Published in final edited form as:

Cogn Affect Behav Neurosci. 2014 June ; 14(2): 561–577. doi:10.3758/s13415-014-0281-z.

Utilization of reward-prospect enhances preparatory attention and reduces stimulus conflict

Berry van den Berg^{a,c}, Ruth M. Krebs^b, Monique M. Lorist^{c,d}, and Marty G. Woldorff^a

Berry van den Berg: berryv.dberg@gmail.com; Ruth M. Krebs: ruth.krebs@ugent.be; Monique M. Lorist: m.m.lorist@rug.nl; Marty G. Woldorff: woldorff@duke.edu

^aCenter for Cognitive Neuroscience, Duke University, Durham, NC 27708, United States

^bDepartment of Experimental Psychology, Ghent University, 9000 Ghent, Belgium ^cBCN Neuroimaging Center, University of Groningen, Groningen, The Netherlands ^dDepartment of Experimental Psychology, University of Groningen, Groningen, The Netherlands

Abstract

The prospect of gaining money is an incentive widely at play in the real world. Such monetary motivation might have particularly strong influence when the cognitive system is challenged, such as when needing to process conflicting stimulus inputs. Here, we employed manipulations of reward-prospect and attentional-preparation levels in a cued-Stroop stimulus-conflict task, along with the high temporal resolution of electrical brain recordings, to provide insight into the mechanisms by which reward-prospect and attention interact and modulate cognitive-task performance. In this task the cue indicated whether or not the subject needed to prepare for an upcoming Stroop stimulus, and if so, whether there was the potential for monetary reward (dependent on performance on that trial). Both cued-attention and cued-reward-prospect enhanced preparatory neural activity, as reflected by increases in the hallmark attention-related negative-polarity ERP slow wave (CNV) and reductions in oscillatory Alpha activity, which was followed by enhanced processing of the subsequent Stroop stimulus. In addition, similar modulations of preparatory neural activity (larger CNVs and reduced Alpha) predicted faster versus slower response times (RTs) to the subsequent target stimulus, consistent with such modulations reflecting trial-to-trial variations in attention. Particularly striking were the individual differences in the utilization of reward-prospect information. In particular, the size of the reward effects on the preparatory neural activity correlated across-subjects with the degree to which reward-prospect both facilitated overall task performance (faster RTs) and reduced conflict-related behavioral interference. Thus, the prospect of reward appears to recruit attentional preparation circuits to enhance processing of task-relevant target information.

Keywords

attention; motivation; event-related potentials; contingent negative variation (CNV); oscillatory Alpha

Introduction

We navigate through life in complex, dynamic environments, in which the relevance of information around us changes continuously. To efficiently deal with these changes, we use attentional-control processes to select that stimulus information which is most important to us at each moment, resulting in improved task performance on those inputs (Pashler, 1998). It is also the case that the possibility of gaining reward, monetary or otherwise, also tends to improve task performance, as has been shown in terms of faster response times (RTs) and higher accuracy (Bijleveld, Custers & Aarts, 2010), improved visual cognition (Engelmann, Damaraju, Padmala & Pessoa, 2009; Engelmann & Pessoa, 2007; Kristjansson, Sigurjonsdottir & Driver, 2010), better cognitive control (Locke & Braver, 2008) and improved memory (Adcock, Thangavel, Whitfield-Gabrieli, Knutson & Gabrieli, 2006; Krebs, Schott, Schutze & Duzel, 2009; Wittmann et al., 2005). Neuroimaging studies have shown some overlap in brain areas that are activated by reward-prospect and those regions implicated in attentional control, suggesting a relation between these two cognition-influencing factors (Chelazzi et al., 2013; Maunsell, 2004; Bendiksbj & Platt, 2006; Pessoa & Engelmann, 2010; Krebs, Boehler, Egner & Woldorff, 2011; Krebs, Boehler, Appelbaum & Woldorff, 2013; Hickey, Chelazzi & Theeuwes, 2010; Krawczyk, Gazzaley & D'Esposito, 2007). Although attentional control and reward-prospect both seem to modulate the way we cope with continuously changing environmental input and goals, the nature of the interactions between these factors remains elusive.

One key way in which attention and reward-prospect seem to interact is in the wide range of preparatory processes that we need to continually perform to most effectively navigate through our environment, as that environment and our goals change from moment to moment. In fMRI studies, attentional preparation has been shown to be reflected in activation of the fronto-parietal attentional-control network, prior to the performance of a task, particularly in demanding ones (reviewed in Corbetta & Shulman, 2002). Electrophysiologically, attentional preparation has been found to be associated with an enhancement of the fronto-central negative-polarity ERP wave known as the contingent negative variation (CNV: Walter, Cooper, Aldridge, McCallum & Winter, 1964), which has been explicitly linked to activity in the fronto-parietal attentional-control network observed with fMRI (Grent-t-Jong & Woldorff, 2007). Another classical marker for increases in attention and attentional preparation are reduced levels of Alpha-band (8–12 Hz) oscillatory EEG activity (Foxe & Snyder, 2011; Grent-t-Jong, Boehler, Kenemans & Woldorff, 2011), both globally when an individual is less attentive and more specifically for local cortical circuits (Worden, Foxe, Wang & Simpson, 2000), although the relationship of these effects to attention-related CNV modulations is not well understood.

Preparatory attention is not consistently implemented across time, however, which can be observed experimentally by its variation across trials in an experimental session. For instance, Hillyard (1969) showed a strong correlation between preparatory activation, as reflected by the CNV, and within-subject RT performance, suggesting that the CNV reflects a '*common and ubiquitous*' preparatory effect. Similarly, using fMRI, Weissman, Roberts, Visser and Woldorff (2006) showed in a cognitive conflict task that decreased prestimulus activity levels in frontal attentional-control areas were associated with slower RTs,

presumably due to trial-to-trial attentional variations. It is also the case that within-subject performance can be predicted by pre-stimulus fluctuations in oscillatory EEG activity in the Alpha (8–12 Hz) frequency band (Hanslmayr et al., 2007). These various studies indicate that variations in these neural markers of attentional preparation can predict trial-by-trial variations in within-subject behavioral performance.

Preparatory attentional control can also be influenced by cued reward-prospect. For example, in a recent fMRI study, Padmala and Pessoa (2011) cued reward-prospect on each trial of a Stroop-like stimulus-conflict task in which the cue on each trial indicated whether there was a prospect of reward on that trial. The classic behavioral finding in Stroop-like conflict tasks is that participants are slower to respond on incongruent trials than on congruent ones (Macleod, 1991; Stroop, 1934). In the Padmala and Pessoa (2011) study, the reward-prospect cueing resulted in a reduction of the interference cost measured behaviorally for the subsequent target stimuli (incongruent-trial RT versus neutral-trial RT [neutral targets stimuli did not contain conflicting information]). In addition, the cues indicating reward-prospect elicited enhanced activity in the fronto-parietal attentional-control network, as well as in subcortical regions such as the ventral striatum (including the nucleus accumbens) that have been associated with the processing of reward (Aarts, Holstein & Cools, 2011; Camara, Rodriguez-Fornells & Münte, 2008; Delgado, 2007; Haber & Knutson, 2010; Knutson, Adams, Fong & Homme, 2001; Schultz, 2000). The modulations of these neural markers of attention by reward-prospect suggest that one key way that the latter might influence behavior is by marshalling the attentional control network.

Another method to manipulate reward-prospect, in contrast to advance cueing, is to use within-trial reward-associations, such that specific stimuli or stimulus features of the task itself are associated with reward or not. For example, in a recent series of stimulus-conflict studies (Krebs et al., 2010, 2011, 2013) a modified version of the color-naming Stroop task was used in which certain font colors were associated with reward-prospect while others were not. In the fMRI version of this paradigm (Krebs et al., 2011) the findings indicated enhanced fMRI activity in both the frontal-parietal control network and the ventral striatum when processing Stroop stimuli that were associated with reward, again implying important functional interactions between reward processing (here, within-trial reward associations) and attentional control. Behaviorally, these studies also found that conflict-induced behavioral interference was reduced for reward-associated Stroop stimuli, in addition to faster overall RTs. And, lastly, in the electrophysiological version of this paradigm (Krebs et al., 2013), it was found that reward-associations led to an earlier instantiation of the negative-polarity ERP incongruency effect that is typically observed in an incongruent-stimulus versus congruent-stimulus contrast (the Ninc/N450; Hanslmayr et al., 2008; Liotti, Woldorff, Perez & Mayberg, 2000). Such a result suggests that reward associations can induce accelerated conflict detection, followed by reduced behavioral interference effects. It is not known, however, whether such effects would occur when the prospect of reward is cued in advance rather than by stimulus associations, nor whether such effects would also be observed just in response to attentional cueing.

