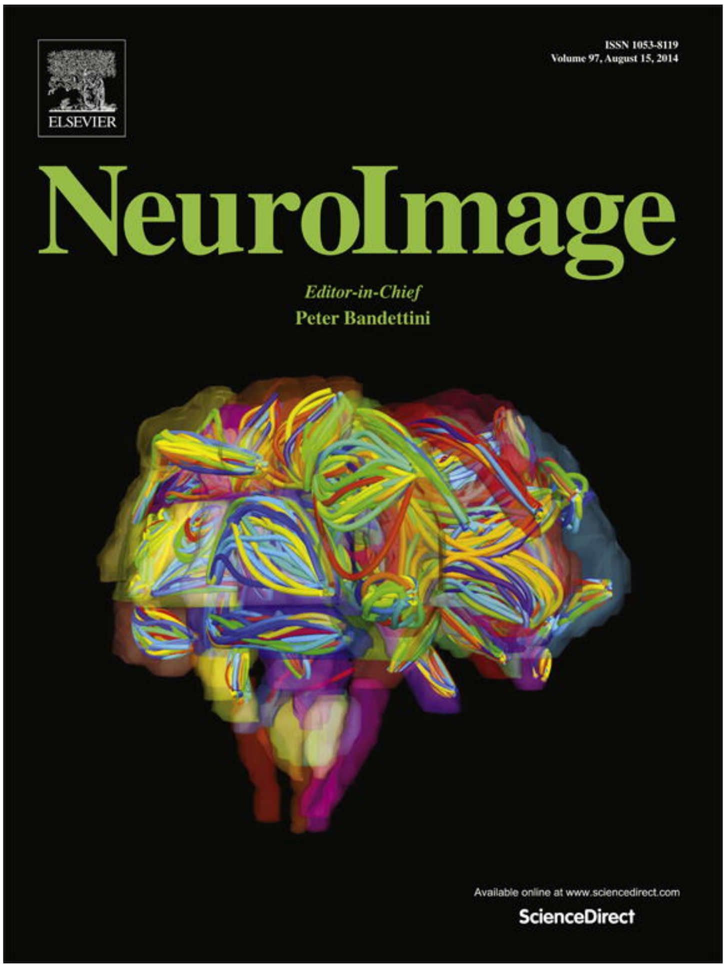
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Sunk costs in the human brain

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ABSTRACT

Rational decision-making should not be influenced by irrecoverable past costs. Human beings, however, often violate this basic rule of economics and take 'sunk' costs into account when making decisions about current or future investments, thus exhibiting a so-called 'sunk cost effect'. Although the sunk cost effect may have serious political, financial or personal consequences, its neural basis is largely unknown. Using functional magnetic resonance imaging (fMRI) and a novel financial decision-making task, we show here that previous investments reduced the contribution of the ventromedial prefrontal cortex (vmPFC) to current decision-making and that this reduction in vmPFC activity correlated with the sunk cost effect. Moreover, activity in the dorsolateral prefrontal cortex (dlPFC) was associated with the norm not to waste resources and negatively correlated with vmPFC activity. The present findings show how past investments may bias decision-making in the human brain, suggesting that the interaction of vmPFC and dlPFC may promote a tendency to throw good money after bad.

Introduction

According to traditional economic theory, rational decision-making should be based on current and future costs and benefits associated with the available alternatives (Bernoulli, 1954; Frank and Bernanke, 2006). Past costs that have already been incurred and cannot be recovered, however, should be ignored when making decisions about present investments. Nevertheless, people are frequently influenced by previous investments in their decision-making, succumbing to a cognitive bias known as the 'sunk cost' effect (Arkes and Ayton, 1999; Arkes and Blumer, 1985). Although the sunk cost effect often leads to adverse financial (McNamara et al., 2002), political (Staw, 1976), or personal consequences (Strube, 1988), its neurobiological underpinnings are largely unknown.

Recent years have seen rapid advances in understanding how decision processes are implemented in the brain (Blakemore and Robbins, 2012; Grabenhorst and Rolls, 2011; Kable and Glimcher, 2009; Rangel et al., 2008). Neurophysiological and neuroimaging studies identified a large network of brain areas relevant for decision-making, including the ventral striatum, the amygdala, the anterior cingulate cortex (ACC), and the parietal cortex (de Martino et al., 2006; Hare et al., 2008; Hunt et al., 2012; Platt and Glimcher, 1999). However, in particular the orbitofrontal cortex (OFC) and the ventromedial prefrontal cortex (vmPFC) are thought to integrate the various dimensions of an option and to compute expected value or utility (Grabenhorst and Rolls, 2011; Kable and Glimcher, 2009; Padoa-Schioppa and Assad, 2006; Schwabe et al., 2012; Valentin et al., 2007) that is central in economic and psychological decision theories (Kahneman and Tversky, 1979; von Neumann and Morgenstern, 1944). Here, we set out to examine how past investments change the contribution of these areas to decision-making and, thus, to characterize the brain mechanisms underlying the sunk cost effect.

