

Monetary reward magnitude effects on behavior and brain function during goal-directed behavior

P. Rosell-Negre¹ · J. C. Bustamante² · P. Fuentes-Claramonte¹ · V. Costumero¹ · S. Benabarre³ · A. Barrós-Loscertales¹

Published online: 29 July 2016
© Springer Science+Business Media New York 2016

Abstract Reward may modulate the cognitive processes required for goal achievement, while individual differences in personality may affect reward modulation. Our aim was to test how different monetary reward magnitudes modulate brain activation and performance during goal-directed behavior, and whether individual differences in reward sensitivity affect this modulation. For this purpose, we scanned 37 subjects with a parametric design in which we varied the magnitude of monetary rewards (€0, €0.01, €0.5, €1 or €1.5) in a blocked fashion while participants performed an interference counting-Stroop condition. The results showed that the brain activity of left dorsolateral prefrontal cortex (DLPFC) and the striatum were modulated by increasing and decreasing reward magnitudes, respectively. Behavioral performance improved as the magnitude of monetary reward increased while comparing the non reward (€0) condition to any other reward condition, or the lower €0.01 to any other reward condition, and this improvement was related with individual differences in reward sensitivity. In conclusion, the locus of influence of monetary incentives overlaps the activity of the regions commonly involved in cognitive control.

Electronic supplementary material The online version of this article (doi:10.1007/s11682-016-9577-7) contains supplementary material, which is available to authorized users.

✉ A. Barrós-Loscertales
barros@uji.es

¹ Departamento de Psicología Básica, Clínica y Psicobiología, Universitat Jaume I, Castellón, Av. de Vicent Sos Baynat, s. /n 12071 Castelló de la Plana, Spain

² Departamento de Psicología y Sociología, Universidad de Zaragoza, Zaragoza, Pedro Cerbuna, 12 50009 Zaragoza, Spain

³ Unidad Docente Medicina Familiar y Comunitaria, Instituto Aragonés de Ciencias de la Salud (IACS), Avenida San Juan Bosco, nº13, 50009 Zaragoza, Spain

Keywords Reward magnitude · Reward sensitivity · fMRI · Stroop

Introduction

Human cognition has the cognitive control capacity to adjust and flexibly guide people's behavior in changing environmental circumstances, especially in situations where distracting information or a prepotent response tendency must be ignored to successfully act in a goal-directed manner (Bunge et al. 2002; Grandjean et al. 2012). Since Stroop (1935) reported the Stroop effect, the Stroop task has become one of the most widely used paradigms to study cognitive control (MacLeod 1991). In this study, we employed the interference counting Stroop condition as a goal-directed behavior, which has been employed as a variant to study the Stroop effect in the functional magnetic resonance imaging (fMRI) context (Barrós-Loscertales et al. 2011; Bush et al. 1998, 1999, 2006; Hayward et al. 2004). In this task, an automatic or predominant response tendency (word reading of number words; i.e., four) must be withheld in favor of a more controlled one (counting naming; i.e., two for “four, four” presentation). Reaction times (RTs) are typically slower for incongruent trials (twice the “four” word) than for congruent trials (four times the “four” word). This phenomenon is known as the Stroop effect, which has been widely replicated across several studies and the experimental conditions that involve participants in overcoming interference as goal behavior (Grandjean et al. 2012).

The Dual Mechanism of Control (DMC) framework hypothesizes that neurobehavioral adjustment, characteristic in cognitive control processes, changes from ‘proactive control’ (to maintain goal-relevant information before cognitively demanding events take place) to the ‘reactive control’ strategy

(to detect and resolve cognitively demanding events after its onset), depending on situational demands or individual differences (Braver 2012). In this study, we focus on analyzing high motivation in a high conflict expectation context, which are task conditions that involve a proactive control strategy (Grandjean et al. 2012; Soutschek et al. 2014; Soutschek et al. 2013). In particular, we tested how increasing monetary reward magnitudes modulate behavioral performance (i.e., reaction time and accuracy) and brain activity by adding a blocked graded parametric variation of reward magnitude contingencies for correct performance under an interference counting Stroop condition with high conflict expectancy (e.g., low proportion of congruent trials).

Behaviorally, enhancement in goal-directed behavior during conflict processing has been related with high conflict expectancy (Carter et al. 2000; Funes et al. 2010; Logan and Zbrodoff 1979; Soutschek et al. 2014; Soutschek et al. 2013) and enhanced levels of motivation (Krebs et al. 2013; 2011; 2010; Padmala and Pessoa 2011; Soutschek et al. 2014; Veling and Aarts 2010). Functionally, conflict expectancy involves frontal regions, including the dorsal ACC (dACC) and the medial superior frontal cortex, whereas reward motivation enhances brain activity in regions associated with proactive control, such as dACC, lateral PFC and the striatum (Soutschek et al. 2014). However, enhanced goal-directed behavior seems to engage similar or mutually influencing processes. Thus high conflict expectancy alone may already lead to an optimal processing mode so that high motivation could not activate any additional proactive processes, and vice versa (Soutschek et al. 2013). Therefore, we considered studying whether blocked conditions of increasing monetary rewards would affect general task performance and brain activation (Engelmann et al. 2009; Stoppel et al. 2011; Veling and Aarts 2010) in an already stable high conflict condition. Consequently, we expected that as magnitude of reward increases, (1) task performance would improve and (2) activity in those brain regions involved in proactive control, such as the lateral PFC (Jimura et al. 2010) or the striatum (Aron, 2011), would change their activation accordingly.

Therefore, as providing a reward does not consistently instill proactive control in participants, because individuals may differ in their reaction to rewards (Braver 2012; Jimura et al. 2010), we studied the relation of reward sensitivity trait to behavior and brain function in our study. Reward sensitivity reflects the persistency of the reward-triggered behaviors regulated by the reward system (Jimura et al. 2010), and helps explain the tendency to adopt a proactive control strategy, particularly under cognitive task conditions with a high reward motivational value (Braver 2012; Jimura et al. 2010). Previous literature has suggested that reward sensitivity personality traits modulate the effects of a motivational context in demanding cognitive situations with greater performance enhancement (van Steenbergen et al. 2009) and brain function

modulation (Braver 2012; Jimura et al. 2010; Locke and Braver 2008). Apart from our main question, we also investigated the effects of individual differences in reward sensitivity on the behavioral performance and brain activation obtained during the parametric modulation of monetary rewards. We speculated that high reward sensitivity trait scores would be related with parametric performance improvement and proactive brain activation.

Material and methods

Participants

Thirty-seven right-handed volunteers (31 men and 6 women) participated in this study. Their mean age was 36.89 years old (standard deviation; SD = 8.94; range = 20–56) and their average years of education were 11.95 (SD = 2.81; range = 8–17). The inclusion criteria to select the sample were: (1) no major medical illnesses or Diagnostic and Statistical Manual of Mental Disorders, Fourth Edition (DSM-IV) Axis I disorders; (2) no history of head injury with loss of consciousness lasting longer than 30 min; (3) no current use of drugs or psychoactive substances. Before the scanner sessions, all the participants completed a Spanish translated version of the Behavioral Inhibition/Behavioral Activation Scales (BIS/BAS; Carver and White 1994). The BIS/BAS questionnaire consists of three scales that measure the traits related to behavioral approach (BAS) and one scale related to responsiveness to punishment cues (BIS). The three scales that comprise BAS are Drive (D), Fun Seeking (FS) and Reward Responsiveness (RR). The D scale comprises items that pertain to the persistent pursuit of desired goals. The FS scale contains items that reflect both a desire for new rewards and a willingness to approach a potentially rewarding event on the spur of the moment. The RR scale includes items that focus on positive responses to occurrence or anticipation of reward. The participants' mean scores for the BAS-FS (mean; $M = 11.19$, $SD = 2.11$, range = 7–15), BAS-D ($M = 11.00$, $SD = 2.61$, range = 4–16), BAS-RR ($M = 16.92$, $SD = 2.27$, range = 13–20) and BIS ($M = 20.19$, $SD = 3.81$, range = 9–27) were similar to the normative sample (Carver and White 1994). We used the BIS/BAS scales to inspect the respective nonparametric test (Kolmogorov–Smirnov [K-S]; RR, $Z = 0.93$, $p = .35$; D, $Z = 0.66$, $p = .78$; FS, $Z = 0.69$, $p = .73$; BIS, $Z = .735$, $p = .653$) to ensure normality in distribution. The scale showed good reliability (Cronbach's $\alpha = .7$). All the participants received information about the nature of the research, provided written informed consent prior to participating in the study, and received a monetary award for their participation in accordance with their performance during the task. The institutional Review Board of the Universitat Jaume I (Castellón, Spain) approved this study.