Task manipulation and hypotheses of the current study

To investigate the relationships between attentional control, reward, and behavioral performance, we implemented reward-prospect cueing in a stimulus-conflict Stroop task while measuring high temporal resolution EEG recordings of brain activity, with a particular focus on the cue-elicited electrophysiological markers closely associated with attentional preparation (i.e., cue-triggered CNV and Alpha activations). We used three manipulations: the first was cueing to prepare versus not-prepare, by including trials that began with a cue indicating that a target would appear on that trial and trials that began with a control cue indicating that no target would appear, similar to several previous attentional cueing paradigms using both ERPs and fMRI (Woldorff et al, 2004; Grent-'t-Jong & Woldorff, 2007). The second manipulation, for trials in which a target would be appearing, was cueing whether there was reward-prospect versus noreward-prospect, similar to the fMRI study of Padmala and Pessoa (2010) but now using electrophysiological measures. These two manipulations allowed us to extract in the same study and participants the effect of cueing for reward-prospect versus cueing for attentional preparation. Thirdly, we looked at trial-by-trial variations in attentional preparatory activity as associated with trial-to-trial variations in task performance (fast versus slow RTs) in order to relate these to neural preparatory activity associated with reward-prospect. Thus, this approach provided three cognitive manipulations (attend versus not attend, reward-prospect versus noreward-prospect, and trial-to-trial variations in performance), which we hypothesized would all induce modulations of the classic neural markers (CNV and Alpha) associated with attentional preparation. Moreover, this approach enabled us to also leverage the high temporal resolution of EEG and ERP recordings to relate these cue-elicited variations in brain activity with modulation of behavioral performance and neural activations for the target Stroop stimulus that followed.

More specifically, in response to the cues we expected that the identification of a cue stimulus indicating reward-prospect compared to noreward-prospect would be associated with a larger occipital N2 wave, due to its presumed greater salience (Folstein & Petten, 2008, Krebs et al., 2013; Hickey & Zoest, 2012). More importantly here, however, we expected that the cueing for attentional preparation (for both reward-prospect and noreward-prospect) versus cueing to not prepare (control cues) would elicit enhanced CNVs and decreased Alpha activity prior to the target Stroop stimulus. We also expected that comparison of cueing for reward-prospect versus cueing for noreward-prospect would also elicit an enhanced CNV and decreased Alpha activity, due to the marshalling of the attentional control circuits. In addition, we hypothesized that the CNV would be larger and Alpha would be more decreased when followed by fast responses versus slow responses to the target Stroop stimulus, although these effects might differ depending on whether the trial included reward-prospect or not.

Following the cue, we also anticipated a number of related behavioral and neural effects on the processing of the subsequent target Stroop stimuli. First, behaviorally we expected faster RTs and fewer errors for congruent compared to incongruent Stroop stimuli, as has been classically shown, as well as for reward-prospect trials versus those without such prospect. In addition, we hypothesized that we might observe a reduced behavioral interference effect

(incongruent RTs versus congruent RTs) for reward-prospect trials versus no-reward-prospect trials, as has been found in some previous studies (Krebs et al., 2010, 2013; Padmala & Pessoa 2011). Neurally, we hypothesized that the enhanced preparatory activity that we expected to observe in response to reward-prospect cues would be followed by attention-related modulations on the processing of the target Stroop stimuli, which would be reflected by larger N2 and P3 waves to those target stimuli. In addition, we anticipated that if advanced cueing of reward-prospect could indeed modulate the processing of stimulus conflict, then we would also see a reduction in the size or latency of the conflict-related negative deflection, the Ninc, and the associated subsequent late positive wave known as the LPC (Liotti, Woldorff, Perez & Mayberg, 2000).

Lastly, to further dissociate the processes involved in attention and reward-prospect, we looked at individual differences in these effects by examining between-subject correlations of task performance with the associated neural activations. More specifically, we hypothesized that participants who were better able to utilize the reward-prospect information, as reflected by larger modulations of the cue-triggered preparatory activity with reward-prospect, would show greater facilitation of the Stroop stimulus processing and in turn greater reduction in conflict-related interference in the context of reward.

Methods

Participants

Twenty-nine healthy volunteers (15 male and 14 female with a mean age of 22.4 [SD: 4.1] and 23.3 [SD: 3.9] years, respectively) participated in the study. All participants had intact color vision and normal or corrected-to-normal visual acuity. Five participants were left-handed while 24 were right-handed. One participant was excluded from the analysis due to excessive noise in the EEG data (i.e., over 50 % of the EEG trials contained artifacts). All participants gave written informed consent as reviewed in accordance with the Declaration of Helsinki by the Duke Medical Center Institutional Review Board. Participants were paid 15 dollars an hour plus reward-associated bonuses accumulated over the experiment (mean bonus = 18.5 dollars, SD = 1.0).

Apparatus

The task was programmed using the Presentation software package (version 14.1, <http://www.neurobs.com/>) for psychological experiment design. Stimuli were randomized using the R statistical programming software package (R Development Core Team, 2013). Stimuli were presented on a 60Hz CRT monitor. Participants interacted with the Presentation software using a Logitech precision gamepad (<http://www.logitech.com/>). EEG was recorded using a 64-channel, custom-designed, extended-coverage Duke electrode cap (Electrocap, Inc., Eaton, OH) connected to a Neuroscan amplifier, using a right-mastoid reference during recording.

Task and Stimuli

In all trials (see Figure 1 for an overview), a cue stimulus (400 ms duration) was presented first. In 80% of the trials, the cue indicated that there would either be reward-prospect (40%

of trials, indicated by a '\$') or no-reward-prospect (40% of trials, indicated by a '&'), and was followed by a Stroop color-word stimulus, to which participants had to respond to the font color by pressing a pre-specified button on the gamepad. These Stroop stimuli consisted of randomly selected color words (i.e., "RED", "GREEN", "BLUE", and "YELLOW"), which were printed in the semantically corresponding font color on half of the trials (congruent targets) and in a different font color on the other half of the trials (incongruent targets). The other 20% of the trials were control trials, in which the cue ('#') indicated that no target Stroop stimulus would follow and thus the subject did not need to prepare for it.

In the reward-prospect trials, participants could either gain 10 cents if they responded correctly and sufficiently quickly (see below for a description of criteria), or lose 10 cents if their response was incorrect or too slow. Participants were given feedback about their performance every 10 trials by a two-second feedback screen containing the acquired monetary reward balance. In the no-reward-prospect trials, there was no gain or loss involved. In both the reward-prospect and no-reward-prospect conditions, the Stroop stimulus would follow at either a short stimulus interval (33% of the trials, SOA of 700 ms [400 ms cue duration + 300 ms fixation]) or a long stimulus interval (66% of the trials, SOA of 1300 ms [400 ms cue duration + 900 ms fixation]). Intertrial-intervals following the reward-prospect and no-reward-prospect trials, during which only a fixation cross was present, were varied between 1000 and 1400 ms. Intertrial-intervals following control trials, during which only a fixation cross was present and no Stroop target word would occur or be expected, were varied between 1600 and 2000 ms.

To account for individual differences in RT and to keep all participants at a reward rate of approximately 70% (equivalent to a gain of around 19 dollars at the end of the experiment), a reward-related response window was set in which the subject needed to respond, with the upper bound of the response window being adjusted dynamically. More specifically, if the hit rate of the last 10 reward-prospect trials was lower or higher than 70%, 10 ms were either added or subtracted to the response window, respectively. Note that these adjustments to the reward-eligible response window only affected the feedback for the participants and were not indicative of whether or not the trial was included in the behavioral and ERP analyses.

Procedure

Participants were positioned with their eyes 60cm from the screen, which resulted in a visual angle of ~1.5 by 5 degrees for the Stroop word stimuli. Participants were instructed to respond as quickly and accurately as possible. Behavioral responses were given with the index and middle finger of both the left and right hand (counterbalanced) using a gamepad in which the front bumpers were assigned to the four possible font colors. After task instructions, a short practice session followed (30 trials), which was repeated until participants achieved a hit rate of over 90%, and in which the participant received positive feedback on reward-prospect trials if they responded correctly and faster than 900 ms. The subsequent experimental session consisted of 11 blocks of 100 trials each. After each block participants could take a break if they wished.

EEG recording and data analysis

For the compound event trials (i.e., having a cue stimulus followed by a Stroop target stimulus), we used a design that had *REWARD* (reward-prospect versus noreward-prospect) and *CONGRUENCY* for the Stroop stimulus (congruent versus incongruent) as independent variables. In addition, for trial-to-trials variations of within-subject task performance we defined the factor *SPEED* (fast RT trials versus slow RT trials), which was based on a median split within each condition and within each subject. Only reward-prospect and noreward-prospect trials that had a long cue-to-Stroop-stimulus interval were included in the behavioral and ERP analysis (~140 trials for each condition), in order to be able to cleanly assess the cue-triggered activity in the cue-target interval. The short cue-to-Stroop-stimulus intervals were included to make sure that participants started preparation for the upcoming target as soon as the cue appeared onscreen. EEG recording was done with electrode impedances below 2 k Ω for the mastoids and ground electrodes below 5 k Ω for the remaining electrodes. All channels were recorded using an online high-pass filter of 0.01 Hz, low-pass filter of 100 Hz, and a sampling rate of 500 Hz. Offline, the data was digitally filtered using a 30 Hz low-pass filter. Additional pre-processing included segmenting the data into time-locked epochs and rereferencing to the algebraically averaged mastoids.