To this end, we collected functional magnetic resonance images (fMRI) while participants performed a novel financial decision-making task in which they first had to decide whether to invest a certain amount of money in a project and were then asked whether they wanted to make additional investments that would be required to continue the project. According to economic theory, the initial investment decision and the decision to make further investments should be independent. Furthermore, the decision whether to continue a project or not should be unaffected by the amount of previous investments but only be influenced by the expected value of the current decision alternatives. We predicted, however, that current decision-making would be biased by past investment decisions and that this bias would be dependent on the amount that has already been invested. We further predicted that this sunk cost effect would be mediated by reduced activity in prefrontal areas that are implicated in expected value representation. Moreover, based on previous behavioral data (Arkes and Ayton, 1999), we expected that the tendency to consider sunk costs in current decision-making would be related to the individual norm not to waste resources and that this norm would be represented by brain areas that

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have been implicated in rule based control before, such as the dorsolateral prefrontal cortex (dlPFC; Koechlin and Summerfield, 2007).

Methods

Behavioral pilot studies

The task described below was first tested in two consecutive behavioral pilot studies. In the first pilot study, 12 healthy, young participants (6 men, 6 women; age range: 18 to 32 years) completed a task version that differed from the task that was finally used in the fMRI study with respect to the probabilities of success (low probability of 25% vs. high probability of 75%) Because these parameters resulted only in limited behavioral variability, we ran a second pilot study, in which 15 healthy participants (7 men, 8 women; age range: 18 to 32 years) were tested and in which the investment task was used with exactly the same parameters as described below ("Investment task").

fMRI study

Participants

Twenty-eight healthy, right-handed volunteers with normal or corrected-to-normal vision and without a history of any psychiatric or neurologic disorders participated in this experiment (15 women; mean age = 24.8 years, age range: 20–31 years). All participants gave written informed consent and were paid for their participation. The study was approved by the Institutional Review Board of the Ruhr-University Bochum.

Investment task

During fMRI scanning, participants performed 324 trials of an investment task. On each trial, they were presented a project that was characterized by its costs and probability of success (Fig. 1). The project costs were 0.20 Euros (low) or 0.55 Euros (high) and the probability of success was 40% (low), 50% (medium), or 60% (high). These stated probabilities of success corresponded exactly to those success probabilities that were actually implemented in the trials. Behavioral pilot studies (see "Behavioral pilot studies") showed that these parameters resulted in sufficient variability in investment decisions. Participants had 5 s to decide whether they wanted to invest the requested amount in the given project or not by pressing the corresponding button on a response box; the location of the "invest" and "do not invest" responses on the screen varied randomly across participants. If they did not respond within 5 s or decided not to invest in the project, the trial was aborted. However, if participants decided to invest in the project, they received either the immediate feedback that the project was successful or not (according to the given probability of success) or they were informed that further investments would be required. In this latter case, participants were next shown the additional costs that would be required and the current probability of success. The additional costs could again be 0.20 Euros or 0.55 Euros and the probability of success could again be 40, 50, or 60%, thus the only difference between the decision scenarios for the initial investment and the follow-up investment was whether or not participants had already invested in the project. Again, participants had 5 s to decide whether to invest the additional costs or whether to stop the project. If participants invested the additional costs, they received immediate feedback on the success of the project, i.e., there was at maximum one follow-up investment. If the participants decided not to invest the additional costs, the trial was aborted.

Each of the six trial types that resulted from the different combinations of project costs (low vs. high) and probability of success (low vs. medium vs. high) was presented 54 times. In order to make sure that there was a sufficient number of trials in which the influence of prior investments on current investment decisions could be tested (i.e., in which participants had decided to invest), two-thirds of all trials were 'follow-up trials'. In these trials, participants were informed that follow-up investments would be required after they had decided to make the initial investment. These follow-up trials were further subdivided into those in which a low initial investment (0.20 Euros) had been made and those in which participants had already invested a high amount of money (0.50 Euros). Apart from the previous investment, 'no prior investment trials', 'low prior investment trials', and 'high prior investment trials' were identical; all possible costs × probability combinations were presented equally often in these trials. The inclusion of low- and high-prior investment trials has the advantage that possible effects of the amount of prior investment on decision-making