Task design

We scanned all the participants while they performed a counting Stroop task with reward contingencies (see Fig. 1). The task was an adaptation from an earlier study (Barrós-Loscertales et al. 2011). Participants viewed sets of one to four identical number words, which appeared on the screen for each trial during the whole paradigm: “one”, “two”, “three” and “four” (“uno”, “dos”, “tres”, “cuatro” in Spanish). We instructed them to respond as quickly as possible by button-pressing on a keypad with two buttons for each hand (Response Grips, NordicNeuroLab, Norway), which is concordant with the number of words in each set. Inside the scanner, subjects performed 10 functional blocks, each consisting of 26 trials, which yielded 260 trials. Each block included a few congruent trials (15 %, $n = 40$, 5 in each block; the number of words was concordant with the word number, e.g., “two” “two”, response: two) among the incongruent trials (85 %, $n = 220$, 21 in each block; the number of words was discordant with the word number, e.g., “one” “one”, response: two), which were jittered within blocks and between conditions. Congruent trials were intermixed between mostly incongruent trials to promote proactive control (Bugg et al. 2008; De Pisapia and Braver 2006; Grandjean et al. 2012; Soutschek et al. 2013), minimize strategy and increase interference (MacLeod 1991). A linear parametric approach was run, which included five “reward” conditions with the possibility of obtaining different monetary incomes (€0, €0.01, €0.5, €1, €1.5) for correct task performance. Participants repeated each condition for two random blocks within a single run. A parametric design was applied to avoid the shortcomings of using a neutral or congruent condition for cognitive subtraction because our goal was to analyze the effects of reward on interference processing. Instead we included a fixation point, shown for 7200 milliseconds (msec.) between

each task block as the baseline, which also precluded carry-over effects.

The fMRI paradigm started with a baseline block. After this first baseline block and in the following ones, task blocks started with a cue (C) that appeared and lasted 2 s (sec.) The cue informed the participants about the amount of money (€0, €0.01, €0.5, €1 or €1.5) they could win for each correct response within each corresponding Stroop block. After each cue, we displayed a fixation point for 500 msec. Just to maintain participants’ attention. Afterward, we presented 26 trials, each lasting 1000 msec. With an inter-trial interval of 400 msec. The duration of each Stroop block was 46.7 s., whereas total task duration was 7 min and 41 s. Participants did not receive feedback on their performance at any time during the task, only at the end. The stimuli presented throughout all the trials were white on a black background (resolution of 800×600 pixels). We controlled the stimulus presentation with the Presentation software (<http://www.neurobs.com>).

Before they entered the scanner, we instructed all the participants about the task by reading identical instructions. The instructions explained that the participants had to respond to the number of words that appeared on the screen, not to the number word. We also told them that before each set of trials, they would see an informative cue that determined the amount of money they would receive for each correct response obtained in each set of trials (e.g., €0.50), and they would receive a monetary reward when participation ended, based on their task performance. Thus, their main goal was to win as much money as possible. After receiving the instructions, the participants completed a practice version with 90 trials to minimize practice effects and get used to matching responses to the button to press.

fMRI acquisition

We acquired blood oxygenation level-dependent (BOLD) fMRI data in a 1.5-Teslas Siemens Avanto (Erlangen, Germany). We helped subjects to enter the MRI scanner and lie in a supine position. We immobilized their heads with cushions to reduce motion artifacts. We presented the stimuli via MRI-compatible goggles, and we used a response system to control performance during the scanning session (Response grips, NordicNeuroLab). We obtained functional scans using a gradient-echo T2*-weighted echo-planar MR sequence (TR = 2000 ms; TE = 48 ms; matrix = 64×64 , voxel size = $3.5 \times 3.5 \times 4$ mm, flip angle = 90° , 4.5-mm thickness, slice gap of 0.5 mm). We acquired 24 interleaved axial slices parallel to the hippocampi and covering the entire brain. Prior to the functional MRI sequences, we acquired structural images using a high-resolution T1-weighted sequence with TR / TE = 2200 / 3.84.9 ms, FOV = 224 mm, matrix = $256 \times 256 \times 160$, voxel size = $1 \times 1 \times 1$ mm, which

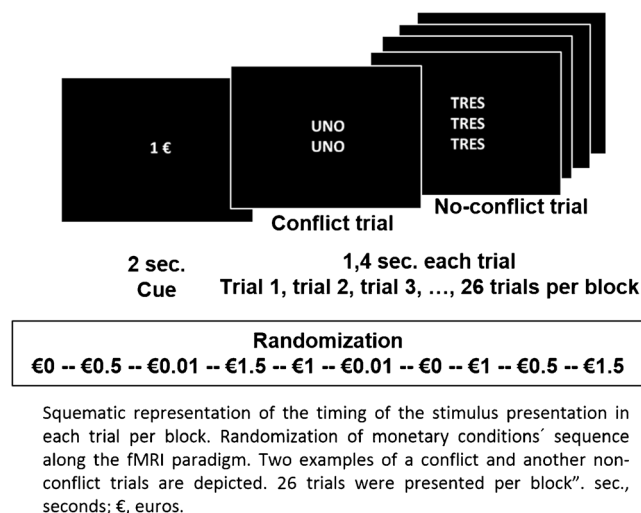


Fig. 1 Schematic representation of the counting Stroop task in an fMRI block-design

facilitated the localization and co-registration of the functional data.

fMRI preprocessing

We preprocessed and analyzed the data with the SPM8 software package (Statistical Parametric Mapping 8; Wellcome Department of Imaging Neuroscience; <http://www.fil.ion.ucl.ac.uk/spm>), as implemented in MATLAB R2007a (Mathworks, Inc., Natick, MA, USA). Preprocessing first included the realignment of each scan per individual to the first scan to correct motion-related artefacts (movement parameters never exceeded 2 mm of translation or 2 degrees of rotation in any direction for any participant). Second, the normalization to a standard EPI template was carried out in accordance with the Montreal Neurological Institute (MNI) template by applying an affine transformation followed by non-linear deformation, and using the basic functions defined in the SPM program. We applied the computed transformation parameters to all the functional images by interpolating them to a final voxel size of $3 \times 3 \times 3$ mm. Finally, we spatially smoothed the images with an $8 \times 8 \times 8$ mm (Full Width at Half Maximum; FWHM) Gaussian kernel.

Statistical analyses

Behavioral analysis

Two variables related to task performance were analyzed: mean RTs to the correct responses (msec.) and error rate (%). We performed two within subjects ANOVAs, including congruency effect (congruent, incongruent) \times reward magnitude (€0, €0.01, €0.5, €1 or €1.5) factors (levels) to test whether increasing monetary reward magnitudes affected task performance. We carried out these analyses by SPSS v.20 (Statistical Package for Social Sciences; SPSS Inc., Chicago, IL, USA).

Distributional analysis

The differences in the congruency effect between the distinct motivational conditions can be a result of the different RTs levels under these conditions rather than motivational effects (Soutschek et al. 2014) as previous studies have showed how the magnitude of the congruency effect decreases with faster responses (Pratte et al. 2010). To this end, we compared the congruency effects under the reward magnitude conditions by means of a distributional analysis to more conclusively support the assumption that anticipation of increasing monetary rewards only affects general task performance without enhancing the level of cognitive control, independently of response speed (Soutschek et al. 2014). These analyses allowed us to evaluate the impact of motivation on interference

processing at the different RTs levels for each reward magnitude. In order to perform the distributional analyses, the RTs of all the responses (including both correct and incorrect responses) were rank-ordered for the different levels of factors congruency effect (congruent and incongruent) and reward magnitude (€0, €0.01, €0.5, €1 or €1.5) separately. Then they were divided into four speed bins of equal size (quartiles) for each subject. Next we calculated the mean RTs (RTs congruent + RTs incongruent)/2 for each quartile and each reward magnitude separately, and excluded error trials. Delta plots for RTs were constructed by plotting congruency effect size (mean RTs incongruent - mean RTs congruent) according to response speed (mean RTs per quartile). Likewise, delta plots for error rate were constructed by plotting congruency effect size (errors incongruent - errors congruent) according to response speed (mean RTs per quartile). We carried out these analyses by SPSS v.20 (Statistical Package for Social Sciences; SPSS Inc., Chicago, IL, USA).

fMRI data analysis

We performed statistical analyses following the General Linear Model (GLM) (Friston et al. 1995). In a block design analysis, we modeled each participant's preprocessed time series under different conditions with a boxcar function convolved with the hemodynamic response function. The model included seven regressors: five regressors that modeled the Stroop blocks for each monetary condition separately (€0, €0.01, €0.5, €1 or €1.5), one regressor that modeled the baseline condition ("*" for 7200 msec.) and another regressor that modeled all the informative cues. We also removed intrinsic autocorrelations by a high-pass filter with a cut-off frequency of 128 Hz, which eliminated low-frequency components. Finally, we included the motion parameters of each subject's realignment correction in the model as "nuisance" variables.