The ERP analysis was based on 2000 ms epochs (including 500 ms before event onset), locked to the onset of the cue for cue-related responses and to the onset of the target Stroop stimulus for the Stroop processing. Epochs containing eye blinks between 100 ms pre-cue / pre-Stroop-stimulus and 200 ms post-cue/post-Stroop-stimulus were rejected, thereby ensuring that participants were actually viewing the stimulus in a given trial. Outside of this window, eye blinks were corrected using independent components analysis (ICA). For each participant, trials in which multiple behavioral responses were recorded, or where the behavioral responses were outside a 200–1200 ms post-Stroop-stimulus response window or outside an interval of ± 2 SD around the mean RT (for that subject and within each condition), were considered outliers and were excluded from the analysis. In addition, trials containing any remaining EEG artifacts (eye movements, muscle activity, drifts; approximately 10% of all data) and trials with incorrect behavioral responses were rejected from inclusion in the analyses. Fast and slow trials were also selectively averaged, using a median split (for each subject) on the RTs within each condition. ERP preprocessing and analysis was performed using the Matlab (MATLAB Release 2013a) in combination with EEGLab (Delorme & Makeig, 2004) and Fieldtrip (Oostenveld, Fries, Maris & Schoffelen, 2011). Time-frequency decomposition was performed using a Hanning taper window with a decreasing width for higher frequencies to control temporal smoothing (seven cycles per time window, resulting in a window of $1/\text{Hz} \times 7$ [e.g., for 12 Hz: $1/12 \times 7 = 580$ ms]) from 4 to 20 Hz in steps of 1 Hz, from 0.5 s pre-cue to 1.5 s post-cue in steps of 50 ms. (To accommodate the wider windows for lower frequencies, longer epochs were generated before performing time-frequency decomposition). For the oscillatory power analyses, a baseline correction from 500–200 ms before cue onset was applied, yielding activity measures in units of dB change compared to baseline.

Statistical Analysis

The following regions of interest (ROIs) were defined: occipital, parietal, centro-parietal, central, fronto-central, and frontal. Intervals for measuring ERP components were defined by collapsing the ERPs over all conditions, using a subsequent orthogonal selection of interval for each component. For the cue-triggered ERPs, the occipital N1 component was defined as activity across the 140–180 ms post cue interval over the occipital ROI. The N2 component (negative occipitally and positive frontally) was calculated as a mean amplitude across the 200–300 ms interval over the occipital and frontal ROIs. The cue-triggered CNV activity was measured in the latter half of the cue-Stroop-stimulus interval (i.e., between 700–1200 ms) in the fronto-central ROI (Grent-‘t-Jong & Woldorff., 2007). For the target-stimulus-locked ERPs, the N2 (also appearing as negative occipitally and positive frontally) was measured as the mean amplitude between 150–200 ms over the occipital and frontal ROIs. This interval was earlier compared to the latency found by Krebs et al. (2013), but because the topography as described in the results section overlapped the topography found by Krebs et al. (2013) we will refer to this component as the N2. The P3 to the Stroop target stimuli was defined by a parietal ROI in the 300–600 ms post-Stroop-stimulus interval. However, the effect of reward-prospect on the target P3 was notably more anterior and started earlier, perhaps reflecting a P3a like enhancement; for this reason; we also selected frontal ROI for the P3 enhancement by reward-prospect in the 200–500 ms post stimulus interval and report the statistics for both the frontal and parietal ROIs. For the conflict-related Ninc component, a centro-parietal ROI over 300–500 ms was used, and for the longer-latency LPC a parietal ROI was used over 700–900 ms post-stimulus interval. For the oscillatory analyses, we used the fronto-central and occipital ROIs to match the CNV and occipital sensory ERP effects. We specifically focused on activity in the Alpha band (9–11 Hz). To make sure we would optimally capture the Alpha effects to the cue, we defined a window from 500–1200 ms post-cue-interval. Statistical analyses were done using the R statistical programming environment (R Development Core Team, 2013). Repeated-measures ANOVAs (rANOVAs) were run on the behavioral and ERP / time-frequency effects. Effect sizes were reported for the rANOVA’s, using the generalized η^2 (η_g^2 ; Bakeman, 2005). For correlations, the R^2 values are reported.

Results

Behavioral Results

Participants responded more slowly to incongruent Stroop stimuli compared to congruent ones (see Figure 2 for RT values; $F_{1,27}=142$, $p<0.0001$, $\eta_g^2=0.11$) and had higher error rates (0.08 versus 0.04, $F_{1,27}=25.0$, $p<0.0001$, $\eta_g^2=0.12$). In addition, for Stroop stimuli cued by reward-prospect participants responded faster compared to trials cued by noreward-prospect (see Figure 2; $F_{1,27}=29.8$, $p<0.0001$, $\eta_g^2=0.026$) and decreased error rates (0.05 versus 0.07; $F_{1,27}=11.8$, $p=0.002$, $\eta_g^2=0.023$). Based on previous studies we expected participants to show reduced behavioral *interference* (incongruent *minus* congruent) in the reward-prospect compared to the noreward-prospect condition. In contrast to this hypothesis, however, no reduction of interference was observed (congruency*reward-prospect: $F_{1,27}=0.27$, n.s.).

However, we did observe a large variability across-subjects in both the size of the interference reduction (mean 2.43 ms, SD: 24.9 ms), and in the reward-prospect effect (reward-prospect minus noreward-prospect; mean 30.9 ms, SD: 29.9). Importantly, there was a robust correlation across participants between the interference effect and the reward-prospect effect ($R^2 = 0.27$, $p = 0.005$; see also Figure 2D), showing a relationship between the utilization of the advanced information about reward-prospect and the degree to which participants were able to actually reduce interference in the reward-prospect condition. In addition, analysis of the standard deviations (SDs) of the RT distributions revealed a decrease in the SDs in the reward-prospect compared to the noreward-prospect condition ($F_{1,27} = 15.6$, $p = 0.0005$, $\eta_g^2 = 0.020$). Similarly, the SD was decreased for congruent compared to incongruent stimuli ($F_{1,27} = 35.0$, $p < 0.0001$, $\eta_g^2 = 0.078$). For the analysis of neural measures we used a median split of RTs for the factor SPEED, which resulted in the following mean RTs ($\pm$ SD): reward-prospect; fast RTs – 517 ms (± 57), reward-prospect; slow RTs – 693 ms (± 74), noreward-prospect; fast RTs 539 ms (± 59), noreward-prospect; slow RTs 731 ms (± 80) (median split was done separately for the congruent and incongruent conditions [using the mean], but is collapsed here).

ERP results

Cue-processing: effects of reward and speed—Cues that indicated reward-prospect compared to noreward-prospect elicited a larger occipital visual N1 around 150 ms (occipital ROI: $F_{1,27} = 11.18$, $p = 0.002$, $\eta_g^2 = 0.015$). This enhanced occipital N1 enhancement with REWARD was followed at 250 ms by an enhanced occipital negativity, presumably an N2 ($F_{1,27} = 21.2$, $p < 0.0001$, $\eta_g^2 = 0.013$) with similar scalp distributions as the N1 enhancement, but with the occipital negativity paired with a larger frontal positivity ($F_{1,27} = 19.0$, $p = 0.0002$, $\eta_g^2 = 0.017$; ERP results are visualized in Figure 3). This complex shows a similar topography as the occipital N2/ frontal P2 complex reported by Krebs et al. (2013). In addition to an enhancing effect of REWARD on the frontal P2 positivity, there was also an interaction between SPEED and REWARD on the frontal ROI at this latency ($F_{1,27} = 8.9$, $p = 0.005$, $\eta_g^2 = 0.004$). Following the N2-latency modulations by REWARD, there was an effect on the parietal P3 (300–600 ms after cue onset) for both REWARD (larger for reward-prospect cues) ($F_{1,27} = 11.8$, $p = 0.002$, $\eta_g^2 = 0.017$) and the interaction between SPEED and REWARD ($F_{1,27} = 7.25$, $p = 0.012$, $\eta_g^2 = 0.003$). A similar enhancement for the P3 was observed when the cue was followed by a fast compared to a slow response on the target noreward-prospect trials.

