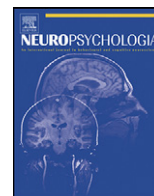




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Modulation of neural activity by motivational and spatial biases

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ABSTRACT

Motivational biases and spatial attention both modulate neural activity and influence behavioural performance. The time course of motivational bias effects, as well as the relationship between motivation and attention across the time course of information processing, however, are relatively unknown. In the present study, event-related potentials (ERPs) were recorded whilst individuals performed a modified Posner task, in which cue stimuli indicated the reward stakes of a given trial and the probable spatial location of a subsequent target stimulus. Reaction times (RTs) were sensitive to motivation and to attention, with faster responses produced on valid and on rewarded trials. In addition, motivation modulated neural activity from the visual analysis of stimuli, with an earlier N1 peak for rewarded compared with non-rewarded stimuli. Effects of motivation were relatively independent from those of attention until late cognitive processing and response production, where motivation and attention interacted to enhance P300-like potentials and the lateralised readiness potential (LRP). The results suggest that multiple sources of modulatory influences may exist, with motivation and attention exerting independent influences over early stimulus and cognitive processing, followed by a late interaction allowing the construction of a comprehensive stimulus representation that contains information pertaining to both motivational and spatial expectations.

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1. Introduction

Our perception is highly biased and adapted to our current behavioural goals. Selective attention is typically considered to be the main set of functions for modulating the processing of incoming information. Top-down signals from a fronto-parietal network of brain regions influence information processing from early perceptual stages through a variety of cellular mechanisms (Corbetta & Shulman, 2002; Kastner & Ungerleider, 2000; Treue, 2003). However, attention is unlikely to provide the only source of bias for perceptual processing.

Functions related to reward and motivation also exercise a powerful influence upon behaviour. Positive consequences increase incidences of behaviour, whilst negative ones diminish it (Skinner, 1966). Given the powerful and evolutionarily pervasive effects of reinforcement learning, a crucial question is whether the reward-related circuitry is also capable of biasing perceptual and cognitive

functions. Whereas much research has demonstrated the powerful role of motivational factors upon motor processing and decision-making (e.g. Rushworth & Behrens, 2008), there has been little investigation of the possible influences of these upon perceptual and cognitive analysis.

The parallels between selective attention and reward-related processing have recently been highlighted. Whereas many studies have conflated manipulations of spatial attention and motivation (Maunsell, 2004), only a few have systematically investigated their separated relative contributions and the relationship between the two (Della Libera & Chelazzi, 2006; Engelmann, Damaraju, Padmala, & Pessoa, 2009; Engelmann & Pessoa, 2007; Kiss, Driver, & Eimer, 2009; Maunsell, 2004; Mohanty, Gitelman, Small, & Mesulam, 2008; Padmala & Pessoa, 2010; Pessoa, 2009; Raymond & O'Brien, 2009; Small et al., 2005). These have not tended to focus on the ability of reward to influence perceptual analysis, although recent studies have begun to examine the effects of reward upon visual search and colour processing (Hickey, Chelazzi, & Theeuwes, 2010; Kiss et al., 2009). Instead, they have mainly focused on how reward and attention may interact to influence overt behaviour (Della Libera & Chelazzi, 2006; Engelmann & Pessoa, 2007; Raymond & O'Brien, 2009) or activity in multisensory brain regions involved in attentional control (Engelmann et al., 2009; Padmala & Pessoa,

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2010; Small et al., 2005). Modulation of activity in visual striate and extrastriate cortex by motivation has been reported in fMRI studies, suggesting motivation is able to modulate perception (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-entrant feedback. To overcome this limitation, in the current study we employ electrophysiological recordings, which have the fine temporal resolution necessary to provide such information.

There are two main possible routes through which reward-related motivational biases could influence perception. Reward and motivation could modulate visual activity indirectly, by acting through the attention system. Regions of prefrontal cortex (such as the anterior or posterior cingulate cortex, ACC and PCC) or posterior parietal cortex are likely target sites for such mediation (Bendiksy & Platt, 2006; Engelmann et al., 2009; Mohanty et al., 2008; Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009; Small et al., 2005). 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 and motivation, independent of the attention system (McDonald, 1998). Prefrontal regions such as the orbitofrontal cortex (OFC) may be the origin of signals that act upon this pathway (Kringelbach & Rolls, 2004). Some combination of the two is also plausible, with interaction between motivation and attention systems at some stages and independence at others.

The primary aims of the present study were to determine whether reward-related motivation biases could influence information processing during perceptual analysis, and to chart the relationship between the effects of motivational bias and spatial attention in modulating information processing. Reward stakes and spatial attention were manipulated on a trial-by-trial basis in a Posner cueing task with a factorial design. Independent and interactive effects of motivational bias and spatial attention were measured on potentials signalling successive stages of information processing between perception and action. Putative perceptual effects were examined on the visual P1 and N1 potentials. Effects upon cognition were examined on the P300 potential, and effects on motor selection and execution were examined on the lateralised readiness potential (LRP). If effects of motivational bias are mediated through the attention system, we would expect to observe interactions in the modulation of potentials by reward stakes and spatial attention. Independent modulation of electrophysiological markers by each factor would suggest separate sources of influences by motivation and attention.