In order to test the neural regions that are sensitive to monetary reward magnitudes while suffering Stroop interference, we generated statistical contrast images to obtain brain activation by subtracting the €0 condition from the other reward magnitudes ($R1 = \text{"€0.01 vs. 0€"}; R2 = \text{"€0.5 vs. €0"}; R3 = \text{"€1 vs. €0"}; R4 = \text{"€1.5 vs. €0"}).$ For a second-level analysis (random effects), we calculated a within-subjects ANOVA on the contrast of the reward magnitude ($R1, R2, R3, R4$) factor (levels) to show the parametric differences for the four conditions using the parameter estimates. For the parametric analysis of reward magnitudes, we fitted a parametric contrast from $R1$ to $R4$ $[-2 -1 1 2]$ as a linear signal increase from $R1$ to $R4$. For the inverse parametric analysis, we fitted a parametric contrast from $R1$ to $R4$ $[2 1 -1 -2]$ as a linear decrease from $R1$ to $R4$. To protect the whole-brain analysis against false-positive activations, we identified the brain activations that showed significant contrasts of parameter estimates by a double-threshold approach; that is, by

combining a voxel-based threshold with a minimum cluster size (Forman et al. 1995). The activations that exceeded this double threshold were, therefore, considered to be activated at an experiment-wise threshold of $p < .05$, corrected for multiple comparisons. We obtained multiple comparisons correction by applying a voxel-wise high threshold of $p .001$ (uncorrected), while cluster size was determined by the algorithm implemented in the CorrClusTh program (<http://www2.warwick.ac.uk/fac/sci/statistics/staff/academic-research/nichols/scripts/spm/johnsgems5/#Gem6>). This resulted in a cluster threshold of 95 voxels. Our hypotheses directed our analysis of reward magnitude in regions of interest (ROIs) such as the striatum given its involvement in reward-related/motivational processes (Aarts et al. 2010; Balleine et al. 2007; Di Martino et al. 2008) and proactive cognitive control (Aron, 2011). The striatum is composed of discrete anatomical regions in which the whole-brain corrected statistical cluster threshold may overcome its own size. Therefore, we defined the bilateral ventral striatum ROI as a 4-mm radius sphere at 10,8,0/–10,10,–2 (x,y,z, MNI coordinates: based on Knutson and Greer 2008) and the bilateral striatum ROIs, including the caudate head and body, putamen and globus pallidus, which were selected from pre-established regions of the PickAtlas toolbox. We used Automatic Atlas Labeling from WFU-PickAtlas (Maldjian et al. 2003). For the ROI analysis, we thresholded the functional effects at the voxel-wise corrected level (FWE-corrected, $p < .05$).

Correlation analysis with BAS scales

We used correlation analyses to test the expected modulation of individual differences in reward sensitivity (BAS scales: RR, D and FS) with the behavioral performance and brain activation obtained during the parametric modulation of monetary rewards. We calculated the monetary differentials (€1.5 minus €0.01) for the RTs and error rate (by taking congruent and incongruent trials together), as well as regional extracted activations from sensitive brain regions to the parametric reward magnitude. Then we correlated them with individual BAS scores. For the PFC, regional activation was extracted using 4-mm radius spheres centered on the local activity maxima of sensitive regions to the parametric effect after FWE correction ($p < .05$, FWE voxel-wise corrected). For the striatal regions, we extracted the mean beta-weights from the cluster that showed a significant parametric effect after voxel-wise correction given its discrete anatomical definition. The correlation analysis threshold was set at $p < .05$, Bonferroni FWE-corrected. Based on this method we divided the a priori selected threshold of $p < .05$ by the number of BAS scales ($k = 3$), which stabilized statistical levels as significant if less than .017. We carried out these analyses with SPSS v.20 (Statistical Package for Social Sciences; SPSS Inc., Chicago, IL, USA).

Results

Behavioral results

Table 1 and Fig. 2 summarize the behavioral results. For the RTs analysis, we observed a significant main effect of reward magnitude ($F(4144) = 26.894$; $p < .001$), a significant main effect of the congruency effect ($F(1,36) = 104.777$; $p < .001$), and a significant reward magnitude \times congruency effect interaction ($F(4144) = 15.743$; $p < .001$) which indicates that congruency effect varied across reward conditions. In the error rate analysis, we observed a significant main effect of reward magnitude ($F(4144) = 4.979$; $p = .001$), a main effect of the congruency effect, ($F(1,36) = 18.651$; $p < .001$) and a significant reward magnitude \times congruency effect interaction ($F(4144) = 3.49$; $p = .009$). Once again the congruency effect varied across reward conditions. The behavioral results showed an unexpected effect on the €0.5 reward condition for RTs and an error rate in the congruent trials, which showed slower RTs and a higher error rate than the incongruent trials. In order to test whether the interaction effect depended on the €0.5 condition, we reran the analysis after excluding the €0.5 level from the reward magnitude factor of the ANOVA. In this way the reward magnitude \times congruency effect interaction remained significant ($F(3108) = 4.826$; $p = .003$) in the RTs variable. So, as we can see in Fig. 2, if we did not take into account the €0.5 reward condition, the remaining interaction effect was due to a different pattern of reduction in the RTs for the congruent and incongruent trials when comparing any reward condition with the non reward one (€0). However, in the error rate analysis, the reward magnitude \times congruency effect interaction did not remain significant ($F(3108) = .415$; $p > .05$) when we removed the €0.5 reward condition. Hence this congruency effect \times reward magnitude interaction depended on the unexpected effect under the €0.5 reward condition. To investigate the nature of these interactions, we calculated the congruency effect variable by subtracting the RTs and error rates in the congruent trials from the incongruent ones (see Table 1) and paired comparisons were run for the congruent and incongruent trials for each reward condition separately (see Fig. 2). Finally, if we focus in the distribution of the more frequent incongruent trials only (see Fig. 2), across the five monetary conditions, we observe that increasing monetary reward improve gradually task performance (RTs ($F(4144) = 13.408$; $p < .001$) and error rate ($F(4144) = 5.036$; $p = .001$)). Moreover, we observed a significant linear (RTs $F(1,36) = 26.055$, $p < .001$; and error rate $F(1,36) = 11.282$, $p = .002$) but also quadratic effects (RTs $F(1,36) = 13.281$, $p = .001$; and error rate $F(1,36) = 7.488$, $p = .01$) when the incongruent trials were analyzed separately.

Distributional results

We decided to group the €0 and €0.01 reward conditions (LR; lower reward) and the €1 and €1.5 reward conditions (HR;

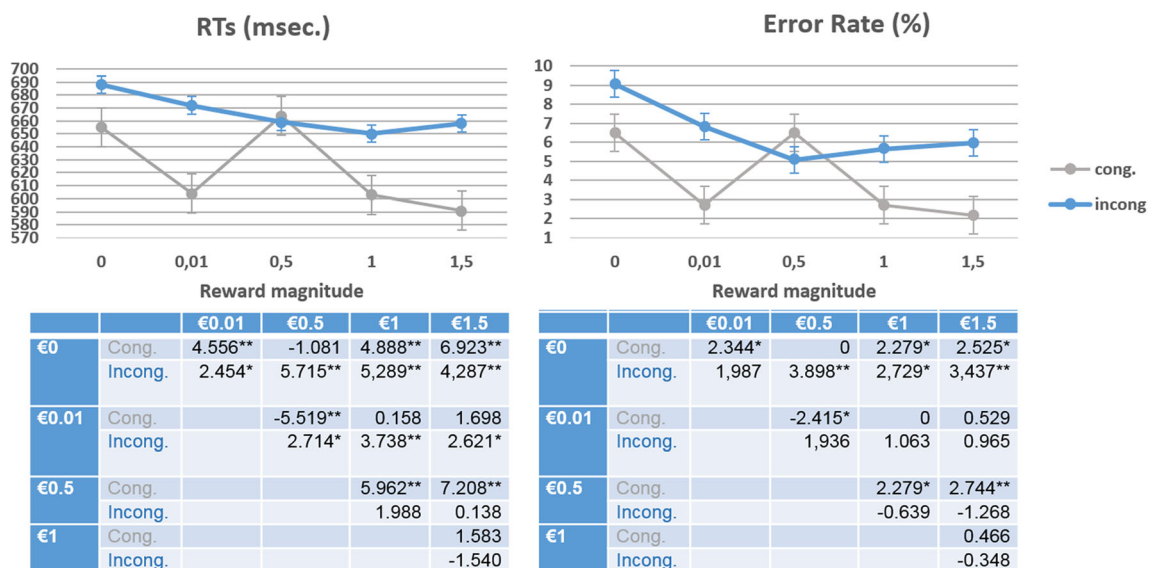
Table 1 Means (standard deviations) of the behavioral variables of interest in each reward magnitude