Between 600 and 1300 ms after cue onset, ERPs elicited by both the noreward-prospect and reward-prospect cues, relative to the control cues, showed a robust enhancement of the fronto-central negative-polarity wave characteristic of the hallmark contingent negative variation (CNV) that is a marker for attentional preparatory activity (Luck 2005). This CNV was largest for reward-prospect, fast RT trials and smallest for noreward-prospect, slow RT trials. The relationship with RTs was most apparent in the later time range of the CNV (Figure 3C). The reward-related CNV enhancement (reward-prospect minus noreward-prospect) started as a negative deflection bilaterally over frontal and central sites and moved

more posteriorly over time, similar to the CNV for the cued-reward and cued-noreward trials relative to the control cues, and similar to previous reports of cued attentional preparatory activity (Grent-‘t-Jong & Woldorff, 2007). The relation between CNV size and behavioral RTs was particularly strong for noreward prospect trials, but mostly disappeared when reward-prospect was at stake. Statistical analyses of the CNV (measured from 700 until 1200 ms with a fronto-central ROI) confirmed these effects: namely, a main effect of SPEED ($F_{1,27} = 6.25$, $p = 0.019$, $\eta_g^2 = 0.011$), a main effect of REWARD ($F_{1,27} = 22.1$, $p < 0.0001$, $\eta_g^2 = 0.10$), and an interaction between SPEED and REWARD ($F_{1,27} = 4.33$, $p = 0.047$, $\eta_g^2 = 0.005$).

The ERPs elicited by the Stroop target stimuli showed no differences with regard to the factors of REWARD or SPEED until 150 ms (Figure 4). On trials with reward-prospect the versus noreward-prospect, target stimuli first elicited a larger frontal positivity in the 150–200 ms latency range ($F_{1,27} = 17.0$, $p = 0.0004$, $\eta_g^2 = 0.018$), which was paired with a simultaneous enhanced bilateral negativity over the occipital channels ($F_{1,27} = 4.7$, $p = 0.04$, $\eta_g^2 = 0.0024$). This effect has a similar topography as the occipital N2/ frontal P2 complex reported by Krebs et al. (2013) and the N2/P2 during the cue phase, although the target-evoked N2/P2 occurred notably earlier, with a latency closer to the N1 in the cue phase. There was also an effect of SPEED (larger occipital N2 for faster RT trials) and an interaction between REWARD and SPEED on the occipital N2 (SPEED: $F_{1,27} = 13.0$, $p = 0.0012$, $\eta_g^2 < 0.01$; SPEED $\times$ REWARD: $F_{1,27} = 4.6$, $p = 0.04$, $\eta_g^2 < 0.01$), with the N2 being larger for rewarded fast trials, but the effect of N2 by SPEED was only significant in the noreward condition. The interaction between SPEED and REWARD on the N2 effect was similar to the CNV enhancements, with the effect of SPEED being mostly absent in the reward-prospect condition.

The above effects of reward-prospect in the 150–200 ms time range were followed by a positivity in the P3 latency range (parietal ROI: $F_{1,27} = 9.6$, $p = 0.005$, $\eta_g^2 = 0.019$; frontal ROI: $F_{1,27} = 29.9$, $p < 0.0001$, $\eta_g^2 = 0.038$). We also observed an effect of SPEED (larger for faster RTs) on this component, as well as an interaction between SPEED and REWARD. The effect of SPEED on the P3 was larger in the reward-prospect condition compared to the noreward-prospect condition (SPEED: parietal ROI: $F_{1,27} = 71$, $p < 0.0001$, $\eta_g^2 = 0.09$, frontal ROI: $F_{1,27} = 37.7$, $p < 0.0001$, $\eta_g^2 = 0.054$; SPEED $\times$ REWARD: parietal ROI: $F_{1,27} = 10.0$, $p = 0.004$, $\eta_g^2 = 0.0024$, frontal ROI: $F_{1,27} = 8.98$, $p = 0.006$, $\eta_g^2 = 0.003$), which was similar to the observed interaction with the P3 enhancement during the processing of the cue, but opposite in direction from the effect of SPEED $\times$ REWARD on the CNV. Note that the reported F-values were extracted from both the parietal ROI and frontal ROI. The parietal ROI would be a typical topographical location of a P3 effect, while topomaps revealed the P3 effect of reward-prospect to be larger more anteriorly, where it started somewhat earlier, perhaps representing more of a P3a-like component.

The hallmark negative-polarity incongruency-related component (Ninc), as defined by comparing incongruent versus congruent target stimuli (), did not differ as a function

of REWARD (Figure 5; Ninc: CONGRUENCY $\times$ REWARD:), paralleling the RT pattern for these factors. In the same comparison, the Ninc was followed by a late positive component (LPC) in both the reward-prospect and noreward-prospect condition, again with no interaction between these factors. (LPC: CONGRUENCY $\times$ REWARD:).

Correlation analyses

To investigate the relationship between the neural and behavioral effects of our manipulations, we defined two behavioral effects that were indicative of how participants used the reward-prospect information and examined how these behavioral effects correlated with REWARD effects in the ERPs. For the first behavioral measurement of reward utilization, we used the overall acceleration of the RT with reward-prospect (reward-prospect minus noreward-prospect). The second measure was the ability to minimize cognitive conflict as a function of REWARD (reduction of behavioral interference with reward-prospect compared to noreward-prospect). Neural reward-prospect effects included the enhancements to the cue and target-elicited responses described above, as well as the conflict-related Ninc and LPC. The neural-behavioral correlations are summarized in Figure 6.

The correlation analyses showed a close relationship across subject between the sizes of neural reward-related enhancements and the two behavioral markers of reward utilization. First, the behavioral RT acceleration correlated with the reward-related enhancements of both the cue-triggered CNV (Figure 6A) and the target-triggered frontal P3 enhancement (Figure 6B) with reward-prospect ($R^2=0.24$, $p=0.008$ and parietal ROI: $R^2=0.24$, $p=0.009$, Frontal ROI: $R^2=0.28$, $p=0.004$). Moreover, these two neural effects of reward-prospect were correlated with each other (parietal ROI: $R^2=0.34$, $p=0.001$, Frontal ROI: $R^2=0.65$, $p<0.0001$), i.e., the larger the reward-prospect effect on the CNV, the larger the P3 enhancement with reward-prospect (and the greater the RT acceleration). As mentioned above, participants showed no overall reduction of interference, measured behaviorally or neurally, on reward-prospect trials. In contrast, across-subjects, there was a neural-behavior relationship between the reward-related reduction of behavioral interference and the CNV and target related P3 enhancement by reward-prospect, with participants who elicit larger cue-triggered CNV and frontal target P3 modulations by reward-prospect also showed reduced behavioral interference with reward-prospect ($R^2=0.28$, $p=0.004$ and parietal ROI: $R^2=0.16$, $p=0.035$, Frontal ROI: $R^2=0.20$, $p=0.017$). Noteworthy, is that between-subjects behavioral variance was not correlated with earlier enhancements in both the cue (N1) and target (N1 and N2) ERPs by reward-prospect.

Effect of reward-prospect on cue-evoked oscillatory Alpha activity

To look at effects on time-locked oscillatory Alpha activity, two ROIs (fronto-central and occipital) were used (for an overview of the time-frequency results see Figure 7). Inspection of the spectra (Figure 7A) revealed a power increase in the low-Alpha-band range (7–9 Hz), over the latency of 100–300 ms after cue onset in the occipital ROI for reward-prospect cues compared to noreward-prospect ones (occipital: $F_{1,27} = 8.82$, $p = 0.0044$, $\eta_p^2=0.02$). This effect may be largely due to an enhancement of the occipital N2 (correlation: $R^2=0.41$,

$p=0.0003$). In the Alpha-band (9–11Hz), during the period of the CNV (500–1200 ms), participants showed an effect of both SPEED and REWARD in the occipital channels (REWARD: $F_{1,27} = 19.9$, $p = 0.0002$, $\eta_g^2=0.09$; SPEED: $F_{1,27} = 12.2$, $p = 0.0016$, $\eta_g^2=0.016$). In the fronto-central channels there was an effect in Alpha for SPEED (more reduction of Alpha for faster trials), for REWARD (more reduction for reward-prospect trials), and an interaction between the two (REWARD: $F_{1,27} = 9.7$, $p = 0.0043$, $\eta_g^2=0.07$; SPEED: $F_{1,27} = 5.05$, $p = 0.033$, $\eta_g^2=0.009$; SPEED $\times$ REWARD: $F_{1,27} = 4.9$, $p = 0.036$, $\eta_g^2=0.01$). Interestingly, this interaction followed the opposite pattern compared to the CNV (Figure 8), with Alpha paralleling the P3 enhancements during the cue and target phase. More specifically, fronto-central Alpha showed a large difference between slow and fast RT trials for the reward-prospect condition, and very little difference in the noreward-prospect condition. This is in sharp contrast to the fronto-central CNV pattern (described above), in which the slow and fast RT trials showed a large difference in the noreward condition. After normalization to control for differences between Alpha and CNV effects, this differential interaction pattern was confirmed by a interaction (SPEED $\times$ REWARD $\times$ NEURAL MEASURE ()).