2. Materials and methods

2.1. Participants

Fourteen healthy, right-handed individuals participated in the task (mean age = 23 years, range = 19–31 years, five females). They 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.

2.2. 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 stake available on the given trial for correct performance. The task is illustrated in Fig. 1A.

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 (100 ms, 1.25 degrees in width) that indicated the reward-stake on the given trial and predicted the location of the upcoming target. Reward-stake cues indicated (with 100% validity) whether the upcoming trial would count towards the final remuneration for task performance. Participants were informed that each correct response within

the RT threshold (for which the “reward” feedback was presented) would add £0.20 to their total earnings. Nothing would be added to their earning for fast, accurate responses on non-reward trials. 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. 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 (reward-stakes and spatial location) was counterbalanced across participants. After a variable SOA (800–1200 ms), 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 whilst 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. Participants were informed that only correct responses that were faster than the RT threshold added money to the total earnings. Feedback was provided (100 ms) by centrally presented compound symbolic stimuli (subtending 1.25 degrees). Feedback indicated whether the response was accurate and within the RT threshold. 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 (1800–2800 ms) intervened before the next trial.

2.3. 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, 100 cm 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 3 h.

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.

2.4. 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 512 Hz sampling rate with 100 Hz low-pass filter and 0.16 Hz high-pass filter.

2.5. ERP processing and analysis

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 1200 ms before target stimulus presentation and ending 600 ms 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 $\pm 150 \mu\text{V}$ in any channel, were excluded. Trials containing blinks, deflections greater than $\pm 70 \mu\text{V}$ 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.