	RTs			Error rate			Congruency effect	
	Cong.	Incong.	Σ	Cong.	Incong.	Σ	RTs	ER
€ ^d 0	655 (92)	688 (88)	671 (85)	6.487 (9.49)	9.073 (6.915)	7.78 (7.224)	34 (60)	2.587 (8.191)
€ ^d 0.01	604 (72)	672 (85)	638 (75)	2.703 (5.60)	6.821 (7.321)	4.762 (5.739)	68 (45)	4.118 (6.182)
€ ^d 0.5	664 (101)	659 (84)	662 (89)	6.487 (9.49)	5.084 (5.388)	5.785 (6.602)	−6 (54)	−1.403 (7.993)
€ ^d 1	603 (82)	650 (79)	627 (78)	2.703 (6.52)	5.663 (6.258)	4.183 (5.393)	47 (41)	2.96 (6.854)
€ ^d 1.5	591 (72)	658 (78)	625 (72)	2.162 (4.79)	5.985 (6.138)	4.073 (4.176)	67 (40)	3.822 (7.178)
Σ	623 (76)	665 (80)		4.108 (4.545)	6.525 (5.216)			

RTs, Reaction Time; €^d, euro; Cong., congruent; Incong., incongruent; Σ, sum

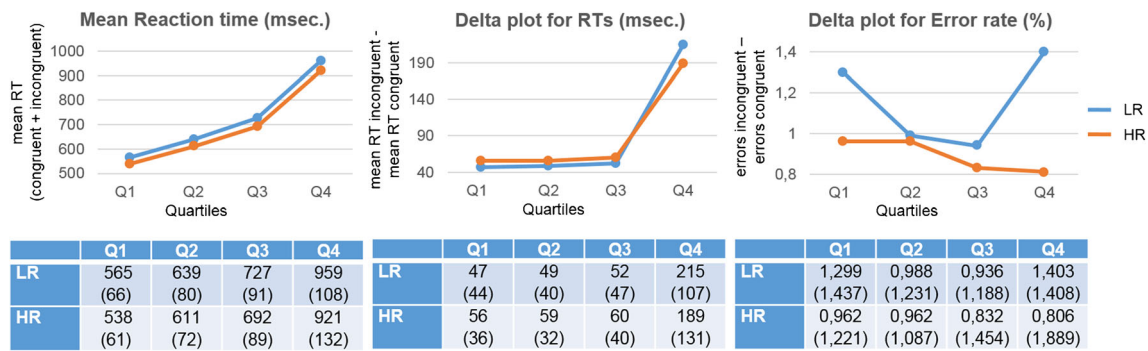
higher reward), and to exclude the €0.5 reward condition given the unexpected effect in the congruent trials for the €0.5 reward condition, and to increase statistical power. The results of the distributional analyses are illustrated in Fig. 3. For the mean RTs, we observed a significant main effect of the reward magnitude ($F(1,36) = 39.519$; $p < .001$) and a significant main effect of the response speed quartile ($F(1108) = 745.371$; $p < .001$) without a significant reward magnitude \times the response speed quartile ($p > .05$), which indicates that the reward effect on the congruency effect depends on the response speed. For the RTs plot, we only observed a significant main effect of the response speed quartile ($F(3108) = 104.745$; $p < .001$), without a significant main effect of the reward magnitude or reward magnitude \times response speed quartile ($p > .05$). Once again, this indicates that the reward effect on the congruency effect depends on the response speed. In the error rate plot, we observed a significant main effect of the reward magnitude ($F(1,36) = 4.963$; $p = .032$),

but no main effect of the response speed quartile and reward magnitude \times response speed quartile ($p > .05$). Once again, this indicates that the reward effect on the congruency effect depends on the response speed. In spite of the lack of any interaction between the reward magnitude and response speed quartile, Fig. 3 revealed that the error rate for Q4 did not behave exactly the same way for LR and HR. In fact, previous works suggest that group differences in the efficiency of inhibition are argued to be most discernible at the slowest segments of the RTs distribution (Burle et al. 2002; Wylie et al. 2009). In order to explore this possibility, we performed a post-hoc analysis by making pairwise comparisons between LR and HR for each quartile. We found a significant difference between LR and HR in the fourth quartile for the error rate effect of the congruency effect $t(36) = 2.737$, $p = .01$. Thus the distributional analyses of the RTs and error rates suggest that motivation implicates a generally faster response speed and no improvement in interference processing, except



The results in the tables under the scatterplots show the pair-wise comparisons t values (*= $p < .05$ and **= $p < .01$). "msec", milliseconds; "cong.", congruent; "incong.", incongruent.

Fig. 2 Graphical representation of congruent and incongruent trials performance for the different behavioral variables and the pair-wise comparisons between reward magnitudes



Related with three within subjects ANOVAs including reward magnitude (LR, HR) x response speed quartile (Q1, Q2, Q3, Q4) in the distributional results section. LR, low reward; HR, high reward; Q1, first quartile; Q2, second quartile; Q3, third quartile; Q4, fourth quartile.

Fig. 3 Graphics from left to right: Mean RTs and delta plots for the congruency effect on RTs and error rate as a function of response speed

for the higher conflict conditions in the error rate (as reflected by a slower quartile). Once again, we emphasize that these results should be cautiously considered given the small number of estimations for the congruent trials under each condition ($n = 10$), and considering that we classified these 10 trials into four quartiles according to their response speed.

Functional results

We observed task-related effects (Stroop-blocks > baseline) throughout the frontal, parietal and striatal regions (see Supplementary Material). The whole brain analysis of the parametric linear increasing of reward magnitude ($R1 < R2 < R3 < R4$) involved a cluster at the left DLPFC ($p < .001$, FWE cluster-corrected), whose activity increased for higher monetary magnitudes. The inverse parametric contrast for linear decreasing ($R1 > R2 > R3 > R4$) involved the left dorsal caudate ($p < .05$, FWE voxel-wise corrected) (see Table 2 and Fig. 4), which indicated less activation for higher monetary rewards. No significant effects were found for any other ROI in the striatum. For illustration purposes, we plotted the parametric effect ($R1 < R2 < R3 < R4$) by extracting the mean beta-weights (parameter estimates) for each separate reward magnitude ($R1 = \text{“€0.01 vs. €0”}$; $R2 = \text{“€0.5 vs. €0”}$; $R3 = \text{“€1 vs. €0”}$; $R4 = \text{“€1.5 vs. €0”}$) from a 4-mm radius sphere centered on the local activity maxima ($p < .001$, FWE cluster-corrected). Likewise, we plotted the inverse parametric effect ($R1 > R2 > R3 > R4$) by extracting the mean beta-weights from the suprathresholded voxels in the dorsal caudate ($p < .05$, FWE voxel-wise corrected). We also performed the corresponding planned pair-wise comparisons

between the reward conditions within both areas with the SPSS software package, v.20 (see Fig. 4). These post hoc analyses were run to examine what drove the parametric effects to obtain a much clearer picture of what drove the effect, but they should not be considered for statistical inference because they were biased estimates of the effects as the ROIs were non independent, but based on the parametric contrast (Poldrack 2007; Kriegeskorte et al. 2009).

Correlation results

The BAS RR scores negatively correlated with monetary differentials (€1.5 minus €0.01) for the RTs ($r(37) = -0.327$, $p = .024$, uncorrected for multiple comparisons; see Fig. 5). We obtained no correlation between any BAS-related trait and brain activation.

Discussion

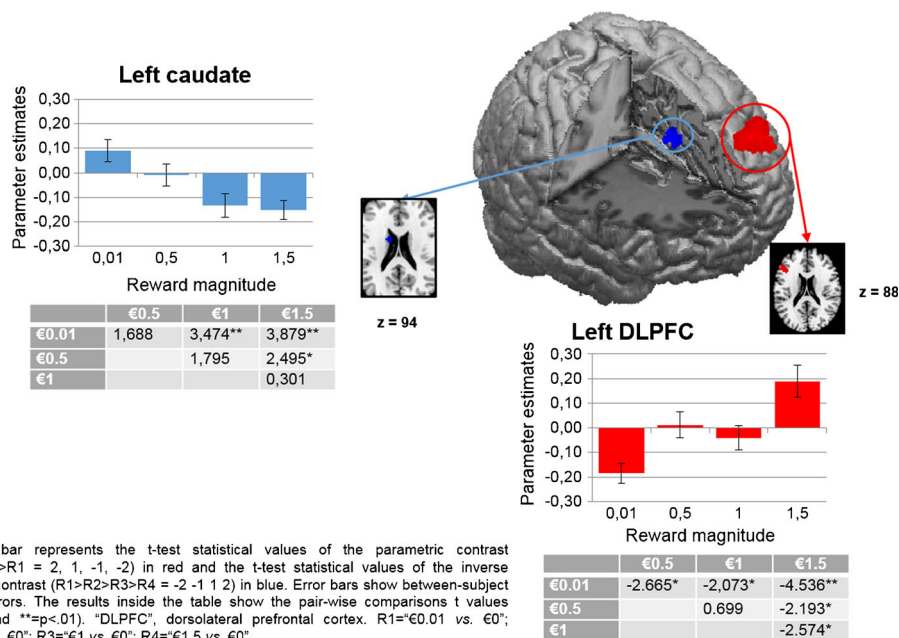
In our fMRI experiment, we wondered how a graded monetary reward magnitude would influence goal-directed behavior and neural activation. To this end, we examined the effects of discrete levels of monetary reward contingencies while performing a Stroop interference condition rather than during a passive conditioning task. In behavioral terms, our study showed that monetary reward cut the RTs and error rate only under certain conditions, and not in a straight linear fashion, which suggests that the prospect of reward improves goal-directed behavior by enhancing neural processing. Thus two reward conditions seem enough to produce enhanced behavior