Modulations of the cue-triggered occipital Alpha did not correlate across-subjects with the reward-prospect RT effect ($R^2 = 0.10$, $p = 0.10$), but data inspection revealed a particularly strong outlier with regard to the occipital Alpha reductions by reward-prospect compared to noreward-prospect (mean: -0.76 dB, SD: 0.91 dB, outlier value: -4.6 dB). We thus ran a form of robust regression known as an M-estimation linear model, which revealed a relationship of occipital Alpha with reward-prospect ($t_{27} = 3.21$, $p = 0.004$). No relationship was found between interference reduction and occipital Alpha ($R^2 = 0.11$, $p = 0.09$). Within the fronto-central ROI, Alpha reductions correlated both with the reward-prospect RT effect and reduced interference (respectively: $R^2=0.15$, $p = 0.039$ and $R^2 = 0.14$, $p = 0.046$, respectively; see also Figure 7) as well as with enhanced CNV size ($R^2 = 0.18$, $p = 0.027$). Specifically, the larger the CNV enhancement, the more the decrease in Alpha.

Discussion

Summary

The overarching goal of the present study was to gain insight into the neural mechanisms by which reward-prospect and attentional control interact, in the context of a task requiring processing of conflicting stimulus inputs. We recorded electrical brain activity during a cued-reward Stroop paradigm, in which we specified three attention related within-subject factors of interest; attentionally prepare versus not-prepare, reward-prospect versus noreward-prospect, and trial-to-trial variations in attention as reflected by slow and fast responses to the subsequent Stroop stimulus). We also looked at how the effects of reward-prospect on preparatory brain activity ramified into task performance on the Stroop stimulus. The results indicate a number of key findings: Behaviorally, participants responded faster when cued with reward-prospect compared to noreward-prospect. Neurally, we saw several effects on the cue-triggered activity: (A) there were effects of attentional preparation, reward-prospect, and within-subject task performance on both the CNV and the pretarget

oscillatory Alpha. (B) Reward-related CNV increases and Alpha decreases within-subjects ramified into faster overall RTs, but not into reductions in either the behavioral or neural markers of conflict processing. (C) Across-subjects, however, reward-related CNV increases and Alpha decreases correlated positively both with overall RT acceleration and with conflict-effect reduction. Interpretation and implications of these results are discussed below.

Reward-predicting cues triggered enhanced early-latency neural activity

Cue stimuli that signalled the prospect of reward induced several relatively early-latency effects on the sensory ERPs to those cues: in particular, enhancements of ERP components in the 100–300 ms range. Most novel in this regard was an enhancement of the cue-triggered N1 component over visual cortices. Modulations of the N1 amplitude have been associated with different forms of selective attention (Mangun & Hillyard, 1991; Hillyard & Anllo-Vento, 1998), suggesting that the observed N1 enhancement likely reflects enhanced sensory processing of the reward-predicting cue due to its greater saliency (see also Hickey, Chelazzi & Theeuwes, 2010; Hickey & Zoet, 2012;). Subsequently, we observed a reward-related enhancement of the occipital N2 component, which had a similar distribution as the early N1 but was paired with a frontal positivity (similar effects were observed by Krebs et al., 2013). N2 amplitude enhancements have been associated with the orientation of attention towards information that is relevant, such as relevant pop-outs in a visual search array (Luck & Ford, 1998) or stimuli associated with reward (Schupp, Flaisch, Stockburger & Junghöfer, 2006). In line with these findings, the enhancement of the N2 would appear to reflect the relevance of reward-prospect and the related increase in attention towards the further processing of this information. In other words, after identifying that a cue predicted reward-prospect (N1), participants seem to allocate more attention towards that reward-predicting stimulus (N2).

Particularly striking in the present results was a robust boosting of the CNV with reward-prospect in the later period of the cue-stimulus interval. This CNV boosting started anteriorly and moved more posteriorly with time. This frontal-to-parietal topographic shift is in line with previous literature on top-down attentional control in the fronto-parietal attentional network (Grent-‘t-Jong & Woldorff, 2007; Buschman & Miller, 2007; Nagai et al., 2004). Moreover, we have recently observed a similar enhancement of the CNV in response to reward-prospect cues in an attentional cuing paradigm (Schevernels, Krebs, Santens, Woldorff & Boehler, 2014). With regard to the underlying neural generators of this reward-elicited CNV modulation it is worth considering the results of a previous fMRI study that employed a cued rewarded Stroop task similar to the current one (Padmala & Pessoa, 2011). Specifically, the authors found enhanced neural activity for reward-prospect compared to noreward-prospect cues in a network of fronto-parietal attentional control regions, which have been closely associated with the generation of the CNV (Grent-‘t-Jong & Woldorff, 2007).

The noticeable CNV increase by reward-prospect, on top of the increased CNV by the active preparation (control cue versus noreward-prospect), along with variations due to within-subject task performance (fast versus slow RTs) is consistent with the interpretation that a

key way by which the reward-prospect influences behavior is by marshalling top-down attentional resources towards the goal of enhancing performance. This is further supported by the large increase in the CNV with reward-prospect being paralleled by an improvement in task performance for the target Stroop stimuli that followed (i.e., faster RTs and higher accuracy). These findings are consistent with previous studies (e.g., Haagh & Brunia, 1985; Hillyard, 1969) showing that CNV size is generally predictive of RTs, supporting the view that the more efficient participants are in preparing their attentional system for an upcoming target stimulus, the faster the RTs to that target (see also Weissman et al., 2006). Interestingly, in the present study we observed a within-subject interaction effect of reward-prospect and within-subject task performance (as reflected by differences between trials with fast and slow RTs) on the CNV size. In particular, the large CNV elicited by the reward-prospect cues did not vary as a function of slow versus fast RTs to the targets for those trials, whereas in the noreward-prospect condition the CNV difference was substantially enhanced for fast versus slow RTs, with a distribution similar to the CNV attentional-preparation effect and that of previous attention-related enhancements of the CNV. This pattern suggests that the CNV in the reward-prospect condition may have been essentially “maxed out”, and that the RT variations in the responses to the later target stimuli derived from a different processing variability. Notably, the CNV variations did not linearly predict RTs, as the fastest noreward-prospect trials were substantially faster compared to the slowest reward-prospect trials, suggesting that a larger CNV does not in and of itself necessarily result in faster RTs -- that is, the CNV does not seem to be the only factor that determines subsequent behavior. Trial-to-trial variations in attentional preparation in the noreward-prospect condition, in which the attentional preparation was presumably not maxed out, as reflected by larger CNV variation, may have more directly ramified to the later RT effects. Consistent with this differential preparatory pattern and a possible ceiling effect for the CNV for reward trials is that the standard deviation of the RTs was significantly lower in the reward-prospect relative to the noreward-prospect condition.

Preparation processes elicited by the cue were also reflected in oscillatory brain activity. Participants showed increases in low-Alpha-band activity with reward-prospect compared to noreward-prospect during the early phase (100–300 ms after cue onset) of the cue-stimulus interval. This low-Alpha-band effect may be largely due to N2 enhancements, as reflected by the high correlation between the two measures. At longer latencies (500–1200 ms) in response to reward-prospect cues there were particularly strong decreases in Alpha power. Such decreases in Alpha power are generally considered to also be a hallmark neural-activity marker for increased attention (Worden, Foxe, Wang & Simpson, 2000).

Our within-subject task performance data provides interesting suggestions for differential roles for preparatory Alpha and preparatory CNV activity. In particular, we observed dissociation between the effects on two cue-elicited neural markers for preparatory attention with regard to the interactions of reward-prospect and RT speed (fast versus slow RTs). As noted above, the large CNV elicited by the reward-prospect cues did not vary as a function of response speed to the targets in these trials, suggesting that preparatory activation reflected by the CNV might have been maxed out in this condition. In the noreward-prospect condition, where lower CNVs were observed, the CNVs were substantially larger for fast versus slow RTs. We also found greater decreases in fronto-central Alpha power for reward-

prospect versus noreward-prospect conditions, consistent with increased preparatory attention. The interaction of reward-prospect with RT speed for the alpha decreases, however, differed relative to the pattern seen for the CNV – named that a robust power reduction was observed for fast versus slow RT trials in the reward-condition (more reduction for fast RTs), but did not differ in the noreward-prospect condition. This differential pattern of results suggests that different preparatory mechanisms are reflected by the Alpha and CNV modulations. It might be hypothesized that Alpha modulations are more closely related to suppression of irrelevant information (e.g., Geerligs, Saliassi, Maurits & Lorist, 2012; Bazanova & Vernon, 2013; Klimesch, Sausen & Hanslmayr, 2007) or perhaps to the task-set mapping (e.g., Grent-‘t-Jong et al., 2011), rather than to selective attention or more general effects as indexed by the CNV. Future studies will be necessary to delineate the functional relationships between these two neural markers for attention-related preparatory processes and their marshalling by reward-prospect.