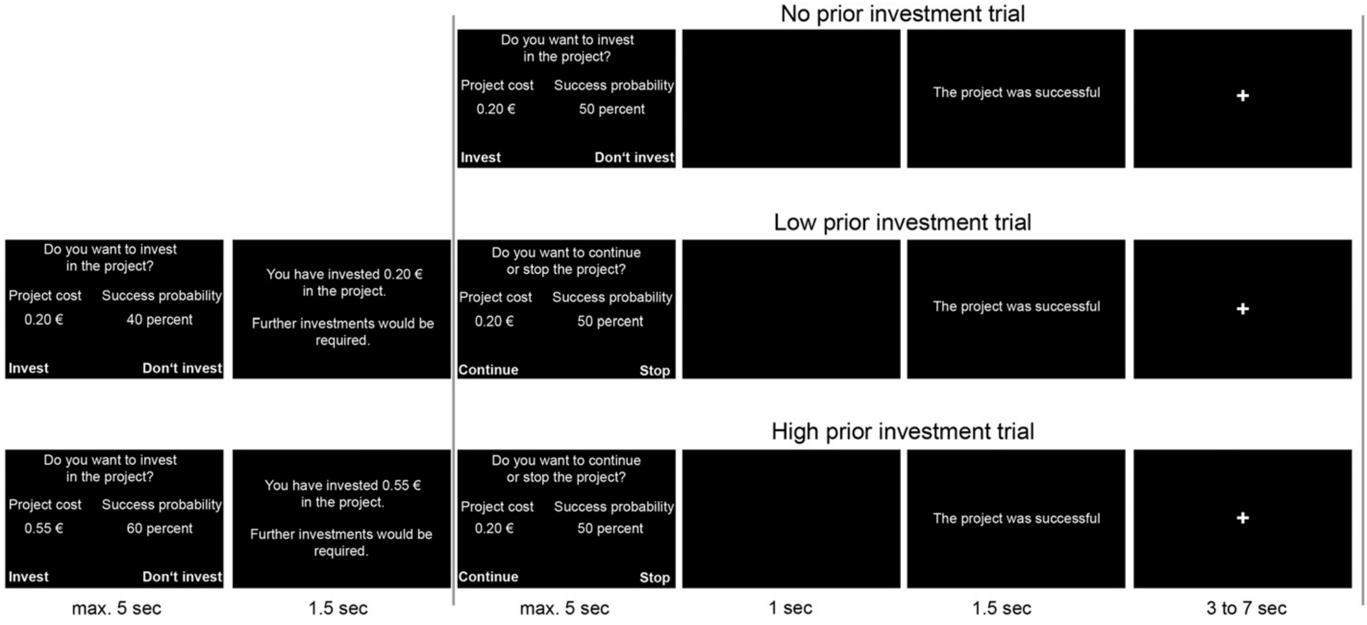

Fig. 1. The investment task. In each trial, participants were presented a project that was characterized by its costs (low vs. high) and probability of success (low vs. medium vs. high). Subjects should decide whether they wanted to invest the requested amount of money in the project or not. If they made the investment, they received either immediate feedback about the project's success (no prior investment trial) or were told that further investments would be required and had to decide whether to invest the additional costs or not (low- and high prior investment trials). The no-, low-, and high prior investment trials differed only in whether and how much participants had already invested in the project.

cannot be explained by any procedural differences (in particular, making one vs. two decisions) that necessarily exist between no prior investment trials and trials in which participants have already made an investment. The different trial types were presented in random order. Between trials, a fixation cross was presented for 3 to 7 s (random jitter: 4 s).

Importantly, participants gained 2 Euros for each project that was completed successfully. However, they also had to pay for the investments they made in a trial, irrespective of a project's success. Participants were informed before the beginning of the investment task that, at the end of the experiment, the computer would randomly select 10 out of the 324 trials and that they would get the money they had gained in these 10 trials in addition to their compensation for participation but that they would also have to pay for any losses that occurred over these 10 trials.

In order to make sure that participants understood the decision-making task, we asked them to repeat the essential features of the task after they had received the task instructions. Possible misconceptions were clarified. In addition, participants performed 3 to 5 training trials out of the scanner and we explained the outcomes achieved in these training trials to the participants. In particular, we emphasized that, in prior investment trials, the probabilities in the initial and follow-up decision scenarios are independent and that any initial investment is lost, irrespective of the follow-up decision.

Wastefulness questionnaire

After completing the investment task, participants filled out a short questionnaire that aimed to assess their desire not to waste resources. This questionnaire consisted of four statements that should be answered on a scale from 1 (“I do not agree”) to 11 (“I completely agree”). The four items were: “It is important for me not to appear wasteful”, “Wasted investments hurt me”, “People who know me think I am wasteful” (inversely coded), and “It annoys me if investments are not successful”. The scores for the 4 items were summed up and this sum score was taken as an indicator of the strength of the individual's desire not to appear wasteful.

Behavioral data analyses

Participants' investment decisions were analyzed by a prior investment (none vs. low vs. high) × project costs (low vs. high) × probability of success (low vs. medium vs. high) ANOVA. Significant main or interaction effects were pursued by appropriate post-hoc tests. All reported *p*-values are two-tailed.

Sunk cost score. In addition, we estimated a sunk cost score for each participant based on their behavioral responses because some of the planned (correlational) analyses required a single parameter that reflects the sunk cost tendency. We calculated for each of the six project costs × probability of success combinations the difference in the percentage of investment decisions between ‘no prior investment trials’ and ‘low prior investment trials’ and between ‘low prior investment trials’ and ‘high prior investment trials’. The average difference was used as an indicator of the individual ‘sunk cost’ tendency. Thus, a higher sunk cost score indicates larger differences between investment decisions in no-, low-, and high-prior investment trials and hence a stronger sunk cost effect.