Table 2 Functional results ($p < 0.001$, FWE cluster-corrected) and (FWE at $p < .05$)

	Brain region	MNI ^d coordinates			Volume (mm ³)	Z score
Parametric effect ($p < 0.001$, FWE cluster-corrected)	Left DLPFC ^c	-51	32	16	2565	4.18
Inverse parametric effect ($p < .05$, FWE voxel-wise corrected)	Left dorsal caudate	-12	-1	22	297	4.31

^a dorsolateral prefrontal cortex; ^b brain regions included inside the main clusters; ^c Montreal Neurologic Institute

Fig. 4 Brain region showing a parametric modulation by reward magnitude and the parameter estimates for each reward magnitude

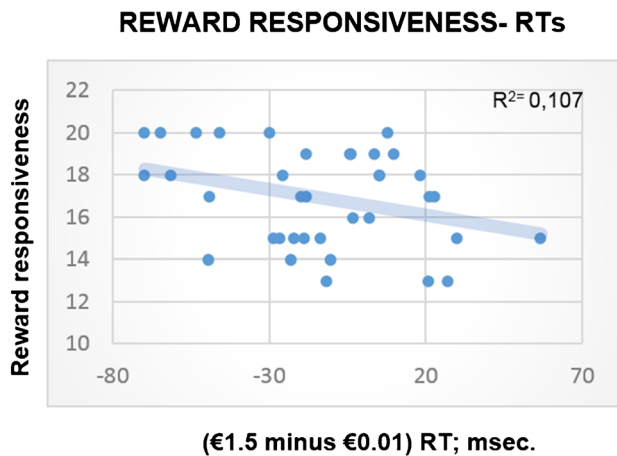


and neural processing, although the inclusion of more than two incentive conditions may have a ceiling effect on improving performance, but not brain function. At the brain level, increasing the reward magnitude enhanced left DLPFC activation, but decreasing the reward magnitude enhanced the left dorsal caudate. The individual differences in reward sensitivity were associated with enhanced behavioral performance. Therefore, the present study presents changes in both behavior and regional brain activation in the DLPFC and the dorsal caudate according to varying reward levels in the Stroop interference context.

Impact of reward on behavioral performance

As far as we know, previous studies have directly analyzed the motivational effects of monetary reward on an Stroop task, including conflict and non conflict conditions (Krebs et al. 2013; 2011, 2010; Veling and Aarts 2010). The results of other studies that have resorted to the picture-word interference task (Padmala and Pessoa 2011; Soutschek et al. 2014) can be compared to classical Stroop tasks (MacLeod and MacDonald 2000). All these previous studies have reported that reward contingencies involve enhanced performance when only two reward and conflict conditions are combined in a factorial design. However, no agreement has been reached about the cognitive mechanism by which such improvement is achieved. Lack of agreement lies in how they differentiate between (1) a more general reward effect that facilitates faster cognitive processing (Veling and Aarts 2010) and (2) a more strategic reward effect that facilitates response selection (Krebs et al. 2013; 2011, 2010; Padmala and Pessoa 2011; Soutschek et al. 2014). Our factorial analysis reported a

congruency by the reward interaction on RTs and ER, but this effect was only confirmed by the distributional analysis for error rate when we removed the €0.5 reward condition. The congruency effects are “higher” at the slow end of the RTs distribution. In fact, based on the activation-suppression hypothesis, Wylie et al. (2009) and Ridderinkhof et al. (2005) consider that inhibition is engaged after the initial activation of a conflicting response and takes time to build-up, which suggests that responses are slowed down when to-be-ignored stimulus features elicit the response opposite to (rather than the response as) that elicited by the target stimulus feature. Therefore, the congruency effect should be minimal for the fastest responses and would grow as RTs slows down. Likewise, Wylie et al. (2009) suggested that group differences in the efficiency of inhibition are argued to be most discernible at the slowest segments of the RTs distribution. Thus our distributional analyses results showed that HR motivational condition did not diminish congruency effect for RTs. However, we observed a non significant reversed congruency effect at the slower quartile (Q4) of the distribution as described by Wylie et al. (2009) according to Burle et al. (2002) (see Fig. 3). On the other hand, we observed a significant reduction in the error rate congruency effect at Q4. In this sense, the most important conclusion we can draw from the distributional analysis is that reward effects on task performance depended on response speed for RTs but they did not for error rate. However, we cannot conclude a parametric effect of reward magnitude on congruency effect, but reward effects were observed when a minimum of two incentive levels were provided. However, our experimental design involved parametric variation in reward magnitude mostly during incongruent trials. Thus our results validated the reward magnitude-related



“msec”, milliseconds;

Fig. 5 Scatterplots displaying the partial correlation between the BAS Reward Responsiveness scores (axes) and the “€1.5 - €0.01” differential for RTs

performance enhancement during complex goal-directed tasks because similar effects were found when comparing a non reward (€0) condition or a low reward magnitude (e.g., €0.01) to higher reward magnitudes (e.g., €0.5, €1 or €1.5); once again, reward effects were observed whenever a minimum of two levels were provided. Previous studies have used only two reward magnitudes (2000 points vs. 0 points in Padmala and Pessoa 2011; \$0 vs. \$0.1 in Krebs et al. 2011; 50 cent vs. 0 cent in Soutschek et al. 2014), which sufficed to discriminate between the mild and strong reward effects on RTs and error rates during cognitive interference. However, our study extends previous results of motivation on goal-directed behavior by evaluating the effects of parametric variations of monetary reward magnitude (€0.01, €0.5, €1 and €1.5) and a control condition (€0), which broadens the known range of monetary reward effects. We showed that performance continued to improve up to the €0.5 reward magnitude from the lower reward conditions, but we observed no differences in task performance between the higher reward magnitudes that we used (€0.5, €1 and €1.5). Indeed, the reward effects on RTs showed both linear and quadratic effects of reward magnitude. The reward effects on RTs in our study must be cautiously considered in line with the both the linear and quadratic effects of reward magnitude. Engelmann et al. (2009) also studied parametric variations of monetary reward magnitude by running a visual attention task using reward magnitudes \$0, \$1 and \$4. However, they only obtained performance improvement for sensitivity scores (d'), but not for RTs, although they did not obtain significant differences for any paired comparison between the reward conditions. They concluded that behavioral performance was enhanced linearly during goal-directed behavior. Yet what we observed for RTs was also a quadratic component that reflected the fact that the increase leveled off, and even fell, in the last measurement(s).

These results suggest that reward magnitude has a ceiling effect on improving performance. According to the magnitudes that we applied in our experiment, a reward magnitude of above €0.5 could suffice to study the magnitude effect of reward on performance in our task. Another plausible explanation is that the parametric variations in the reward magnitude effects depend on the differential reward ratio between conditions. We observed differences between: €0.01 and €0.5, which involved a €1:50 reward ratio; €0.5 and €1, and €0.5 and €1.5, where the ratio was 1:2 and 1:3, respectively; between €1 and €1.5, where the ratio was 1:0.5. In other words, the effects of a certain reward might depend on a relative comparison made with other rewards, rather than the intrinsic or absolute value of this reward (Veling and Aarts 2010), which suggests a relative over an absolute value coding scheme. Future studies could clarify whether using higher reward magnitudes, higher ratios or merely using reward (vs. non reward) is the best strategy to study reward-related effects on goal-directed behavior.

Impact of reward on prefrontal and striatal brain activity

At the brain level, the reward effect showed that the higher the reward magnitude, the greater DLPFC activation became. MacDonald et al. (2000) related the DLPFC with strategic processing and Stroop task implementation, and stressed its key role during the representation and active maintenance of task goal information under proactive control (Grandjean et al. 2012; Lesh et al. 2013). However, recent studies have indicated that reward quality, quantity and the motivational context modulate the task-related activity in the DLPFC, which suggests that it plays a role in integrating cognitive and motivational information processing (Ichihara-Takeda and Funahashi 2008; Watanabe et al. 2007). In fact, Krebs et al. (2011) reported right DLPFC activation when comparing activity for reward trials to non reward trials. Note that the work of Krebs et al. (2011) located DLPFC activation in the right hemisphere, but our work located it in the left hemisphere. Suggestions have been made that different up-regulation mechanisms are activated in the right and left DLPFC while suffering Stroop interference. Accordingly, some works have associated the right DLPFC with an online up-regulation of macro-adjustments in goal-directed behavior, while other have based the left DLPFC role on the temporal up-regulation of the attentional set whenever required by the context (Vanderhasselt and De Raedt 2009), such as reward. This interpretation agrees with the proactive temporal up-regulation of the attentional set for goal attainment with the increasing reward magnitudes found herein. Therefore, our results suggest that the overlapping neural regions involved in cognitive processing also track reward magnitude during task performance.