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

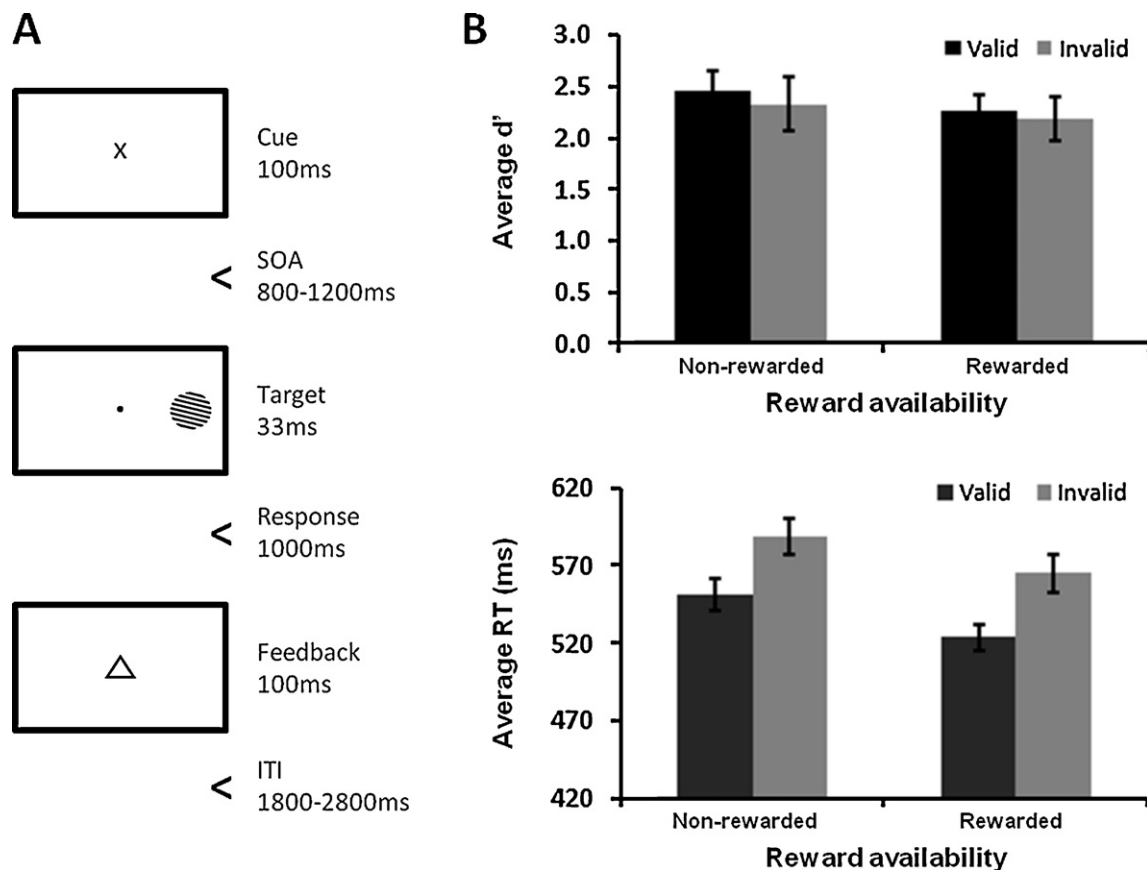


Fig. 1. Task schematic and behavioural results for the experiment of Chapter 5. (A) Trials began with presentation of the cue (100 ms). A variable SOA (800–1200 ms) was followed by presentation of the target stimulus (33 ms). After response, feedback was presented (100 ms), followed by a variable ITI (1800–2800 ms) 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 grey. Error bars use the standard error of the mean.

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 motivation by reward stake and spatial attention on later stages of information processing focused on analysis of the P300 potential, over central electrodes.

In order to investigate how spatial attention and motivation change the time course of the processes that translate perceptual and cognitive analysis into response selection and preparation, the stimulus-locked lateralised potential (LRP) was calculated. The LRP was computed using electrodes C3/C4, located over motor and premotor cortices, using the following formula (Coles, 1989):

$$LRP = \frac{\text{mean}(C4 - C3)_{\text{left-hand}} + \text{mean}(C3 - C4)_{\text{right-hand}}}{2}$$

The LRP reflects the relative lateralisation of neural activity over motor and premotor areas contralateral versus ipsilateral to the responding hand. Because response hand was manipulated orthogonally to the other variables in the task (target location, attention condition, motivation condition), the LRP captures only neural effects that are related to response variables. Time locking to the stimulus emphasises the initial processes of response selection and preparation, rather than the later processes related to response execution (Leuthold, 2003; Leuthold, Sommer, & Ulrich, 1996; Osman & Moore, 1993).

3. Results

3.1. Behavioural results

The effects of reward-related motivation and spatial attention were tested using a repeated-measures analysis of variance (ANOVA) with two within-subjects factors: reward stake (rewarded, non-rewarded) and attention (valid, invalid). Accuracy and RT were analysed. Only correct responses were included in the RT analysis.

Results are shown in Fig. 1B. Performance in the task was highly accurate. Accuracy was 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 stake upon accuracy ($F(1, 13) = 2.52, p = .14$) and no interaction between the two factors ($F(1, 13) < 1, p = .87$). RT was sensitive to both reward stake and attention. Responses were significantly faster for rewarded (mean = 545 ms, SD = 44 ms) than non-rewarded (mean = 570 ms, SD = 45 ms) trials ($F(1, 13) = 21.20, p < .01$). RTs were also faster for valid (mean = 537 ms, SD = 37 ms) than invalid (mean = 577 ms, SD = 46 ms) trials ($F(1, 13) = 30.54, p < .01$). The effects of the two factors upon RT were independent, with no significant interaction between reward stake and attention ($F(1, 13) = 1.43, p = .25$).

3.2. ERP results

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 140 ms post stimulus. The N1 extended slightly more posteriorly in topographical distribution than the P1 and peaked at approximately 190 ms post stimulus. Two late positive peaks were observed, both maximal over central electrode sites. The two were both posterior in distribution, making it unlikely that the first peak was a novelty-induced P3A. The potentials were therefore termed P3₁ and P3₂. The P3₁ extended slightly more anteriorly than the P3₂ and peaked around 330 ms post stimulus. The P3₂ reached a peak at approximately 515 ms post stimulus. The LRP was concentrated over electrode sites C3/C4. This was a slowly developing