fMRI data acquisition

Imaging was performed on a 3 T Philips Achieva scanner. All images were acquired using a 32-channel head coil. Three-dimensional T1-weighted anatomical scans were acquired with high resolution 1-mm slice thickness. For BOLD scanning T2*-weighted echoplanar (EPI) images were acquired parallel to the AC–PC plane using the following parameters: repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, 30 slices without gap, slice thickness 3 mm, 2 mm × 2 mm pixel size, 200 mm field of view (FOV). The first 3 images were discarded to allow T1 equilibration.

fMRI data analysis

Preprocessing and analysis of the fMRI data were performed using SPM8 (Wellcome Trust Center for Neuroimaging, University College London). Functional data were corrected for slice-timing and head motion. Structural images were segmented into gray matter, white matter, and cerebrospinal fluid. Gray matter images were normalized to the MNI template image. Normalized gray matter images were used for normalization of the structural and functional images. Finally, data were spatially smoothed using an 8 mm full-width half-maximum Gaussian kernel.

For the data of each participant, we performed a general linear model (GLM) using the factorial design option as implemented in SPM8. We specified the three factors investment (3 levels: no prior investment, low prior investment, high prior investment), project costs (2 levels: low, high), and probability of success (3 levels: low, medium, high) and entered the six project costs × probability of success trial types for no-, low-, and high prior investment trials accordingly as regressors (18 regressors in total). For these events, we used the time point of the button press as onset (duration: 0 s). Thus, in prior investment trials, there was an interval of about 5 s between the feedback on the initial decision and the actually coded follow-up decision. In addition to these regressors of interest, we included solely the six movement regressors counting information about motion correction into our model. All trial types were modeled in the same way. Regressors of interest were constructed by a stick function convolved by a hemodynamic response function (HRF). The data were filtered in the temporal domain using a nonlinear high-pass filter with a 128 s cut-off.

Subject-specific estimates for each effect of interest were then entered into a second-level (group) one-sample *t*-test. In addition, on the second level, we also conducted whole brain correlation analyses (simple regression) as implemented in SPM8, in which we correlated brain activity in the conjunction contrast no–low prior investment trials ∩ low–high prior investment trials (and the reverse contrasts) with the individual sunk cost and wastefulness score, respectively. Moreover, we examined functional connectivity from the prior investment × project costs × success probability interaction cluster in the right vmPFC as a source region to test which regions of interest covaried with this brain area. To this end, we first extracted the deconvolved time series from this cluster as a seed region (centered at 18, 14, −12; with a 6-mm radius). The psychophysiological interaction (PPI) was then calculated as the element-by-element product of the BOLD signal time course from this sphere and a vector coding for the interactive effect of prior investment, project costs, and probability of success. For each subject, we created a new statistical model containing the PPI as regressor together with the physiological and the psychological vectors. Subjects' specific contrast images were then entered into random effects group (i.e., second-level) analyses.

Our analyses focused on pre-defined regions of interest (ROIs). A priori ROIs were the nucleus accumbens, the amygdala, the anterior cingulate cortex (ACC), the orbitofrontal cortex (OFC), the ventromedial prefrontal cortex (vmPFC) and the dorsolateral prefrontal cortex (dlPFC) because these structures have been consistently implicated in value-based decision making processes (Blakemore and Robbins, 2012; Gold and Shadlen, 2007; Grabenhorst and Rolls, 2011; Kable and Glimcher, 2009; Rangel et al., 2008). The referring masks were taken from the Harvard-Oxford subcortical and cortical atlases (provided by the Harvard Center for Morphometric Analysis; http://www.cma.mgh.harvard.edu) or, for the vmPFC and dlPFC, created with MARINA software (Bender Institute of Neuroimaging, Giessen, Germany; http://www.bion.de/eng/MARINA.php). ROI analyses were performed using the small volume correction (SVC) options of SPM8 with a threshold of $p < .05$, family-wise error (FWE) corrected, and a minimum cluster size of 5 voxels.

Results

Behavioral pilot studies

In a first behavioral pilot study, we used the investment task as described above but with probabilities of success of either 25% (low) or 75% (high). These parameters, however, resulted only in very limited behavioral variability, i.e., in trials with a probability of success of 25% virtually all participants decided in all trials not to invest in the project, whereas in trials with a probability of 75% almost all participants invested in the project. We then ran a second pilot study, in which the procedure of the investment task was exactly the same as in the fMRI study. An investment × project costs × probability of success ANOVA on participants' investment decisions in this behavioral pilot study revealed in addition to main effects of investment ($F(2, 28) = 35.70$, $p < .001$), project costs ($F(1, 14) = 17.64$, $p < .005$), and probability of success ($F(2, 28) = 14.91$, $p < .005$), a significant three-way interaction between these factors ($F(4, 40) = 3.61$, $p = .01$). Follow-up tests showed that the expected value of a project (i.e., the combination of costs and probability of success) influenced investment decisions when no prior investment was made ($F(2, 28) = 4.53$, $p = .02$) but not when a low ($F(2, 28) = 2.32$, $p = .11$) or high ($F(2, 28) = 1.15$, $p = .34$) amount of money had already been invested in the project. As shown in Fig. 2, the influence of prior investments on participants' decisions increased with decreasing expected value of a project and was also dependent on the amount of money that had already been invested in the project.