The reward effect also showed that caudate activation decreases as reward magnitude increases. The left caudate has been implicated in the goal-directed behavior during interference processing (Ali et al. 2010). Previous literature has implicated the dorsal striatum in action-contingent learning; that is, learning about the action and its reward consequences (Balleine et al. 2007; Tricomi et al. 2004), as opposed to more passive forms of appetitive conditioning that have been found to depend on the ventral striatum (Knutson et al. 2001). In fact, we observed no involvement of the ventral striatum. Our task design involved the prospect of reward, and the ventral striatum has been involved in reward anticipation (Knutson et al. 2001), outcome (Delgado et al. 2005; Knutson et al. 2003) and reward learning (Haruno et al. 2004). In our opinion, ventral striatum activation in referenced and other studies is usually captured during transient event-related brain responses. So perhaps its role in signaling sustained reward contexts may be secondary when goal-directed processes are involved (Rothkirch et al. 2014), or it may be blurred by temporal aspects of its reward information coding (Dreher et al. 2006). Our results suggested that left dorsal caudate activation may reduce with the enhancement of goal-directed behavior facilitated by high-magnitude reward contingencies. However, the striatum has usually shown linear increasing trends of activation for higher reward feedback magnitudes (Delgado et al. 2003; Delgado et al. 2005; Smith et al. 2016). As far as we know, there is only a single study that has shown reduced striatum activation while anticipating increasing reward magnitudes in a reward reappraisal context. Staudinger et al. (2011) showed that cognitive emotion regulation decreased responsivity to higher monetary rewards when comparing the anticipation of two reward conditions (€0.5 > €1). Interestingly, the attenuated reward response in the striatum was associated with increased DLPFC activation under emotion regulation in a psychophysiological interaction (PPI) Analysis. Thus our results might suggest a regulatory process in which increased DLPFC and reduced striatum activation may contribute to improve the reward regulation of goal-directed behavior. We ran a post hoc PPI analysis between the activation obtained at the DLPFC and the striatum in our study, but we did not observe a direct association between the activation of both regions in either direction. Nonetheless, Staudinger et al. (2011) located a DLPFC-striatum reward top-down regulation in the putamen, while our effect was located in the dorsal caudate. Dorsal caudate activation has been implicated in goal-directed instrumental behavior that is sensitive to reward outcomes as a subsystem of the associative cortico-basal ganglia networks (Balleine and O'Doherty 2010), although this function is spread over several brain regions that link reward to behavior (Lerchner et al. 2007). Likewise, its role in short-term reward anticipation contrasts with the role of the DLPFC in long-term reward prediction (Tanaka et al. 2016). So we speculate that

reduced dorsal striatum activation may serve to improve task performance, along with increased DLPFC activation, to regulate behavior, and in such a way that cognitive processing improves by maximizing reward outcome. However, our results did not show an association between the DLPFC and the dorsal caudate at a functional level, likely due to the mediation of other acting brain regions. Future studies may serve to test the mediation of the dorsal caudate in the association of DLPFC with reward and behavioral outcomes.

Reward sensitivity and performance

We also found that individual differences in reward sensitivity negatively modulate monetary differential effects on goal-directed behavior for the RTs; that is, high BAS RR scores were associated with less performance improvement from the €0.01 to the €1.5 monetary reward. Previous studies have shown that reward sensitivity trait effects on goal-directed tasks involve motivational contingencies (Aarts et al. 2011; Braver 2012; Braver et al. 2014; Jimura et al. 2010; Locke and Braver 2008; Padmala and Pessoa 2011; van Steenbergen et al. 2009). In our study, we observed a negative relation between reward sensitivity and performance improvement associated with increasing reward, which could be explained by the hypersensitivity of high reward sensitivity subjects to already low monetary rewards, which may even reverse the patterns of expected correlations, as other studies have previously observed (Pickering and Gray 1999).

We did not observe any modulation in the BAS scores for the monetary differential effects on brain activation, which hints at a dissociation between the reward magnitude effects at the behavioral and brain levels as an increasing reward magnitude effect at the brain level was observed from €0.01 to the highest magnitude at €1.5 for fMRI, which was €0.5 at the behavioral level. Therefore, further increased activity does not parallel behavioral effects, which supports the role of these regions in coding the reward value within a goal-directed behavior.

Limitations

Our methodological approach is not without its limitations. The gender distribution between males and females was not equal, although the main results were still significant after regressing out gender effects. We applied an fMRI block design, which entails problems such as habituation and anticipation, and facilitates the application of stimulus processing-related strategic factors. To avoid these effects, we included no-conflict trials among conflict ones (an approximate ratio of 1:4 for no-conflict:conflict trials) but we only varied the parametric effect of reward, and kept a constant high level of interference (e.g. 85 % interference trials per block). Categorical approaches that have subtracted a control

condition from a task condition have assumed that the component of interest is purely inserted into the task condition. In contrast, a parametric approach has systematically tested the relationships between reward parameters and MRI signals to help avoid many cognitive subtraction shortcomings (Friston et al. 1997; Kikyo et al. 2002). Thus we did not control for a condition that involved no-conflict stimuli (e.g., random set of Xs, scrambled color words, or neutral words such as “far”) or only congruent trials (e.g., “two, two”), which is in line with previous parametric studies (Büchel et al. 1998; Elliott et al. 2003; Harris et al. 2000; Kikyo et al. 2002; Seidman et al. 1998). This also avoids a situation in which reward effects on task performance depend on the control condition choice (MacLeod 1991). This design allowed us to test for the reward effects under a cognitive control condition, but we were unable to dissociate the reward effects on interference. We expect that future studies will overcome the limitations of our study.

Regarding behavioral results, the €0.5 reward condition shows odd congruency effects compared to the other reward conditions as congruent trials are slower than incongruent ones. The unexpected congruency effect for the €0.5 condition explained the congruency \times reward interaction with the error rate, but this was not the case with RTs. Likely, a high proportion of incongruent trials vs. congruent ones may reverse the congruency effect, and involve conflict adaptation according to Logan and Zbrodoff (1979) and as shown by Panadero et al. (2015). Soutschek et al. (2013) also observed that given the high expectancy of the incongruent trials (10 % congruent and 90 % incongruent), the congruency effect did not diminish with the possibility of obtaining a high reward (€2 per block) compared to a low reward (€0), and that it even increased, exactly as we observed in the factorial analysis in our study. However, the reported congruency effects should be considered with caution given the odd effect restricted to a single condition, and also given the low proportion and absolute number of congruency trials. Furthermore, regarding incongruent trials, we observed a ceiling effect for enhancing behavioral performance. We cannot rule out that reward involves a quadratic performance trend over reward magnitudes above €1.5, which we did not apply in our study. Yet our results indicated a quadratic effect for accuracy (error rate, $F(1,36) = 7.49$, $p < 0.05$) and RTs ($F(1,36) = 13.28$, $p < 0.005$). In any case, the quadratic effect was less significant than the linear one.

Conclusions

This study has investigated the effects of parametric increasing reward magnitudes (€0, €0.01, €0.5, €1 or €1.5) on goal-directed behavior. We found that increasing reward magnitudes was associated with improved performance in RTs and

accuracy terms, and that this improvement was associated with the reward sensitivity trait in RTs. We found that reward-related left DLPFC and dorsal caudate activation were associated with opposite effects of parametric increasing reward magnitudes. Together with previous reports, this study highlights the reward effects on cognitive performance at the behavioral and brain levels, and restricts this effect to monetary differentials for certain reward magnitudes.

Acknowledgments This research has been supported by Grants PSI2012-33054 from the Spanish Ministry of Economy and Competitiveness, and by 2011I040 from the Spanish National Drug Strategy to ABL. Rosell-Negre P, Bustamante JC, Fuentes P, Costumero V, Benabarre S and Barrós Loscertales declare that they have no conflict of interest.

All the procedures followed were in accordance with the ethical standards of the responsible committee on human experimentation (institutional and national) and with the Declaration of Helsinki (1975), and the applicable revisions at the time that this research was underway. Informed consent to be included in the study was obtained from all the patients.