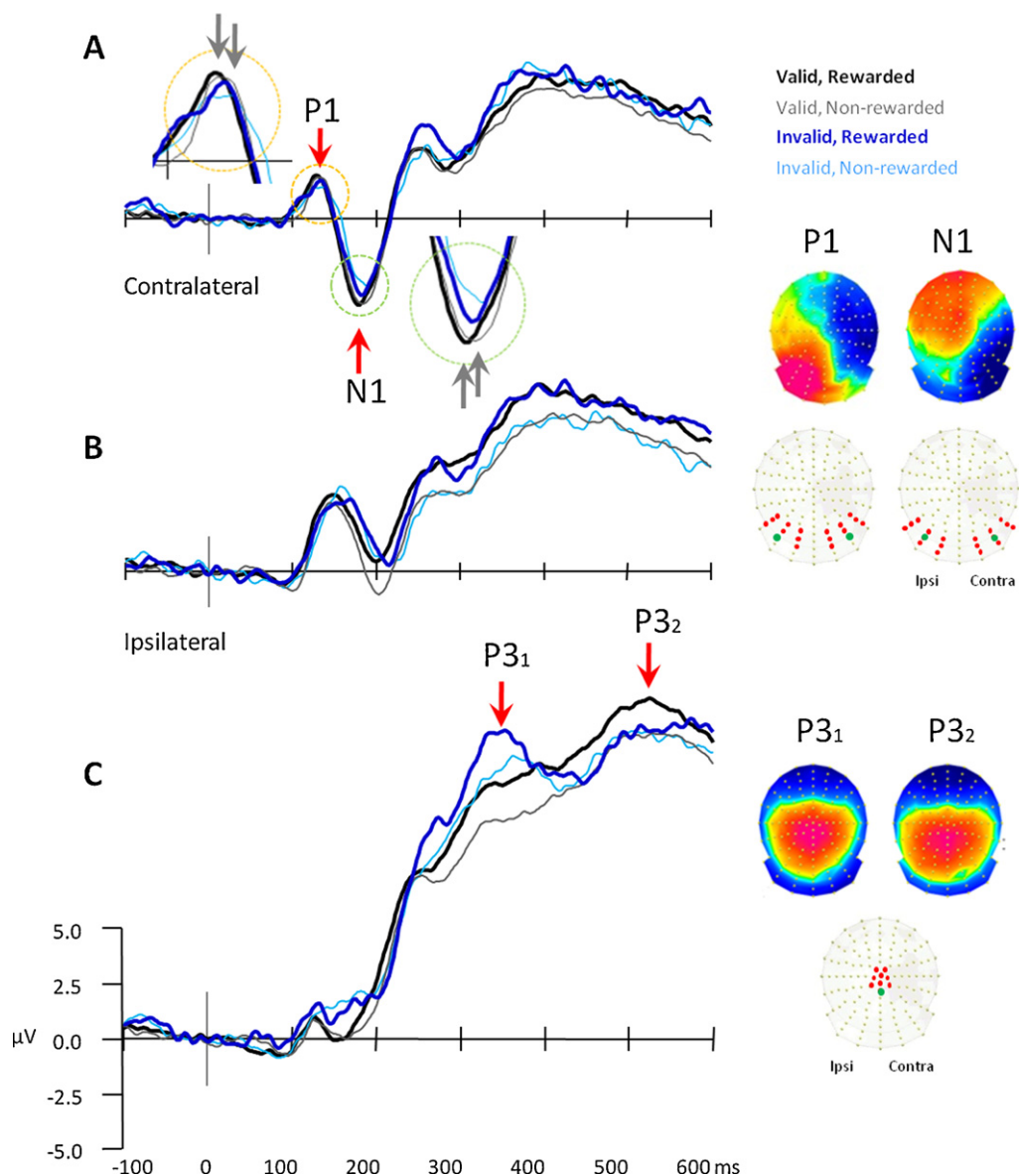


Fig. 2. Grand average waveforms showing the potentials produced in response to presentation of the target stimulus. (A) Grand average waveforms showing the P1 and N1 potentials at the contralateral electrode site. (B) Grand average waveforms showing the P1 and N1 potentials at the ipsilateral electrode site. The topographies of the P1 and N1 potentials are shown on the right. (C) The panel on the left shows the grand average waveforms with the two P300-like potentials indicated. The topographies of these potentials are shown on the right. For all 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, with electrodes plotted in the figures denoted in green. Positive voltage is plotted upwards. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

negative potential, maximal between 350 and 500 ms post stimulus.

The effects of reward stake and spatial attention upon information processing were subjected to repeated-measures ANOVA with factors of reward stake (rewarded, non-rewarded), spatial attention (valid, invalid), hemisphere (ipsilateral, contralateral) and electrode.

3.2.1. Early potentials

The early potentials are illustrated in Fig. 2A and B. The first potential of interest was the P1, peaking around 130 or 140 ms (depending upon hemisphere) at lateral parieto-occipital electrode sites (Fig. 2A). The P1 was analysed 20 ms around the average peak latency at each hemisphere (between 120 and 140 ms contralaterally and 130 and 150 ms 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 or reward stake, nor did the two interact (all $F_s < 1$).

To test for the modulation of latencies of visual potentials by stake and attention, peak detection was performed using the pair of electrodes at which the amplitude for P1 and N1 was maximal. There was an effect of attention on P1 latency ($F(1, 13) = 5.97, p = .03$). The P1 peaked earlier for valid (mean latency = 139 ms, standard error = 3 ms) compared with invalid trials (mean latency = 147 ms, standard error = 6 ms). There was no effect of reward stake ($F(1, 13) = 1.95, p = .19$). The two did not interact ($F(1, 13) = 0.33, p = .58$).