Neural signature of the sunk cost effect

Overall, participants' choice behavior in the fMRI study was influenced by the costs, probability of success, and the combination of costs and success probability (all $F > 25$, all $p < .001$). In addition, the behavioral data in the financial decision-making task showed also a significant effect of prior investment ($F(2, 54) = 52.46$, $p < .001$), indicating a pronounced sunk cost effect (Fig. 3): participants decided significantly more often to invest the requested amount of money in low- compared to no prior investment trials ($F(1, 27) = 55.01$, $p < .001$) and in high- compared to low prior investment trials ($F(1, 27) = 11.07$, $p < .01$). Strikingly, the influence of prior investments was strongest for projects with a relatively low expected value and the impact of the expected value decreased when prior investments had been made (prior investment × costs × success probability interaction: $F(4, 108) = 4.65$, $p < .01$).

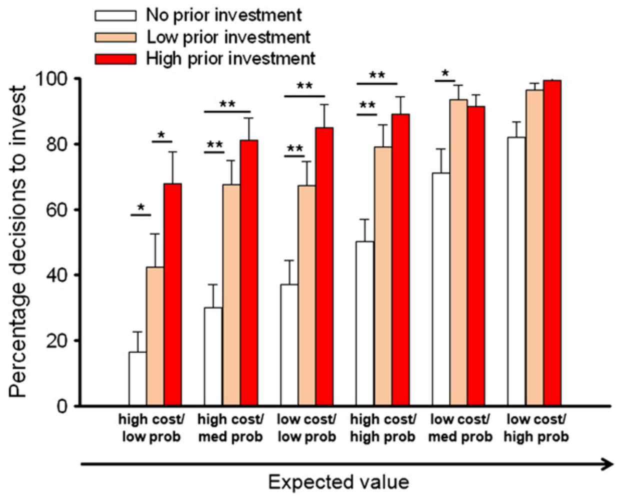

Fig. 2. Data of the behavioral pilot study. Although decisions to invest were generally dependent on the expected value of the project, the influence of the expected value decreased significantly if participants had already invested in the project. Participants showed a strong tendency to further invest in a project if they had already invested in this project, particularly if the prior investment was high. Data represent mean ± standard error of the mean. $^{*}p < .05$, $^{**}p < .01$; *p*-values corrected for multiple comparisons.

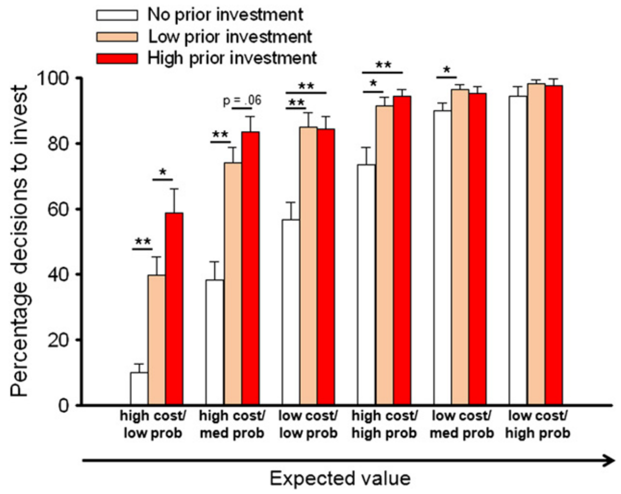

Fig. 3. Behavioral results in the fMRI study. Participants' decisions were biased by previous investments, indicating a sunk cost effect. The sunk cost effect was most pronounced for options with a low expected value. Error bars denote standard errors. $^{**}p < 0.01$, $^{*}p \leq 0.05$; *p*-values corrected for multiple comparisons.

In order to assess the effects of different amounts of prior investments specifically, we performed the above prior investment × costs × probability of success again for the low- and high-probability of success trials only. This ANOVA yielded again, in addition to significant main effects of costs and probability of success and a costs × probability of success interaction (all $F > 20$, all $p < .001$), a significant main effect of the amount of prior investment ($F(1, 27) = 11.07$, $p < .01$) and a significant prior investment × costs × probability of success interaction ($F(2, 54) = 3.46$, $p < .05$). As shown in Fig. 3, investment decisions in low- and high-prior investment trials differed mainly when the expected value was low.

Across all costs × probability of success conditions, the rate for decisions not to (further) invest was 40.6% (range: 11 to 53%) in the initial decision and 16.9% (range: 0.8 to 49%) in the follow-up decision ($t(27) = 8.41$, $p < .001$), which further underlines the pronounced sunk cost effect.