Reward-prospect resulted in enhanced target stimulus processing

Following the preparatory effects in the cue-stimulus interval, we observed an enhanced N2 in response to the Stroop target stimulus when there was the prospect of reward. A similar effect was observed by Krebs et al. (2013) in response to Stroop stimuli whose font color was associated with reward (rather than the prospect of reward being cued from trial to trial, as was done here). However, the N2 component described by Krebs et al. (2013) was later compared to the N2 found here, which may be due to the effect of cueing in the present study. The enhanced N2 for both the cue and the target seems likely to reflect the orientation of attention towards a stimulus with reward possibilities. Notably, this measure was not correlated with behavioral improvements in reward utilization across-subjects, which supports the view that the occipital N2 enhancements are related to an attentional/salience-related enhancement of an identification process, which does not necessarily have consequences for the actual improvement of performance due to utilization of reward-prospect occurring in a later stage. With respect to the target, this enhanced N2 also indicates that participants were able to rapidly boost early processing of relevant information if they are cued with reward information. The early occipital brain activity was again paired with a frontal positivity and was followed by a notably more frontal P3 wave, perhaps a P3a like component (Luck, 2004; Luck & Kappenman, 2011; Polich, 2007), which would appear to reflect the reward-related boosting to improve processing of the target (Krebs et al., 2013; Goldstein et al., 2006; Marini, Marzi & Viggiano, 2011; Wu & Zhou, 2009).

Utilization of cued reward-prospect information improves target stimulus processing

In the present dataset we observed large individual differences in the degree and nature of the improvement of performance with reward-prospect. Those participants showing large improvements in behavioral performance with reward-prospect also showed more pronounced modulations of neural activity patterns. Most importantly, we observed a robust relationship across-subjects between CNV enhancement and the behavioral RT effect (larger reward-related CNVs correlated with greater reward-related acceleration of the RTs), showing that the enhanced CNV activation was predictive of behavioral performance. The same across-subjects relationship held for the reductions of the fronto-central Alpha activity, which also correlated with the CNV enhancements. Modulations of the N1/N2 components

elicited by target Stroop stimuli did not appear to predict performance across-subject, however, indicating that these relative early ERP components more likely reflect the detection of reward-prospect (reflecting enhanced saliency), rather than being a marker for actual utilization of that reward prospect information. In other words, people that were less sensitive to reward-prospect still appeared to identify the information as effectively as the reward-sensitive group, but they did not necessarily utilize this information as effectively for optimizing future information processing.

Increased utilization of reward-prospect information reduces behavioral interference

One of our initial hypotheses was that cued reward-prospect, with its expected marshalling of preparatory attentional resources, would reduce stimulus conflict effects. Behaviorally, we expected that as a result the RT difference between incongruent and congruent Stroop words would become smaller in the reward-prospect condition compared to the noreward-prospect condition. Although we did not find this interaction between reward-prospect and the amount of behavioral interference, we did observe that the amount of reward-related reductions in behavioral interference was correlated (across-subjects) with the overall effect of reward-prospect in faster RTs, the enhanced cue-triggered CNVs, the degree of reduction of cue-triggered fronto-central Alpha, and the size of the target-triggered P3. Notably, no correlation was found between the conflict-related Ninc or LPC and the reduction of interference by reward-prospect. In other words, these findings imply that conflict-related processes underlying the Ninc and the LPC are not sensitive to reward-prospect when that prospect is cued ahead of time. These findings indicate that the reduction of interference across-subjects was more likely related to the effectiveness of the utilization of the reward-prospect information, and to the corresponding changes in neural preparation and subsequent target processing, than to an earlier or more efficient processing of conflict (Ninc and LPC).

In contrast to the between-subject correlations, we did not find an overall effect of cued reward-prospect on conflict-related interference, measured either behaviorally or neurally. This would seem to be in disagreement with several previous studies that have reported main effects of reward on conflict processing (Krebs et al., 2010, 2013; Padmala & Pessoa, 2011). There are several possible reasons for this discrepancy. First, it is important to distinguish between paradigms (and behavioral circumstances) that entail cued-reward or *reward anticipation* (e.g., the present study and Padmala & Pessoa, 2011) and ones that entail *reward association* of certain target stimuli or features (e.g., the Krebs et al. studies). Reward anticipation, such as was used here, is induced by cueing the participant on each trial as to whether there would or would not be the prospect of reward on that trial. In such a circumstance, a reduction of conflict interference requires that the reward anticipation (and any attentional variation it might induce) leads to activation of a top-down preparatory mechanism that either enhances the processing of the relevant features of the target that follows or suppresses the processing of its irrelevant, conflicting features (or both). If, however, the preparatory processes lead to an overall enhancement of the processing of the target stimulus (that is, of ALL its features), it will not necessarily reduce conflict processing, because the processing of both the relevant and conflicting task-irrelevant features will be enhanced. In a reward-association conflict paradigm, on the other hand, such

as in the Krebs et al. studies (2010, 2013), there is no cueing. Rather, a specific feature of the target stimulus is associated with reward during the whole session. In this circumstance the processing of reward-associated relevant features will tend to be selectively boosted in a more bottom-up manner due to their acquired saliency from the reward association, relative to the processing of the irrelevant features. This selective enhancement of processing would then tend to reduce the behavioral costs related to conflict processing in incongruent trials. This distinction between reward cueing and reward association is thus an important one to make, given that they may well invoke different mechanisms by which reward can influence processing, which might explain why conflict-reduction effects would be more likely observed in the association paradigms.

Based on the above considerations, it is important to also discuss why the results differ between the current study and Padmala and Pessoa (2011), since both employed a trial-by-trial cueing approach in a Stroop-like task. A possible explanation may derive from key differences in the specific Stroop tasks and stimuli that were employed, and, moreover, may be related to the selectivity hypothesis detailed above. More specifically, in our study we used classic Stroop words, with color words in different font colors that were either congruent or incongruent. In such a paradigm, the relevant feature (i.e., the font-color) is fully integrated into the same object with the irrelevant feature (i.e., the word meaning). In contrast, Padmala and Pessoa (2011) used pictures overlaid with words that were either congruent or incongruent, and thus the relevant and irrelevant stimuli were separate (and perhaps more separable) objects. Accordingly, we speculate that in the reward-cueing condition in the Padmala and Pessoa study, participants were able to more selectively filter out the irrelevant stimuli and focus more on the relevant one, whereas in our study it was more difficult to selectively filter out the irrelevant feature from the relevant one as they were integrated into the same object.

Furthermore, but perhaps more speculatively, it is possible that the inconsistent findings in these studies are due to differences in intrinsic motivation. Multiple studies have shown that an extrinsic reward can undermine intrinsic motivation (for a review see: Deci, Koestner & Ryan, 1999). Specifically, high compared to low levels of intrinsic motivation may result in higher levels of accuracy and a diminished effect of extrinsic reward. Indeed, studies that reported reduced interference in reward conditions (Krebs et al., 2010, 2013; Padmala and Pessoa, 2010) also reported substantially lower accuracy for incongruent noreward-prospect trials compared to rewarded ones (differences ~8%). In contrast, the studies that did not report reduced interference in reward trials (the present study and Krebs et al., 2011) showed only a marginal reduction in accuracy (~2%). Thus, the individual level of intrinsic motivation may be another important factor to consider in studies investigating reward processing (Wu et al., 2014). More generally, future research will be needed to verify the exact conditions under which a reward-related reduction of interference will occur.

As noted above, although we did not find a main effect of conflict reduction, we did find an across-subject correlation indicating that the more the participants utilized the reward-prospect information, measured both neurally and behaviorally, the more reduction there was in conflict-induced costs. Thus, this may reflect a strategy or ability difference between the participants, in that some of them may be able to use the advance cueing information

effectively to selectively enhance relevant features or suppress irrelevant features in the same object. In contrast, it is possible that other individuals use the reward-prospect mainly to enhance processing of the entire target stimulus input, including all its features. In this latter group of individuals, reward-prospect would not be expected to lead to interference reduction, and could possibly even lead to greater conflict.

Conclusions

By using a cue to inform the participant about the reward-prospect on each trial, the present experiment provides a mapping for the cascade of neural processes underlying the utilization of reward information. Key results include that reward-prospect resulted in enhancement of neural markers reflecting attentional preparation and target stimulus processing, as well as in an overall acceleration of behavioral responses. In addition, across-subjects the degree of preparatory attentional processes with reward-prospect (as measured by enhancements of their preparatory CNV activity and reductions in their Alpha-band activity) correlated with the reduction of behavioral measures of conflict. Together, these findings suggest that the utilization of reward-prospect information provided by a cue stimulus results in specific enhancement of attentional-control processes used to improve stimulus processing and the reduction of stimulus conflict.