References

- Aarts, E., Roelofs, A., Franke, B., Rijpkema, M., Fernández, G., Helmich, R. C., & Cools, R. (2010). Striatal dopamine mediates the interface between motivational and cognitive control in humans: evidence from genetic imaging. *Neuropsychopharmacology: Official Publication of the American College of Neuropsychopharmacology*, 35(9), 1943–1951. doi:10.1038/npp.2010.68.
- Aarts, E., van Holstein, M., & Cools, R. (2011). Striatal dopamine and the Interface between motivation and cognition. *Frontiers in Psychology*, 2(July), 163. doi:10.3389/fpsyg.2011.00163
- Ali, N., Green, D. W., Kherif, F., Devlin, J. T., & Price, C. J. (2010). The role of the left head of caudate in suppressing irrelevant words. *Journal of Cognitive Neuroscience*, 22(10), 2369–2386. doi:10.1162/jocn.2009.21352
- Aron AR. From reactive to proactive and selective control: developing a richer model for stopping inappropriate responses. *Biological Psychiatry* [Internet]. Elsevier Inc.; 2011 Jun 15 [cited 2014 Jul 15];69(12):e55–68. Available from: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3039712&tool=pmcentrez&rendertype=abstract>
- Balleine, B. W., & O'Doherty, J. P. (2010). Human and rodent homologies in action control: corticostriatal determinants of goal-directed and habitual action. *Neuropsychopharmacology: Official Publication of the American College of Neuropsychopharmacology*, 35(1), 48–69. doi:10.1038/npp.2009.131.
- Balleine, B. W., Delgado, M. R., & Hikosaka, O. (2007). The role of the dorsal striatum in reward and decision-making. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 27(31), 8161–8165. doi:10.1523/JNEUROSCI.1554-07.2007
- Barrós-Loscertales, A., Bustamante, J. C., Ventura-Campos, N., Llopi, J. J., Parcet, M. A., & Ávila, C. (2011). Lower activation in the right frontoparietal network during a counting stroop task in a cocaine-dependent group. *Psychiatry Research - Neuroimaging*, 194(2), 111–118. doi:10.1016/j.psychres.2011.05.001
- Braver, T. S. (2012). The variable nature of cognitive control: a dual mechanisms framework. *Trends in Cognitive Sciences*, 16(2), 106–113. doi:10.1016/j.tics.2011.12.010.
- Braver, T. S., Krug, M. K., Chiew, K. S., Kool, W., Westbrook, J. A., Clement, N. J., & Somerville, L. H. (2014). Mechanisms of