N1 was examined 40 ms around the average peak latency for each hemisphere (160–200 ms contralaterally and 180–220 ms ipsilaterally) (Fig. 2B). A slightly more lateral set of nine electrodes in each hemisphere than examined for P1 was used for analysis, corresponding to cluster around PO7/8, P7/8 and O1/2. There was a significant main effect of attention ($F(1, 13) = 9.11$,

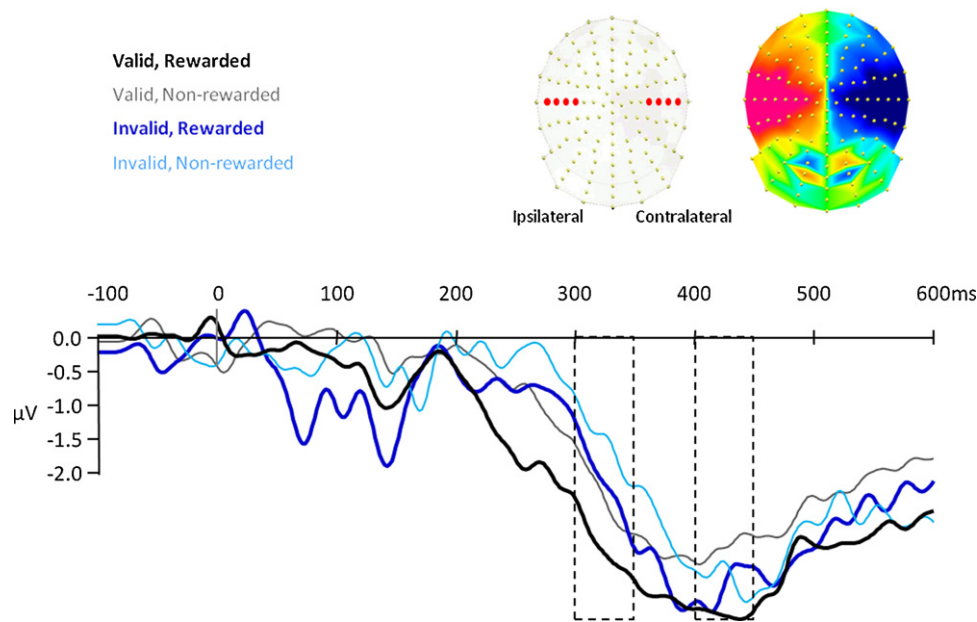


Fig. 3. Grand average waveforms illustrating the derived stimulus-locked LRP potential. Waveforms averaged across the electrodes used for analysis are shown. Dashed boxes illustrate the time periods during which significant modulation of LRP amplitude occurred. Valid trials are plotted in shades of grey, 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

$p = .01$). N1 amplitude was more negative for valid (mean amplitude = $-1.16 \mu\text{V}$, standard error = $0.55 \mu\text{V}$) than invalid (mean amplitude = $-0.46 \mu\text{V}$, standard error = $0.59 \mu\text{V}$) 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 stake ($F(1, 13) = 0.15$, $p = .71$). Reward stake and attention did not interact ($F(1, 13) = 2.71$, $p = .12$).

Peak latency analysis was performed in the same manner as for P1. N1 peak latency was modulated by reward stake ($F(1, 13) = 7.93$, $p = .02$). The N1 peaked earlier for rewarded (mean latency = 190 ms, standard error = 3 ms) than non-rewarded (mean latency = 197 ms, standard error = 2 ms) trials. Validity also tended to decrease the N1 latency, but the effect of attention did not reach significance ($F(1, 13) = 3.32$, $p = .09$). There was no interaction between the factors ($F(1, 13) = .10$, $p = .76$).

3.2.2. Later potentials

Two distinct late positive peaks were observed during the time period of the P300 potential (Fig. 2C). The first P300-like potential ($P3_1$) was prominent over central electrode sites, peaking at approximately 330 ms post stimulus. It was analysed between 300 and 350 ms post stimulus at four electrode sites in each hemisphere and at the midline, surrounding Cz. Reward stake and attention both modulated the amplitude of $P3_1$, and did so independently from one another. There was a main effect of reward stake ($F(1, 13) = 14.17$, $p < .01$). $P3_1$ amplitude was larger for rewarded (mean amplitude = $9.85 \mu\text{V}$, standard error = $1.06 \mu\text{V}$) than non-rewarded (mean amplitude = $8.45 \mu\text{V}$, standard error = $1.16 \mu\text{V}$) 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 = $10.20 \mu\text{V}$, standard error = $1.32 \mu\text{V}$) than valid (mean amplitude = $8.12 \mu\text{V}$, standard error = $0.99 \mu\text{V}$) 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 stake 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 550 ms post-stimulus. This potential differed from the $P3_1$ with a slightly more posterior topography. The CarTool segmentation program identified separate, but highly correlated topographies ($r = 0.94$). The two P300-like potentials were maximal over the same scalp region, thus the $P3_2$ was identified at the same four electrode sites in each hemisphere and at the midline around Cz as were used for $P3_1$ analysis. There was a significant interaction between reward stake 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 stake on valid ($F(1, 13) = 6.56$, $p = .02$) but not invalid ($F(1, 13) = 0.07$, $p = .79$) trials. The $P3_2$ was larger for rewarded (mean amplitude = $12.60 \mu\text{V}$, standard error = $1.06 \mu\text{V}$) than non-rewarded (mean amplitude = $11.31 \mu\text{V}$, standard error = $1.32 \mu\text{V}$) valid 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.