To identify the neural mechanisms involved in the sunk cost effect, we first looked for brain regions that showed significantly decreased or increased activation during decision-making as a function of prior investments. To do so, we performed a conjunction analysis, testing for regions that were active during no- compared to low prior investment trials and during low- compared to high prior investment trials (no–low investment ∩ low–high investment). This analysis showed significant activation in the bilateral nucleus accumbens ($-8, 8, -10$, $Z = 3.97$, $p = .01$, SVC, FWE-corrected; $8, 10, -8$, $Z = 3.62$, $p < .001$, SVC, FWE-corrected) and the right vmPFC ($15, 52, -4$, $Z = 3.76$, $p = .08$, SVC, FWE-corrected), indicating that these areas were less active with increasing prior investments (Figs. 4A and B). Conversely, a conjunction analysis testing for regions that were more active in high- compared to low prior investment trials and in low- compared to no prior investment trials (high–low investment ∩ low–no investment) revealed significantly increased activation in the bilateral amygdala ($-28, -4, -26$, $Z = 4.37$, $p = .001$, SVC, FWE-corrected; $18, -2, -22$, $Z = 3.35$, $p = .08$, SVC, FWE-corrected), ACC ($-4, 36, 20$, $Z = 4.23$, $p = .01$, SVC, FWE-corrected), and right dlPFC ($48, 26, 44$, $Z = 4.35$, $p < .05$, SVC, FWE-corrected; Figs. 4A and B). To assess whether these prior investment-related alterations in brain activity were associated with participants' tendency to consider sunk costs in their decisions, we calculated a sunk cost score that reflects the impact of previous investments on participants' decision-making (see "Behavioral

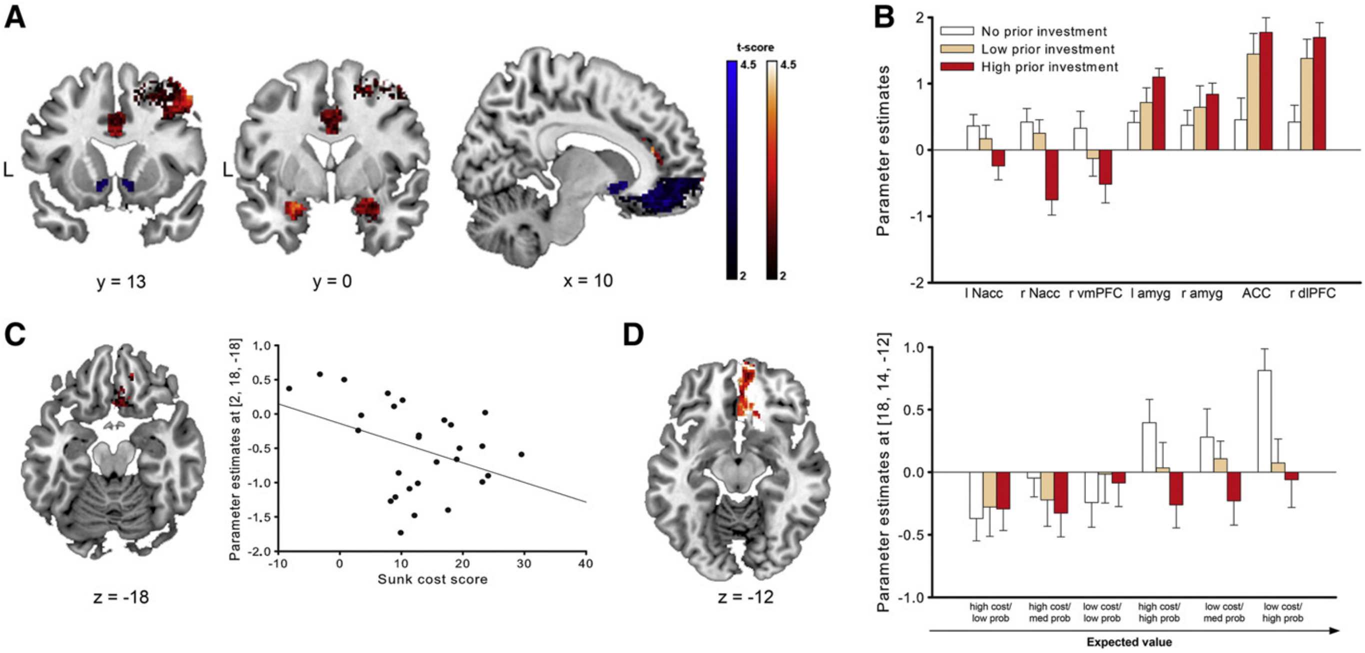

Fig. 4. Neural signature of the sunk cost effect. (A) Brain activations in the conjunction contrasts no–low investment ∩ low–high investment (blue) and high–low investment ∩ low–no investment (red/yellow): (high) previous investments were associated with decreased activity in the nucleus accumbens (Nacc) and vmPFC but with increased activity in the amygdala (amyg), ACC, and, dlPFC. (B) Parameter estimates of the peak voxel for these areas. (C) The activity in the right vmPFC that was associated with high vs. low vs. no prior investments correlated negatively with the sunk cost score. The scatterplot illustrates the correlation between brain activity and the sunk cost score. The analysis, however, was conducted at the whole-brain level. (D) Moreover, an invest × cost × probability interaction in the vmPFC indicated that this region tracked the expected value of a project only when participants had not yet invested in this project. Error bars denote standard errors. L — left, r — right.

data analyses") and correlated this sunk cost score with brain activity in the conjunction contrasts. Interestingly, we obtained a negative correlation between the activation of the right vmPFC (2, 18, −18, $Z = 4.02$, $p < .05$, SVC, FWE-corrected) in the contrast high–low investment ∩ low–no investment and the sunk cost score (Fig. 4C), indicating that reduced activity of the vmPFC in the face of low or high previous investments was associated with a larger sunk cost score. Furthermore, we obtained a positive correlation between activation of the right dlPFC (20, 66, 10, $Z = 2.81$, $p = .002$, uncorrected) in this conjunction contrast and the sunk cost score, which, however, became significant only when a more lenient threshold of $p = .005$ was used.