- motivation-cognition interaction: challenges and opportunities. *Cognitive, Affective, & Behavioral Neuroscience*, 14(2), 443–472. doi:10.3758/s13415-014-0300-0.
- Büchel, C., Holmes, A. P., Rees, G., & Friston, K. J. (1998). Characterizing stimulus-response functions using nonlinear regressors in parametric fMRI experiments. *NeuroImage*, 8(2), 140–148. doi:10.1006/nimg.1998.0351.
- Bugg, J. M., Jacoby, L. L., & Toth, J. P. (2008). Multiple levels of control in the Stroop task. *Memory & Cognition* 36(8), 1484–1494. doi:10.3758/MC.36.8.1484
- Bunge, S. A., Bunge, S. A., Dudukovic, N. M., Dudukovic, N. M., Thomason, M. E., Thomason, M. E., & Gabrieli, J. D. E. (2002). Immature frontal lobe contributions to cognitive control in children: evidence from fMRI. *Neuron*, 33(2), 301–311. doi:10.1016/S0896-6273(01)00583-9.
- Burle, B., Possamaï, C. A., Vidal, F., Bonnet, M., & Hasbroucq, T. (2002). Executive control in the Simon effect: an electromyographic and distributional analysis. *Psychological Research*, 66(4), 324–336. doi:10.1007/s00426-002-0105-6.
- Bush, G., Whalen, P. J., Rosen, B. R., Jenike, M. A., McInerney, S. C., & Rauch, S. L. (1998). The counting stroop: an interference task specialized for functional neuroimaging—validation study with functional MRI. *Human Brain Mapping*, 6(4), 270–282 Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9704265>.
- Bush, G., Frazier, J. A., Rauch, S. L., Seidman, L. J., Whalen, P. J., Jenike, M. A., & Biederman, J. (1999). Anterior cingulate cortex dysfunction in attention-deficit/hyperactivity disorder revealed by fMRI and the counting stroop. *Biological Psychiatry*, 45(12), 1542–1552 Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10376114>.
- Bush, G., Whalen, P. J., Shin, L. M., & Rauch, S. L. (2006). The counting stroop: a cognitive interference task. *Nature Protocols*, 1(1), 230–233. doi:10.1038/nprot.2006.35.
- Carter, C. S., Macdonald, A. M., Botvinick, M., Ross, L. L., Stenger, V. A., Noll, D., & Cohen, J. D. (2000). Parsing executive processes: strategic vs. evaluative functions of the anterior cingulate cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 97(4), 1944–1948. doi:10.1073/pnas.97.4.1944
- Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: the BIS/BAS Scales. *Journal of Personality and Social Psychology*, 67(2), 319–333. doi:10.1037/0022-3514.67.2.319.
- De Pisapia, N., & Braver, T. S. (2006). A model of dual control mechanisms through anterior cingulate and prefrontal cortex interactions. *Neurocomputing*, 69(10–12), 1322–1326. doi:10.1016/j.neucom.2005.12.100.
- Delgado, M. R., Locke, H. M., Stenger, V. A., & Fiez, J. A. (2003). Dorsal striatum responses to reward and punishment: effects of valence and magnitude manipulations. *Cognitive, Affective, & Behavioral Neuroscience*, 3(1), 27–38 Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/12822596>.
- Delgado, M. R., Miller, M. M., Inati, S., & Phelps, E. A. (2005). An fMRI study of reward-related probability learning. *NeuroImage*, 24(3), 862–873. doi:10.1016/j.neuroimage.2004.10.002.
- Di Martino, A., Scheres, A., Margulies, D. S., Kelly, A. M. C., Uddin, L. Q., Shehzad, Z., & Milham, M. P. (2008). Functional connectivity of human striatum: a resting state FMRI study. *Cerebral Cortex (New York, N.Y. : 1991)*, 18(12), 2735–2747. doi:10.1093/cercor/bhn041.
- Dreher, J.-C., Kohn, P., & Berman, K. F. (2006). Neural coding of distinct statistical properties of reward information in humans. *Cerebral Cortex (New York, N.Y. : 1991)*, 16(4), 561–573. doi:10.1093/cercor/bhj004
- Elliott, R., Newman, J. L., Longe, O. A., & Deakin, J. F. W. (2003). Differential response patterns in the striatum and orbitofrontal cortex to financial reward in humans: a parametric functional magnetic resonance imaging study. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 23(1), 303–307. <http://doi.org/23/1/303>
- Engelmann, J. B., Damaraju, E., Padmala, S., & Pessoa, L. (2009). Combined effects of attention and motivation on visual task performance: transient and sustained motivational effects. *Frontiers in Human Neuroscience*, 3(March), 4. doi:10.3389/neuro.09.004.2009
- Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of cluster-size threshold. *Magn Reson Med*, 33(5):636–47.
- Friston, K. J., Holmes, A. P., Poline, J. B., Grasby, P. J., Williams, S. C., Frackowiak, R. S., & Turner, R. (1995). Analysis of fMRI time-series revisited. *NeuroImage* doi:10.1006/nimg.1995.1007
- Friston, K., Price, C., Buechel, C., & Frackowiak, R. (1997). A taxonomy of study design, (i), 1–22.
- Funes, M. J., Lupiáñez, J., & Humphreys, G. (2010). Sustained vs. transient cognitive control: evidence of a behavioral dissociation. *Cognition*, 114(3), 338–347. doi:10.1016/j.cognition.2009.10.007.
- Grandjean, J., D’Ostilio, K., Phillips, C., Baletau, E., Degueldre, C., Luxen, A., & Collette, F. (2012). Modulation of brain activity during a stroop inhibitory task by the kind of cognitive control required. *PLoS One*, 7(7), e41513. doi:10.1371/journal.pone.0041513.
- Harris, I. M., Egan, G. F., Sonkkila, C., Tochon-Danguy, H. J., Paxinos, G., & Watson, J. D. (2000). Selective right parietal lobe activation during mental rotation: a parametric PET study. *Brain: A Journal of Neurology* 123 (Pt 1), 65–73. doi:10.1093/brain/123.1.65
- Haruno, M., Kuroda, T., Doya, K., Toyama, K., Kimura, M., Samejima, K., & Kawato, M. (2004). A Neural Correlate of Reward-Based Behavioral Learning in Caudate Nucleus. *A Functional Magnetic Resonance Imaging Study of a Stochastic Decision Task*, 24(7), 1660–1665. doi:10.1523/JNEUROSCI.3417-03.2004.
- Hayward, G., Goodwin, G. M., & Harmer, C. J. (2004). The role of the anterior cingulate cortex in the counting stroop task. *Experimental Brain Research*, 154(3), 355–358. doi:10.1007/s00221-003-1665-4.
- Ichihara-Takeda, S., & Funahashi, S. (2008). Activity of primate orbitofrontal and dorsolateral prefrontal neurons: effect of reward schedule on task-related activity. *Journal of Cognitive Neuroscience*, 20(4), 563–579. doi:10.1162/jocn.2008.20047.
- Jimura, K., Locke, H. S., & Braver, T. S. (2010). Prefrontal cortex mediation of cognitive enhancement in rewarding motivational contexts. *Proceedings of the National Academy of Sciences of the United States of America*, 107(19), 8871–8876. doi:10.1073/pnas.1002007107.
- Kikyo, H., Ohki, K., & Miyashita, Y. (2002). Neural correlates for feeling-of-knowing. *Neuron*, 36(1), 177–186. doi:10.1016/S0896-6273(02)00939-X.
- Knutson, B., & Greer, S. M. (2008). Anticipatory affect: neural correlates and consequences for choice. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 363(1511), 3771–3786. doi:10.1098/rstb.2008.0155
- Knutson, B., Adams, C. M., Fong, G. W., & Hommer, D. (2001). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 21(16), RC159. <http://doi.org/20015472>
- Knutson, B., Fong, G. W., Bennett, S. M., Adams, C. M., & Hommer, D. (2003). A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: characterization with rapid event-related fMRI. *NeuroImage*, 18(2), 263–272. doi:10.1016/S1053-8119(02)00057-5.
- Krebs, R. M., Boehler, C. N., & Woldorff, M. G. (2010). The influence of reward associations on conflict processing in the stroop task. *Cognition*, 117(3), 341–347. doi:10.1016/j.cognition.2010.08.018.
- Krebs, R. M., Boehler, C. N., Egner, T., & Woldorff, M. G. (2011). 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*, 31(26), 9752–9759. doi:10.1523/JNEUROSCI.0732-11.2011.
- Krebs, R. M., Boehler, C. N., Appelbaum, L. G., & Woldorff, M. G. (2013). Reward associations reduce behavioral interference by changing the temporal dynamics of conflict processing. *PLoS One*, 8(1), e53894. doi:10.1371/journal.pone.0053894.
- Kriegeskorte, N., Simmons, W. K., Bellgowan, P., & Baker, C. I. (2009). Circular analysis in systems neuroscience - the dangers of double dipping. *Nat Neurosci*, 12(5):535–540. doi:10.1038/nn.2303.
- Lechner, A., La Camera, G., & Richmond, B. (2007). Knowing without doing. *Nature Neuroscience*, 10, 15–17. doi:10.1038/nn0107-15.
- Lesh, T. A., Westphal, A. J., Niendam, T. A., Yoon, J. H., Minzenberg, M. J., Ragland, J. D., & Carter, C. S. (2013). Proactive and reactive cognitive control and dorsolateral prefrontal cortex dysfunction in first episode schizophrenia. *NeuroImage: Clinical*, 2(1), 590–599. doi:10.1016/j.nicl.2013.04.010.
- Locke, H. S., & Braver, T. S. (2008). Motivational influences on cognitive control: behavior, brain activation, and individual differences. *Cognitive, Affective, & Behavioral Neuroscience*, 8(1), 99–112. doi:10.3758/cabn.8.1.99.
- Logan, G. D., & Zbrodoff, N. J. (1979). When it helps to be misled: Facilitative effects of increasing the frequency of conflicting stimuli in a Stroop-like task. *Memory & Cognition*, 7(3), 166–174. doi:10.3758/BF03197535.
- MacDonald, A. W., Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science (New York, N.Y.)*, 288(5472), 1835–1838. doi:10.1126/science.288.5472.1835.
- MacLeod, C. M. (1991). Half a century of research on the stroop effect: an integrative review. *Psychological Bulletin*, 109(2), 163–203. doi:10.1037//0033-2909.109.2.163.
- MacLeod, C. M., & MacDonald, P. A. (2000). Interdimensional interference in the stroop effect: uncovering the cognitive and neural anatomy of attention. *Trends in Cognitive Sciences*, 4(10), 383–391. doi:10.1016/S1364-6613(00)01530-8.
- Maldjian, J. A., Laurienti, P. J., Kraft, R. A., & Burdette, J. H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *NeuroImage*, 19(3), 1233–1239. doi:10.1016/S1053-8119(03)00169-1.
- Padmala, S., & Pessoa, L. (2011). Reward reduces conflict by enhancing attentional control and biasing visual cortical processing. *Journal of Cognitive Neuroscience*, 23(11), 3419–3432. doi:10.1162/jocn_a.00011.
- Panadero, A., Castellanos, M.C. & Tudela P. (2015). Unconscious context-specific proportion congruency effect in a stroop-like task. *Consciousness and cognition*, 31:35–45
- Pickering, A.D. & Gray, J. (1999). Dopamine, appetitive reinforcement, and the neuropsychology of human learning: An individual differences approach Personality and Neuropsychology Possible Personality-Sensitive Processes Affecting Learning.
- Poldrack, R. A. (2007). Region of interest analysis for fMRI. *Scan*, 2, 67–70.
- Pratte, M., Rouder, J., Morey, R., & Feng, C. (2010). Exploring the differences in distributional properties between stroop and Simon effects using delta plots. *Attention, Perception, & Psychophysics*, 72(7), 2013–2025. doi:10.3758/APP.
- Ridderinkhof, K. R., Scheres, A., Oosterlaan, J., & Sergeant, J. A. (2005). Delta plots in the study of individual differences: new tools reveal response inhibition deficits in the AD/HD that are eliminated by methylphenidate treatment. *Journal of Abnormal Psychology*, 114(2), 197–215. doi:10.1037/0021-842X.114.2.197/APP.
- Rothkirch, M., Schmack, K., Deserno, L., Darmohray, D., & Sterzer, P. (2014). Attentional modulation of reward processing in the human brain. *Human Brain Mapping*, 35(7), 3036–3051. doi:10.1002/hbm.22383.
- Seidman, L. J., Breiter, H. C., Goodman, J. M., Goldstein, J. M., Woodruff, P. W., O'Craven, K., Rosen, B. R. (1998). A functional magnetic resonance imaging study of auditory vigilance with low and high information processing demands. *Neuropsychology*, 12(4), 505–518. doi:10.1037/0894-4105.12.4.505.
- Smith, D. V., Rigney, A. E., & Delgado, M. R. (2016). Distinct reward properties are encoded via corticostriatal interactions. *Scientific Reports*, 6(August 2015), 20093. doi:10.1038/srep20093.
- Soutschek, A., Strobach, T., & Schubert, T. (2013). Motivational and cognitive determinants of control during conflict processing. *Cognition & Emotion*, 00(May 2014), 37–41. doi:10.1080/02699931.2013.870134.
- Soutschek, A., Stelzel, C., Paschke, L., Walter, H., & Schubert, T. (2014). Dissociable effects of motivation and expectancy on conflict processing: an fMRI study. *Journal of Cognitive Neuroscience*, 1–10. doi:10.1162/jocn.
- Staudinger, M. R., Erk, S., & Walter, H. (2011). Dorsolateral prefrontal cortex modulates striatal reward encoding during reappraisal of reward anticipation. *Cerebral Cortex (New York, N.Y. : 1991)*, 21(11), 2578–2588. doi:10.1093/cercor/bhr041.
- Stoppel, C. M., Boehler, C. N., Strumpf, H., Heinze, H. J., Hopf, J. M., & Schoenfeld, M. A. (2011). Neural processing of reward magnitude under varying attentional demands. *Brain Research*, 1383, 218–229. doi:10.1016/j.brainres.2011.01.095.
- Stroop, J. R. (1935). Studies of Interference in Serial Verbal Reactions, 18(6), 643–662.
- Tanaka, S. C., Doya, K., Okada, G., Ueda, K., Okamoto, Y., & Yamawaki, S. (2016). Prediction of immediate and future rewards differentially recruits cortico-basal ganglia loops. *Behavioral Economics of Preferences, Choices, and Happiness*, (June), 593–616. doi:10.1007/978-4-431-55402-8_22.
- Tricomi, E. M., Delgado, M. R., & Fiez, J. A. (2004). Modulation of caudate activity by action contingency. *Neuron*, 41(2), 281–292. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/14741108>.
- van Steenbergen, H., Band, G. P. H., & Hommel, B. (2009). Reward counteracts conflict adaptation. Evidence for a role of affect in executive control. *Psychological Science*, 20(12), 1473–1477. doi:10.1111/j.1467-9280.2009.02470.x.
- Vanderhasselt, M. A., & De Raedt, R. (2009). Impairments in cognitive control persist during remission from depression and are related to the number of past episodes: an event related potentials study. *Biological Psychology*, 81(3), 169–176. doi:10.1016/j.biopsycho.2009.03.009.
- Veling, H., & Aarts, H. (2010). Cueing task goals and earning money: relatively high monetary rewards reduce failures to act on goals in a stroop task. *Motivation and Emotion*, 34(2), 184–190. doi:10.1007/s11031-010-9160-2.
- Watanabe, M., & Sakagami, M. (2007). Integration of cognitive and motivational context information in the primate prefrontal cortex. *Cerebral Cortex (New York, N.Y. : 1991)*, 17 Suppl 1, i101–i109. doi:10.1093/cercor/bhm067.
- Wylie, S. A., van der Wildenberg, W. P. M., Ridderinkhof, K. R., Bashore, T. R., Powel, V. D., Manning, C. A., & Wooten, G. F. (2009). The effect of Parkinson's disease on interference control during action selection. *Neuropsychologia*, 47(1), 145–157. doi:10.1016/j.neuropsychologia.2008.08.001.