3.2.3. 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 (Fig. 3). This was a slowly developing negative potential, evolving from around 250 ms post stimulus and peaking around 400 ms post stimulus. In order to chart the temporal evolution of the LRP, mean amplitude was analysed in 50 ms time windows between 250 and 500 ms post stimulus at four electrode sites in each hemisphere analogous to the C3/C4 position. The first effects of reward stake and spatial attention on response selection and preparation were independent, and occurred between 300 and 350 ms. In this time window, reward stake modulated LRP amplitude ($F(1, 13) = 5.00$, $p = .04$). The LRP was larger on rewarded (mean = $-1.35 \mu\text{V}$, standard error = $0.26 \mu\text{V}$) than non-rewarded (mean = $-0.82 \mu\text{V}$, standard error = $0.19 \mu\text{V}$) trials. Attention also modulated the LRP during this time window ($F(1, 13) = 7.02$,

$p = .02$). The LRP was larger on valid (mean = $-1.33 \mu\text{V}$, standard error = $0.22 \mu\text{V}$) than invalid (mean = $-0.84 \mu\text{V}$, standard error = $0.22 \mu\text{V}$) trials. Reward and attention did not interact ($F(1, 13) = 0.15, p = .70$). There was no effect of either factor, nor was there an interaction between attention and reward stake, in the 350–400 ms time window (all $F_s < 1$).

In the 400–450 ms time window reward stake and attention interacted to modulate LRP amplitude ($F(1, 13) = 5.04, p = .04$). There was no main effect of reward stake ($F(1, 13) = 2.50, p = .14$) 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 = $-1.72 \mu\text{V}$, standard error = $0.28 \mu\text{V}$) than non-rewarded (mean = $-0.84 \mu\text{V}$, standard error = $0.25 \mu\text{V}$) trials.

4. Discussion

The results of this study extended those of the previous literature by demonstrating clear effects of motivational bias and spatial attention upon behaviour and at multiple stages of information processing. In this experiment, effects of motivation induced by reward stake were evident from the visual analysis of stimuli. Effects of reward stake were primarily independent from those of attention until late cognitive processing ($P3_2$) and later stages of response selection and preparation (late portion of the LRP). This suggested that motivational and attentional systems may have operated in parallel until late stages of processing, where information with respect to reward stake and spatial expectations was integrated for the construction of accurate representations of the current environment and the production of responses.

The present study illustrated the ability of motivational bias to influence behaviour. RT was the sensitive behavioural measure, with responses faster when produced in expectation of reward. There was no effect of reward stake on d' . This suggested reward-related motivational bias may have acted upon the process most relevant to optimisation of behaviour and maximisation of earnings, in this case speed of response. In addition, the effects of reward stake upon RT were independent from those of attention. This suggests that motivation and attention may impact upon behavioural RT measures via largely separate mechanisms. The behavioural measures are unable, however, to show effects at successive stages of processing, providing instead a depiction at the end point of processing. Examination of RT cannot, therefore, rule out the possibility of earlier interactions between reward and attention which are simply not visible at the time of response production. ERPs were therefore also used, to allow for such clarification.

The effects of reward stake upon RT but not accuracy differ from some previous reports of improved accuracy or d' with increased magnitude of expected reward (Della Libera & Chelazzi, 2006; Engelmann et al., 2009; Engelmann & Pessoa, 2007; Raymond & O'Brien, 2009). It is possible that differences in specific task parameters may have led to the discrepancies in the nature of the reward effects. A recent study by Padmala and Pessoa (2010) suggested the relationship between attention and motivation may be greatly dependent upon task parameters. Though both this task and those of Engelmann and colleagues required participants to discriminate visual stimuli, the degraded or faint stimuli utilised in the two studies of Engelmann et al. (Engelmann et al., 2009; Engelmann & Pessoa, 2007) may have placed a greater emphasis on stimulus discrimination, whilst the emphasis was on speed of response in this task. The discrepancy in measures influenced by reward was therefore consistent with the argument that reward targets the process most relevant to performance and payoff optimisation.

Though motivational bias did not modulate accuracy, spatial attention led to improvements in this measure, as well as speeding RTs. These effects replicated that of the prevailing literature (Posner, Snyder, & Davidson, 1977, 1980). This suggests that the absence of motivational effects was not due to deficient task parameters. The attention effects on accuracy suggest there were not ceiling or floor effects that would have precluded the ability to see motivation effects. Furthermore, there were a sufficient number of trials and participants to reveal effects of similar magnitude as those of spatial attention. It is therefore likely that the inability to observe effects of motivational bias on accuracy was due to an absence of effect, rather than a deficiency in the task.