References

- Aarts E, van Holstein M, Cools R. Striatal Dopamine and the Interface between Motivation and Cognition. *Frontiers in psychology*. 2011; 2:163. [PubMed: 21808629]
- Adcock RA, Thangavel A, Whitfield-Gabrieli S, Knutson B, Gabrieli JDE. Reward-motivated learning: mesolimbic activation precedes memory formation. *Neuron*. 2006; 50(3)
- Bakeman R. Recommended effect size statistics for repeated measures designs. *Behavior Research Methods*. 2005; 37(3):379–384. [PubMed: 16405133]
- Bazanova OM, Vernon D. Interpreting EEG Alpha activity. *Neuroscience and Biobehavioral Reviews*. 2013
- Bendiksy MS, Platt ML. Neural correlates of reward and attention in macaque area LIP. *Neuropsychologia*. 2006; 44(12):2411–2420. [PubMed: 16757005]
- Bijleveld E, Custers R, Aarts H. Unconscious reward cues increase invested effort, but do not change speed-accuracy tradeoffs. *Cognition*. 2010; 115(2):330–335. [PubMed: 20089247]
- Buschman T, Miller E. Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*. 2007; 315(5820):1860–1862. [PubMed: 17395832]
- Camara E, Rodriguez-Fornells A, Münte TF. Functional connectivity of reward processing in the brain. *Frontiers in human neuroscience*. 2008; 2:19. [PubMed: 19242558]
- Chelazzi L, Perlato A, Santandrea E, Della Libera C. Rewards teach visual selective attention. *Vision Research*. 2013; 85:58–72. [PubMed: 23262054]
- Corbetta M, Shulman GL. Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*. 2002; 3(3):201–215.
- Deci EL, Koestner R, Ryan RM. A meta-analytic review of experiments examining the effects of extrinsic rewards on intrinsic motivation. *Psychological bulletin*. 1999; 125(6):627–668. discussion 692–700. [PubMed: 10589297]
- Delgado MR. Reward-related responses in the human striatum. *Annals of the New York Academy of Sciences*. 2007; 1104:70–88. [PubMed: 17344522]
- Delorme A, Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics. *Journal of Neuroscience Methods*. 2004; 134:9–21. [PubMed: 15102499]

- Engelmann JB, Damaraju E, Padmala S, Pessoa L. Combined effects of attention and motivation on visual task performance: transient and sustained motivational effects. *Frontiers in human neuroscience*. 2009; 3:1–4. [PubMed: 19255629]
- Engelmann JB, Pessoa L. Motivation sharpens exogenous spatial attention. *Emotion*. 2007; 7(3):668–674. [PubMed: 17683222]
- Folstein J, Petten, Van C. Influence of cognitive control and mismatch on the N2 component of the ERP: a review. *Psychophysiology*. 2008; 45(1):152–170. [PubMed: 17850238]
- Foxe JJ, Snyder AC. The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. *Frontiers in Psychology*. 2011; 2:154. [PubMed: 21779269]
- Geerligs L, Saliassi E, Maurits NM, Lorist MM. Compensation through increased functional connectivity: neural correlates of inhibition in old and young. *Journal of cognitive neuroscience*. 2012; 24(10):2057–2069. [PubMed: 22816367]
- Grent-'t-Jong T, Boehler CN, Kenemans JL, Woldorff MG. Differential functional roles of slow-wave and oscillatory- α activity in visual sensory cortex during anticipatory visual-spatial attention. *Cerebral cortex*. 2011; 21(10):2204–2216. [PubMed: 21372123]
- Grent-'t-Jong T, Woldorff MG. Timing and sequence of brain activity in top-down control of visual-spatial attention. *PLoS biology*. 2007; 5(1):e12. [PubMed: 17199410]
- Goldstein RZ, Cottone La, Jia Z, Maloney T, Volkow ND, Squires NK. The effect of graded monetary reward on cognitive event-related potentials and behavior in young healthy adults. *International Journal of Psychophysiology : Official Journal of the International Organization of Psychophysiology*. 2006; 62(2):272–279. [PubMed: 16876894]
- Haagh S, Brunia C. Anticipatory response-relevant muscle activity, CNV amplitude and simple reaction time. *Electroencephalography and Clinical Neurophysiology*. 1985:30–39. [PubMed: 2408861]
- Haber SN, Knutson B. The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology : official publication of the American College of Neuropsychopharmacology*. 2010; 35(1):4–26. [PubMed: 19812543]
- Hanslmayr S, Aslan A, Staudigl T, Klimesch W, Herrmann CS, Bäuml K-H. Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*. 2007; 37(4):1465–1473. [PubMed: 17706433]
- Hanslmayr S, Pastotter B, Bäuml K-H, Gruber S, Wimber M, Klimesch W. The electrophysiological dynamics of interference during the Stroop task. *Journal of Cognitive Neuroscience*. 2008; 20(2):215–225. [PubMed: 18275330]
- Hickey C, van Zoest W. Reward creates oculomotor salience. *Current Biology*. 2012; 22(7):219–220.
- Hickey C, Chelazzi L, Theeuwes J. Reward changes salience in human vision via the anterior cingulate. *The Journal of neuroscience : the official journal of the Society for Neuroscience*. 2010; 30(33):11096–11103. [PubMed: 20720117]
- Hillyard S. Relationships between the contingent negative variation (CNV) and reaction time. *Physiology & Behavior*. 1969; 4:351–357.
- Hillyard S, Anllo-Vento L. Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences*. 1998; 95:781–787.
- Klimesch W, Sauseng P, Hanslmayr S. EEG Alpha oscillations: the inhibition-timing hypothesis. *Brain Research Reviews*. 2007; 53(1)
- Knutson B, Adams CM, Fong GW, Hommer D. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *The Journal of Neuroscience : the official journal of the Society for Neuroscience*. 2001; 21(16):RC159. [PubMed: 11459880]
- Krawczyk DC, Gazzaley A, D'Esposito M. Reward modulation of prefrontal and visual association cortex during an incentive working memory task. *Brain research*. 2007; 1141:168–177. [PubMed: 17320835]
- Krebs RM, Boehler CN, Woldorff MG. The influence of reward associations on conflict processing in the Stroop task. *Cognition*. 2010; 117(3):341–347. [PubMed: 20864094]
- Krebs RM, Boehler CN, Egner T, Woldorff MG. The neural underpinnings of how reward associations can both guide and misguide attention. *The Journal of Neuroscience : the official journal of the Society for Neuroscience*. 2011; 31(26):9752–9759. [PubMed: 21715640]

- Krebs RM, Boehler CN, Roberts KC, Song AW, Woldorff MG. The Involvement of the Dopaminergic Midbrain and Cortico-Striatal-Thalamic Circuits in the Integration of Reward Prospect and Attentional Task Demands. *Cerebral cortex*. 2012; 22(3):607–615. [PubMed: 21680848]
- Krebs RM, Boehler CN, Appelbaum LG, Woldorff MG. Reward associations reduce behavioral interference by changing the temporal dynamics of conflict processing. *PloS One*. 2013; 8(1)
- Krebs RM, Schott BH, Schütze H, Düzel E. The novelty exploration bonus and its attentional modulation. *Neuropsychologia*. 2009; 47(11):2272–2281. [PubMed: 19524091]
- Kristjánsson Á, Sigurjónsdóttir Ó, Driver J. Fortune and reversals of fortune in visual search: Reward contingencies for pop-out targets affect search efficiency and target repetition effects. *Attention, Perception, & Psychophysics*. 2010; 72(5):1229–1236.
- Liotti M, Woldorff MG, Perez R, Mayberg HS. An ERP study of the temporal course of the Stroop color-word interference effect. *Neuropsychologia*. 2000; 38(5):701–711. [PubMed: 10689046]
- Locke HS, Braver TS. Motivational influences on cognitive control: Behavior, brain activation, and individual differences. *Cognitive, Affective, & Behavioral Neuroscience*. 2008; 8(1):99–112.
- Luck SJ, Ford Ma. On the role of selective attention in visual perception. *Proceedings of the National Academy of Sciences of the United States of America*. 1998; 95(3):825–830. [PubMed: 9448247]
- Luck SJ. *An Introduction to the Event-Related Potential Technique (Cognitive Neuroscience)*. A Bradford Book (1 edition). 2005
- Luck, SJ.; Kappenman, ES., editors. *The Oxford Handbook of Event-Related Potential Components*. Oxford University Press; 2011.
- MacLeod CM. Half a century of research on the Stroop effect: An integrative review. *Psychological Bulletin*. 1991; 109(2):163–203.
- Mangun GR, Hillyard Sa. Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *Journal of experimental psychology. Human Perception and Performance*. 1991; 17(4):1057–1074. [PubMed: 1837297]
- Marini F, Marzi T, Viggiano MP. "Wanted!" the effects of reward on face recognition: electrophysiological correlates. *Cognitive, affective & behavioral neuroscience*. 2011; 11(4): 627-3.
- Maunsell JHR. Neuronal representations of cognitive state: reward or attention? *Trends in cognitive sciences*. 2004; 8(6):261–265. [PubMed: 15165551]
- Nagai Y, Critchley HD, Featherstone E, Fenwick PBC, Trimble MR, Dolan RJ. Brain activity relating to the contingent negative variation: an fMRI investigation. *NeuroImage*. 2004; 21(4):1232–1241. [PubMed: 15050551]
- Oostenveld R, Fries P, Maris E, Schoffelen JM. FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational intelligence and neuroscience*. 2011; 2011:1568–1569.
- Padmala S, Pessoa L. Reward reduces conflict by enhancing attentional control and biasing visual cortical processing. *Journal of cognitive neuroscience*. 2011; 23(11):3419–3432. [PubMed: 21452938]
- Pashler HE. *The psychology of attention*. Book. 1998; 41
- Pessoa L, Engelmann JB. Embedding reward signals into perception and cognition. *Frontiers in neuroscience*. 2010; 4:2–8. [PubMed: 20582255]
- Polich J. Updating P300: an integrative theory of P3a and P3b. *Clinical neurophysiology*. 2007; 118(10):2128–2148. [PubMed: 17573239]
- R Development Core Team. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing; 2013. ISBN 3-900051-07-0, URL: <http://www.R-project.org/>.
- Schevernels H, Krebs RM, Santens P, Woldorff MG, Boehler CN. Task preparation processes related to reward prediction precede those related to task-difficulty expectation. *NeuroImage*. 2014; 84:639–647. [PubMed: 24064071]
- Schultz W. Multiple reward signals in the brain. *Nature Reviews Neuroscience*. 2000; 1:199–207.
- Schupp HT, Flaisch T, Stockburger J, Junghöfer M. Emotion and attention: event-related brain potential studies. *Progress in brain research*. 2006; 156:31–51. [PubMed: 17015073]