Next, we subjected our fMRI data to a factorial model with the factors prior investment, costs, and probability. Corroborating earlier reports (de Martino et al., 2006; Rangel et al., 2008), this analysis yielded significant activation of the nucleus accumbens, amygdala, ACC, OFC, dlPFC, and vmPFC, depending on the project costs and the probability of success (Supplementary Tables S1 to S3). Most importantly, however, we obtained also a significant investment × costs × probability interaction in the right vmPFC (18, 14, −12, $Z = 5.60$, $p < .001$, SVC, FWE-corrected), showing that this area tracked the expected value of a project if no prior investment had been made but not if participants had already invested a low or high amount of money in the project (Fig. 4D).

Negative interaction between ventromedial and dorsolateral prefrontal cortices

It has been suggested that the sunk cost effect may be due to people's desire not to appear wasteful (Arkes and Blumer, 1985). We therefore measured participants' desire not to appear wasteful with a short questionnaire (see "Wastefulness questionnaire") and observed a strong correlation between this desire and the sunk cost score ($r = 0.48$, $p < .001$; Fig. 5A), suggesting that participants' tendency to consider past costs in decision-making is indeed related to their desire not to appear wasteful. For this reason, we next asked which brain areas were associated with the influence of the desire not to appear wasteful on decision-making. Therefore, we correlated the score of the wastefulness

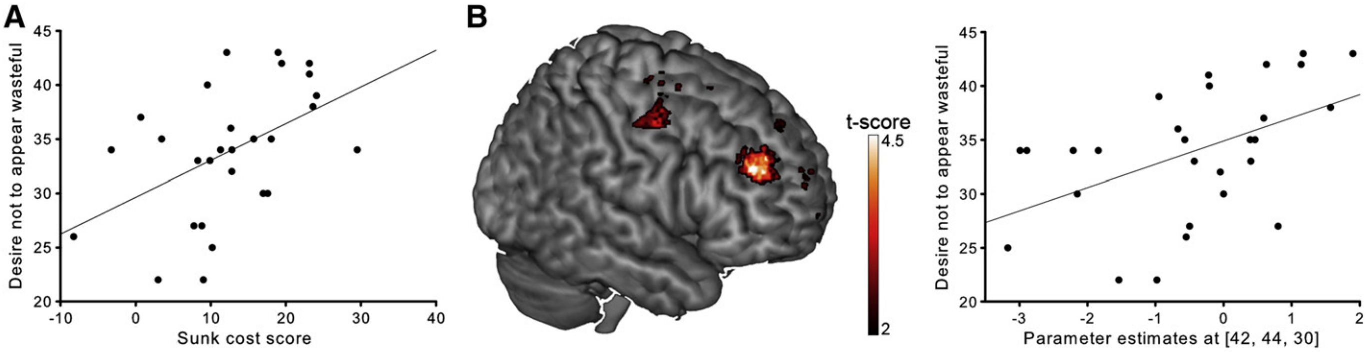

Fig. 5. Impact of the desire not to appear wasteful. (A) The desire not to appear wasteful correlated positively with the sunk cost score. (B) Activity in the dlPFC in the conjunction contrast high–low investment ∩ low–no investment was correlated with the desire not to appear wasteful. The scatterplot illustrates the correlation between brain activity and the desire not to appear wasteful. The analysis, however, was conducted at the whole-brain level. Error bars denote standard errors.

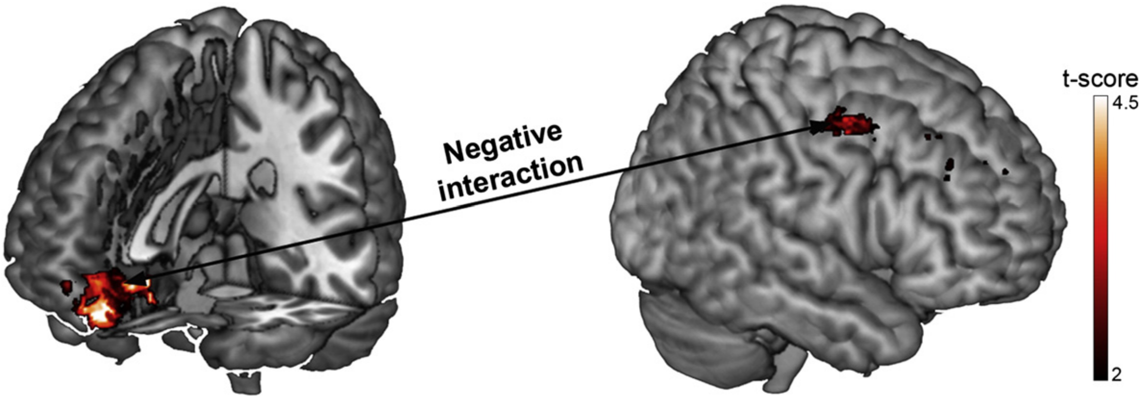

Fig. 6. Interaction of vmPFC and dlPFC. Psychophysiological interaction (PPI) analyses showed that the vmPFC exhibited negative functional connectivity with the dlPFC.