In addition to the effects upon behaviour, motivational bias influenced neural activity at multiple stages from perception to action, beginning with visual analysis of stimuli. Reward-stake cues led to a modulation of the latency of the N1 potential, such that peak were reached earlier for targets in reward trials. The N1 is thought to index discriminative processing of visual stimuli (Hopf, Vogel, Woodman, Heinze, & Luck, 2002). These results thus suggest that discriminative processing may have been more rapidly triggered or was accelerated overall when motivation was increased by means of the reward-signalling cue. This was consistent with the previous argument that reward availability targeted processes most pertinent to optimal task performance, given the necessity to discriminate the tilt of the target grating correctly and rapidly in order to maximise earnings on this task. This early effect of motivational bias demonstrated the ability of the reward system to modulate visual processing on a trial-by-trial basis. This effect is unlikely to be solely due to an increase in arousal, as effects of arousal typically begin later than this stage of processing (Keil et al., 2008; Olofsson, Nordin, Sequeira, & Polich, 2008; Olofsson & Polich, 2007; Palomba, Angrilli, & Mini, 1997; Rozenkrants, Olofsson, & Polich, 2008).

At the early visual analysis stages of processing, the effects of motivation and attention were independent. Whilst both motivation and attention modulated the N1 potential, the modulation by each factor was achieved through different means. Motivation 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). Furthermore, attention, but not motivation, modulated the latency and amplitude of the P1 potential. It is possible that at this stage of processing attention optimised processing to an extent that no effects of motivation could be seen. Alternatively, motivation may not influence processing at this early stage. It must be noted that reward has been demonstrated to influence P1 amplitude when associated with a highly salient stimulus feature such as colour. Hickey et al. (2010) observed an increase in P1 amplitude for stimuli bearing a colour associated with high reward. This amplitude modulation was irrespective of task relevance, occurring for target and distractor stimuli. It is important to note, however, that physical salience is likely to induce a bottom-up capture of attention. This may account for the difference from the lack of P1 effects in the present study, where the reward signal was not attached to a physical feature of the target stimulus. Rather than attracting attention to the reward-associated feature through physical salience, the reward-stake cue in this study likely initiated a different strategy, possibly leading to a greater degree of preparatory processes from the time of cue presentation. These early effects of the reward-signalling cue were likely to occur separately from the changes in processing initiated by the attentional aspects of the cue, given the lack of an interaction of reward and attention upon visual potentials.

Motivational bias continued to influence neural activity at later stages of processing. The amplitudes of both late positive P300-like

potentials were enhanced for rewarded relative to non-rewarded trials. For the earlier P₃₁ potential, this was independent from the action of the attention system. The posterior P300, which both P₃₁ and P₃₂ are likely to reflect, has been hypothesised to reflect contextual updating (Donchin & Coles, 1988; Johnson, 1986; Nieuwenhuis, Aston-Jones, & Cohen, 2005). This suggested stimuli associated with reward in this study received priority for encoding into working memory, or were valued more highly in the construction and updating of stimulus representations (Donchin & Coles, 1988; Johnson, 1986; Nieuwenhuis et al., 2005; Yeung & Sanfey, 2004). The actual outcome of a trial may be compared with expected outcome, with new stimulus information integrated with reinforcement history, behavioural goals and attentional biases in the updating of stimulus-outcome representations (Rushworth & Behrens, 2008; Walton, Crosson, Behrens, Kennerley, & Rushworth, 2007; Walton, Devlin, & Rushworth, 2004).

Attention also modulated the P₃₁, with amplitude larger for invalid spatial cues. Increased P300 amplitude has been observed for less probable, infrequent or novel stimuli (Donchin & Coles, 1988; Johnson, 1986; Nieuwenhuis et al., 2005). 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 motivation and attention modulated P₃₁ 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.

In the later P₃₂ time window, the effects shifted from independence to interaction. As with P₃₁, motivation 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 motivation effects remained consistent with the enhancement by reward of P₃₁ amplitude, the attention effect shifted from greater amplitude of P₃₁ for invalid trials to greater P₃₂ 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 P₃₂ amplitude. Given the greater need to update expectations when predictions were violated, the earlier influence of invalid stimuli was understandable. At this late processing stage the reward and attention systems may have acted to construct a coherent stimulus-outcome representation that encompassed both motivational bias 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.

