $P3_1$ potentials, with a shift to later interaction in the modulation of $P3_2$. It was perhaps surprising that reward and attention interacted late during motor preparation, given the independent effects of each upon RT. It is possible that the interaction was short in duration, however, with later stages of motor processing, such as response selection, being independently influenced by the two systems.

The pattern of modulation of the LRP differed in Chapter 6. Initially all three experimental factors – target reward, distractor reward and target presence – modulated LRP amplitude in

an interactive manner. The effects of distractor type did not endure beyond early motor preparation (150-200ms post stimulus). In later time windows both target reward and target presence enhanced motor preparation, and did so independently. Though the pattern of modulation differed from that of Chapter 5, the effects were consistent with the pattern of modulation of visual processing in Chapter 6, with an early influence of distractor reward information that did not persist in later stages of processing due to the suppression of the influence of these stimuli. This consistency across visual/cognitive processing and the LRP in chapters 5 and 6 suggested there may be a similar activity of reward and attention upon visual and motor processing.

7.3 Neural Circuitry

The spatial resolution of the ERP method does not allow for precise inference as to the sources of neural activity. Examination of the pattern of modulation of the ERPs in this thesis by reward and attention and their topographical distribution in the context of spatial information gained from neuroimaging, single-unit and lesion studies does, however, allow for speculation as to the underlying neural circuitry responsible for the activity studied in this thesis. The predominantly independent effects of reward and attention until a very late stage of processing suggest the two systems may operate primarily in parallel in the modulation of information processing. Each may generate its own top-down biasing signal, which is used to modulate processing in extrastriate visual regions. One potential source of the reward system biasing signal may be the OFC. This region receives information from subcortical reward regions such as the striatum and amygdala as well as multisensory stimulus information (Kringelbach, 2005; Kringelbach, et al., 2003; Kringelbach & Rolls, 2004; Schultz, 2000). This

would allow integration of visual stimulus information with that of current behavioural goals and trial outcomes, consistent with the proposed role of the OFC in tracking the relative value of rewards for different stimulus options. New outcome information is used to update these stimulus-reward representations under changing environmental conditions (Kringelbach, 2005; Kringelbach, et al., 2003; Kringelbach & Rolls, 2004; Schultz, 2000). This is consistent with the influence of reward upon the contextual updating process, as indexed by the P300, in this thesis. This information could then be used to bias processing on subsequent trials. In addition to this top-down bias, interconnection of reward regions such as the amygdala with extrastriate visual regions may have allowed an early direct influence of the reward system upon visual processing, perhaps partially responsible for the modulation of N1 latency in Chapter 5 (McDonald, 1998).

The sources of attentional biasing signals have been well documented. The FEF is a likely source of the top-down attentional bias signal. The FEF is activated during attentional orienting (Corbetta, 1993, 1998, 2002; Corbetta, et al., 1998; Gitelman, et al., 1999; Kim, et al., 1999; Nobre, et al., 1997). Moreover, stimulation of the FEF modulates firing in extrastriate visual cortical regions such as V4 and enhances the competitive weights of stimuli located at the locus of spatial attention (Armstrong, et al., 2006; Armstrong & Moore, 2007; Moore & Armstrong, 2003; Moore & Fallah, 2004; Ruff, et al., 2008; Ruff, et al., 2006; Taylor, et al., 2007a; Taylor, Nobre, & Rushworth, 2007b). The modulation of visual potentials by attention observed in this thesis might be achieved by means of a biasing signal deriving from the FEF.

In addition to the parallel operation of the two systems, the late-stage interaction upon the $P3_2$suggests there may be some interaction between the reward and attention systems in a

higher processing region. It is possible information from both the reward and attention systems pertaining to the expectations and current context is integrated to form a cohesive, system-independent representation of the current stimulus environment. A likely location of such integration is the ACC. The ACC is highly interconnected with such regions of the attention network as the FEF and PPC (Gitelman, et al., 1999; Kim, et al., 1999; Mesulam, 1999; Nobre, et al., 1997). It also has extensive connections with subcortical reward regions, such as the dopaminergic midbrain (Montague, et al., 2004). The ACC is thus anatomically well-placed to integrate information deriving from the reward and attention systems. As such, the ACC has been functionally implicated reward and attentional processes. ACC activity appears to track the reward prediction error and is vital in the use of recent reinforcement history in the optimisation of behaviour (Amiez, et al., 2005; Amiez, et al., 2006; Walton, et al., 2007). The ACC is also consistently active during attention shifts and orienting of spatial attention (Gitelman, et al., 1999; Kim, et al., 1999; Mesulam, 1999; Nobre, et al., 1997). Cingulate activity has also been demonstrated to be modulated by both attention and reward in studies manipulating both factors. BOLD activity correlated more closely with attentional cue benefit scores when these cues indicated an impending stimulus of motivational significance, such as monetary reward or food under conditions of hunger (Mohanty, et al., 2008; Small, et al., 2005). Such an effect is comparable with the increased use of attentional cues when reward was available in Chapter 3. It must be noted that it was the posterior, rather than anterior, cingulate in which these effects were observed, however. The role of the ACC in the tracking and updating of expectations to guide behaviour with respect to both reward and attention is consistent with the interaction at the contextual updating $P3_2$ processing stage in this thesis.