- Stroop JR. Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*. 1934; 18(6):643–662.
- Walter WG, Cooper R, Aldridge VJ, McCallum WC, Winter AAL. Contingent negative variation: An electrical sign of sensorimotor association and expectancy in the human brain. *Nature*. 1964; 203:380–384. [PubMed: 14197376]
- Weissman DH, Roberts KC, Visscher KM, Woldorff MG. The neural bases of momentary lapses in attention. *Nature neuroscience*. 2006; 9(7):971–978.
- Wittmann BC, Schott BH, Guderian S, Frey JU, Heinze H-J, Düzel E. Reward-related FMRI activation of dopaminergic midbrain is associated with enhanced hippocampus-dependent long-term memory formation. *Neuron*. 2005; 45(3):459–467. [PubMed: 15694331]
- Woldorff MG, Hazlett CJ, Fichtenholtz HM, Weissman DH, Dale AM, Song AW. Functional parcellation of attentional control regions of the brain. *Journal of cognitive neuroscience*. 2004; 16(1):149–165. [PubMed: 15006044]
- Worden MS, Foxe JJ, Wang N, Simpson GV. Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *The Journal of Neuroscience : the official journal of the Society for Neuroscience*. 2000; 20(6):RC63. [PubMed: 10704517]
- Wu CC, Samanez-Larkin GR, Katovich K, Knutson B. Affective traits link to reliable neural markers of incentive anticipation. *NeuroImage*. 2014; 84:279–289. [PubMed: 24001457]
- Wu Y, Zhou X. The P300 and reward valence, magnitude, and expectancy in outcome evaluation. *Brain Research*. 2009; 1286:114–122. [PubMed: 19539614]

Figure 1. Trial structure

Each trial started with a cue: '\$' for trials with reward-prospect, '&' for noreward-prospect trials, and '#' for control trials. All cues were followed by a fixation cross and, in the reward-prospect and noreward-prospect trials, by a Stroop stimulus to which participants needed to respond. Control cues indicated that no Stroop stimulus would follow and thus that there was no need to prepare for it. Note that in all the figures 'reward' and 'noreward' refer to the reward-prospect and noreward-prospect conditions, respectively.

behavioral effects

Figure 2. Behavioral RT data

A) The RT data averaged over the various conditions. **B)** The within-subject conflict-related interference effects (RTs for the incongruent trials minus the congruent ones), showing that these effects did not differ in the reward-prospect and noreward-prospect conditions. **C)** The RTs for the main effect of interference (incongruent minus congruent), main effect of REWARD (reward-prospect minus noreward-prospect) and the interaction of the two (reduction of interference as a function of REWARD), showing a main effect of interference (incongruent versus congruent), a main effect of reward-prospect (reward-prospect versus noreward-prospect), but not interaction between the two. **D)** The correlation across participants between the overall RT acceleration with reward-prospect (reward-prospect RT minus noreward-prospect RT) and the reward-related reduction in behavioral interference (the more positive the value, the more the reduction in interference with reward). The plot shows that the greater the RT acceleration with reward, the greater the reward-related reduction in behavioral interference. Error bars represent standard error of the mean.

Figure 3. Cue-elicited ERP effects

A) The ERP waveforms for reward-prospect and noreward-prospect, split out into cue-evoked ERPs which preceded ‘fast’ RTs or ‘slow’ RTs (median split) for the behavioral responses to the target. Effects of reward-prospect were observed on the occipital N1, N2, frontal P2, P3 and a fronto-central CNV enhancement. The effect of SPEED was most pronounced on the CNV in the noreward-prospect condition. **B)** Topographic scalp maps of the ‘early’ enhancement effects after cue onset showed the difference between ERPs evoked by reward-prospect cues minus noreward-prospect cues. The topomaps reveal the effect of

reward-prospect on the N1, N2 and P2. C) Topomaps of the ‘late’ enhancements of the effect REWARD in response to the cue and SPEED as defined by the RTs on the subsequent target. The comparison between noreward-prospect and control cues reveals a characteristic fronto-central negative wave (CNV). The comparison between fast-RT and slow-RT noreward-prospect trials revealed that fast RT-trials were preceded by an enhanced negative fronto-central CNV deflection starting around 800 ms. The comparison between reward-prospect and noreward-prospect cues showed a larger parietal P3 followed by a CNV enhancement for reward-prospect cues compared to noreward-prospect cues, with a distribution similar to the SPEED effect. The CNV enhancement was also similar to the comparison of noreward-prospect cues minus control cues.

Figure 4. ERPs elicited by the target stimuli, for fast and slow RT trials

A) The ERPs elicited by reward-prospect and noreward-prospect cues. There was an effect of reward-prospect on the occipital N2 and the temporally paired frontal positive P2, followed by an effect of both SPEED and reward-prospect on the P3. The dashed versus solid line ERPs indicate the potentials preceding fast or slow RTs by participants. **B)**

Topographic maps indicate the difference between potential reward and noreward targets and illustrate the locations of the reward-prospect effect in the N2, P2 and P3 intervals. Note that the N2 is somewhat earlier compared to other studies, but has a similar topography as the N2 enhancement by reward as reported by Krebs et al., (2013).

incongruency related target ERPs

Figure 5. Conflict-related ERP effects elicited by the target Stroop stimuli

A) The ERPs for the REWARD and CONGRUENCY conditions for the central ROI. There was a clear hallmark conflict-processing marker, the central-parietal Ninc, followed by a parietal LPC. **B)** The difference wave between incongruent minus congruent Stroop stimuli for reward-prospect and noreward-prospect. Scalp maps on the right illustrate that the Ninc and LPC do differ between reward-prospect and noreward-prospect trials.

Figure 6. Correlations between behavior and the cue and target ERPs

Between-subject correlations were based on the mean RTs of the reward-prospect effect, the reduction in conflict-related interference effect, the neural mean amplitudes of the cue-evoked reward effect on the fronto-central CNV (700–1200 ms) and the target evoked reward effect on the frontal P3 (200–500 ms). **A**) Left plot: correlation between the cue-evoked CNV (x-axis) and the target-evoked frontal P3 (y-axis). Middle and right plots show the correlations between the reward effect on the cue CNV (x-axis) and the reward effects on the overall RTs and on the behavioral interference effect, respectively (y-axis). **B**) Correlation between P3 component of the target-evoked ERPs (x-axis) and behavioral markers for reward utilization (y-axis). Fitted lines are based on a linear model fit, and shaded areas show a 95% confidence interval for the fitted line.

cue evoked oscillatory activity

Figure 7. Effects of oscillatory EEG activity

(A) The spectrograms illustrate the effect of reward-prospect and within-subject task performance (fast RTs versus slow RTs) for different frequencies and time. Note that the effect of oscillatory Alpha for REWARD is substantially larger than that for SPEED. (B) Traces reflect oscillatory Alpha for their respective ROI and condition. (C) The scalp distribution of Alpha that was largest over the occipital channels. (D) Plots showing significant correlations between reward utilization measures (reward-prospect RT effect and reduced interference) and fronto-central Alpha.

Figure 8. Differential REWARD × SPEED interactions for CNV and Alpha

Cue evoked oscillatory Alpha and CNV activity showed differential patterns with respect to the effect of reward-prospect and within-subject task performance. Error bars reflect the standard error of the mean.