Effects of motivational bias upon response selection and preparation were examined upon the stimulus-locked LRP to determine whether motivational biases can speed up anticipatory motor preparation and/or whether the neural signals related to motor preparation were intensified by reward stake. Furthermore, the mechanisms of motivational bias were compared to those of attentional bias. The analysis of motor potentials complemented that of visual potentials. Response selection and preparation was influenced by both motivation and attention. Paralleling the results on perceptual and cognitive potentials, the effects on response selection and preparation were initially independent, becoming

integrated only at later stages of the LRP. Motivation enhanced LRP amplitude, suggesting that a greater degree of response selection and 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 response selection and preparation. As with the motivational effect, this was consistent with the behavioural results. Later response-related variables were modulated by motivation and attention in an interactive manner. Reward was observed to boost response selection and preparation for targets occurring at the expected location. This was consistent with the ability of both motivation 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 motivational 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 motivational 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).

In this task, transient changes in arousal may have ensued with presentation of the reward-signalling cues, leading to the observed changes in behaviour and neural activity. Indeed it is possible that changes in arousal may be intrinsic to manipulations signalling that reward is at stake. The faster RTs for reward-cued trials are consistent with a speeding of RTs with increased physiological arousal (Foucher, Otzenberger, & Gounot, 2004; Makeig & Inlow, 1993). In addition, slow positive-wave ERPs are typically enhanced for high versus low arousal, whether arousal level is manipulated by threat of shock or emotional content (Eason, Harter, & White, 1969; Keil et al., 2008; Olofsson et al., 2008; Olofsson & Polich, 2007; Palomba et al., 1997; Rozenkrants et al., 2008). The observation of increased P300 amplitude with reward-signalling cues in this task is consistent with this. It is important to note, however, that accounts of arousal typically suggest increased arousal leads to an increased allocation of attention. Arousal effects are maximal over parietal scalp sites. In addition, the increase in P300 amplitude correlates with a greater likelihood of subsequent recall (Keil et al., 2008; Olofsson et al., 2008; Olofsson & Polich, 2007; Palomba et al., 1997; Rozenkrants et al., 2008). Both of these factors are consistent with greater attentive processing for stimuli associated with increased arousal level. In our task, both the P300 modulation and the effect on RT by reward cues were independent from effects of attention. It is interesting to note that many past manipulations of arousal relate to motivational factors. The threat of shock in the study of Eason et al. (1969) increased motivation to respond correctly. Furthermore, positive emotional images, which typically produce the greatest arousal-related increase in P300 amplitude (despite unpleasant images being rather greater in arousal level) are inherently rewarding (Sabatinelli, Bradley, Lang, Costa, & Versace, 2007). It may be the case that only stimuli or manipulations that have motivational consequences can change arousal. Future experiments will be necessary to disentangle the contributions of reward- and arousal-related mechanisms in the brain. Overall, however, our findings show an additional source of influence over perceptual, cognitive and motor functions, which at certain stages may operate separately from top-down biasing by spatial attention.

Our ERP results cannot address the source of the signals carrying motivational biases to act upon visual processing regions. Identifying the circuitry involved will benefit from single-unit, imaging and lesion studies. Such studies suggest that a potential

pathway by which the observed modulation of visual processing by reward in this study may have occurred is via the striatal-OFC circuit (Hollerman, Tremblay, & Schultz, 1998; Kringelbach, 2005; Tremblay, Hollerman, & Schultz, 1998). The OFC receives sensory input and is a site of integration of sensory and motivational information, and this circuit appears to code and dynamically track the current relative value of stimuli (Kringelbach, 2005; O'Doherty, 2004; Rushworth & Behrens, 2008). It will be of great interest to test such speculations in future work, perhaps with the use of magnetoencephalography, with its greater spatial resolution to allow source localisation, or combined EEG–fMRI.

Previous studies examining the mechanisms of motivation and attention have suggested a predominantly interactive relationship, whereby reward expectation boosts allocation of attention towards stimuli or locations most likely to be associated with reward, or associated with a larger expected reward (Della Libera & Chelazzi, 2006; Engelmann et al., 2009; Engelmann & Pessoa, 2007; Mohanty et al., 2008; Padmala & Pessoa, 2010; Raymond & O'Brien, 2009; Small et al., 2005). In this study we independently manipulated motivational bias and spatial attention, allowing examination of effects of each factor in isolation, as well as a combination of the two. Furthermore, use of the ERP method allows for a more precise tracking of the effects of reward stakes manipulation and attention across the information processing time course, a capability not possible with functional neuroimaging and behavioural measures. The results of this study suggest that it is possible for motivation and attention to influence information processing independently at multiple stages. In this case, the two acted with relative independence until late during processes related to decision making or response production. Given the dependence of the exact pattern behavioural effects on task parameters, however, it is important to note that the precise pattern of independence and interactivity may depend upon task demands. In this task, accuracy results suggest perceptual demands were relatively simple, with greater emphasis upon speed of response (manifest in the motivational effects upon RT but not accuracy). It is possible that with greater perceptual demands, the level at which interactions occur may differ. Further studies will be required to test whether the stages at and mechanisms through which spatial and motivational expectations influence processing and come together are fixed or dependent on the task parameters and goals.

Conflict of interest

The authors have no conflicts of interest to declare.

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