A further potential region in which reward and attention signals may be integrated is the PPC, in particular the LIP/IPS. The PPC appears to have a role in stimulus salience, whether that be physical salience for use by the attention system or motivational salience of import to the reward system (Bisley & Goldberg, 2003; Goldberg, Bisley, Powell, Gottlieb, & Kusunoki, 2002; Gottlieb, 2007; Gottlieb & Goldberg, 1999; Gottlieb, et al., 1998; Platt & Glimcher, 1999). The study of Peck and colleagues (2009) suggested reward could bias the allocation of attention to a given spatial location. In human studies BOLD activation in inferior parietal cortex was modulated by both reward information and attention. Not only did activation increase linearly with incentive (Engelmann, et al., 2009), but a similar correlation between BOLD activation and cue benefit score as occurred in cingulate cortex was observed (Mohanty, et al., 2008; Small, et al., 2005). The ability of reward-associated yet task-irrelevant stimuli to capture attentional resources in Chapter 6 may be mediated by parietal regions in which reward and attention information converges.

It should be noted that there was a greater degree of interaction between reward and attention in Chapter 6, where targets appeared in a multi-stimulus array and thus greater competition for processing resources ensued. It is possible that the relationship between the reward and attention systems is fluid, with the degree of interaction between the two dependent upon current task conditions. When demands upon processing are high, the systems may interact at more stages of processing and also in more anatomical regions, to ensure the prioritisation for processing of the most relevant stimuli to optimisation of performance. It is therefore possible that parietal regions are sites of integration only when processing demands are sufficiently high. This may account for the lack of an interaction between reward and attention in the study of Bendiksby and Platt (2006). Attentional

demands may not have been great enough to drive an interaction between the two systems in this case.

7.4 Future Directions

The experiments of this thesis have examined the ability of reward expectation to modulate neural activity and behaviour. The results suggested that reward could influence information processing at multiple stages. The exact nature of the effects was highly dependent on task parameters, but overall many of the effects tended to occur independently from attention. Some degree of interaction between the systems was evident, however. This suggested reward may have been able to influence neural processing independently, but that information pertaining to reward and attention may be integrated, particularly in late stages of contextual updating. This would allow for a highly sensitive system, whereby multiple top-down bias signals carrying information with respect to reward contingencies and spatial expectations were able to target processing stages most relevant to the optimisation of task performance, whilst still providing a cohesive representation of the stimulus environment, in terms of reward history, target location, and so forth and allow for the dynamic adaptation to changes in environmental information.

An interesting direction for future research would be to take the concepts and results of this thesis and test them within the context of experiments with a more naturalistic setting. Given the ability of reward information to influence behaviour and information processing in a dynamic manner and also for individuals to learn information relating to stimulus and reward

contingencies, it would be of great interest to study how reward information influences this learning process, both with respect to behaviour and neural activity. Of particular interest would be the way in which reward influences the learning of contingencies relating to reward and attention in a dynamically changing environment, by comparing behaviour and neural activity trial-by-trial during the learning of these contingencies. Research with monkeys and humans has examined the way in which reinforcement history influences choice behaviour (Behrens, et al., 2007; Kennerley, et al., 2006; Rushworth & Behrens, 2008; Walton, et al., 2007; Walton, et al., 2004; Walton, Kennerley, Bannerman, Phillips, & Rushworth, 2006). It would be interesting to extend this work to examine effects across the time course of information processing, which is not possible with the fMRI and lesion studies typically used. It would also be of interest to examine the direct effects upon the more difficult perceptual discrimination tasks, such as utilised in this thesis, rather than the effects upon choice behaviour. One potential course of future study could use natural scenes as the presentation environment, with inherent properties embedded in these stimuli providing predictive information from which reward and attentional contingencies could be cultivated. For example, a scene including trees might indicate that reward was more likely to be available, whilst a car might be a more likely location at which a stimulus will appear. It would be interesting to test stimuli across a range of visibility parameters. This would enable the derivation of measures of modulation on psychophysical perceptual functions and allow for the charting of changes in threshold salience required for stimulus detection with changes in reward information.

It would also be of interest to apply the concepts of this thesis to other experimental methods. Future research could also optimise this course of study methodologically with the use of magnetoencephalography (MEG). The additional spatial sensitivity provided by this method

would allow for greater conclusions as to the location or source of effects. The combination of this increased resolution with the exquisite temporal resolution of the ERP method would provide an even more comprehensive illustration of the effects of reward expectation during information processing. MEG may also help bridge electrophysiological findings with results obtained with the use of fMRI.

Pharmacological manipulations would also be of great interest in helping to unravel the mechanisms for modulation of information processing by reward expectation and attention. Given the vital role of the dopamine system in reward learning, manipulation of dopamine levels to examine the impacts upon behaviour would be of great interest (Fiorillo, et al., 2003; Schultz, 2000). Dopamine levels also influence attentional performance. Accuracy on the five choice serial RT task in rats is improved with the D1 receptor partial agonist SKF 38393, whilst lower accuracy and slower responses result from application of D1 receptor antagonist SCH 23390 (Granon, et al., 2000; Pezze, Dalley, & Robbins, 2007). Manipulating dopamine levels in tasks of the nature of this thesis, as well as that outlined above, would be useful in examining how dopamine levels contribute to task performance with respect to the activity of the reward and attention systems.

The serotonergic system may also play a vital role in probabilistic learning, especially with motivationally relevant feedback. In probabilistic reversal-learning tasks, depletion of serotonin results in impaired reversal learning. There is a greater likelihood to alter response (lose-switch behaviour) on the subsequent trial following negative feedback (Bari, et al., 2010). This is comparable with the increased salience of negative feedback in patients diagnosed with depression (Bari, et al., 2010). Furthermore, the dopaminergic and serotonergic systems may

act as opponent systems, with dopamine tracking reward rate and serotonin tracking punishment rate in a similar manner (Daw, Kakade, & Dayan, 2002). The systematic manipulation of dopamine and serotonin levels during performance of tasks involving the learning and utilisation of reward (and punishment) and spatial contingencies would therefore be of great interest, as well as potentially having clinical applications in disorders such as depression and addiction.

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