questionnaire with whole brain activation in the conjunction contrasts. We found a positive correlation between the desire not to appear wasteful and the activity of the dlPFC (42, 44, 30, $Z = 4.70$, $p = .01$, SVC, FWE-corrected) in the contrast high–low investment ∩ low–no investment (Figs. 5B and C), indicating that a stronger desire not to appear wasteful was associated with increased activation of the dlPFC in high- compared to low prior investment trials and in low- compared to no prior investment trials.

Because our data suggest that the sunk cost effect is associated with reduced vmPFC activity and that the desire not to appear wasteful is correlated with the dlPFC, we also investigated whether these two areas exhibit functional connectivity during the investment task by means of a psychophysiological interaction (PPI) analysis using the right vmPFC as a seed region. Interestingly, this analysis revealed negative connectivity between the vmPFC and the dlPFC (54, 2, 52, $Z = 3.32$, $p < .05$, SVC, FWE-corrected; Fig. 6), suggesting that the coupling between these two regions during decision-making increased when prior investments were made. When a more lenient threshold of $p = .001$ was used, there was also a positive correlation between the coupling of vmPFC and dlPFC (16, 32, 38, $Z = 2.98$, $p = .001$, uncorrected) with the sunk cost score.

Discussion

The sunk cost effect is one of the most consequential biases in human decision-making. It can explain why people remain in a failing relationship (Strube, 1988) or why they are unable to leave a dissatisfying job (Arkes and Blumer, 1985), it may push up prices in auctions (Murnighan, 2002), drive wars or keep failing policies alive (Staw, 1976). Here, we provide insight into how the sunk cost effect is represented in the human brain. Using a novel decision-making task, we show that a number of prefrontal, striatal, and limbic areas are involved in expected value-based decision-making, in line with several previous reports (Christopoulos et al., 2009; de Martino et al., 2006; Dreher et al., 2006; Hayden et al., 2009; Hunt et al., 2012; Kahnt and Tobler, 2013; Knutson et al., 2005; Yacubian et al., 2007). Importantly, however, our neuroimaging data demonstrate that the contribution of some of these areas to decision-making is significantly altered if a prior investment has been made.

Particularly, the present findings point to a key role of the vmPFC in the sunk cost effect. The vmPFC was less activated during decision-making if participants had already made an investment. Moreover, reduced activation of the vmPFC was associated with participants' tendency to consider previous investments in their current decisions. The vmPFC plays a crucial role in decision-making in general (Bechara et al., 2000) and in the representation of expected value in particular (Chib et al., 2009; Grabenhorst and Rolls, 2011; Kable and Glimcher, 2009). In line with this idea, we found here that vmPFC activity tracked the expected value of a project if participants had not yet invested in this project. However, as indicated by our full factorial model analysis, if an investment had already been made, the contribution of the vmPFC to decision-making was significantly reduced. Thus, if an investment has been made, the vmPFC, the brain area that integrates costs and potential gains (Grabenhorst and Rolls, 2011; Kable and Glimcher, 2009), is less activated and individuals become prone to invest, irrespective of the expected value of a decision alternative. The activation of the nucleus accumbens, another region critical for value-based decision-making (Kable and Glimcher, 2009), was also diminished if participants had already made an investment. In sum, these findings suggest that the influence of previous investments on current decisions is mediated by a reduced involvement of areas representing the value of an option during decision-making.

Once an investment has been made, subsequent decisions are less dependent on the expected value of the decision alternatives. Instead, after an initial investment people's decisions seem to be (at least partly) based on the need to justify the previous investment (Brockner, 1992) and on the desire not to appear wasteful (Arkes and Blumer, 1985). Our data show that the desire not to appear wasteful was associated with enhanced activation of the dlPFC. The dlPFC has previously been implicated in strategic behavior (Steinbeis et al., 2012), cognitive control (MacDonald et al., 2000), self-control (Hare et al., 2009), and norm-related behavior (Sanfey et al., 2003). Together with the present data, these findings suggest a role of the dlPFC in the representation of abstract rules, norms or other higher-order factors that may govern decision-making. Thus, whereas the vmPFC is implicated in value representation, the dlPFC seems to be linked to rule based control (Koechlin and Summerfield, 2007; Rangel and Clithero, 2013). Moreover and in line with the observed negative interaction between the dlPFC and vmPFC, the dlPFC exerts at least some of its effects via modulation of the vmPFC (Baumgartner et al., 2011; Hare et al., 2009). Hence, our data suggest that the dlPFC, representing the norm not to waste resources, is activated once an investment has been made and may override the vmPFC, thus hampering expected value-based decision-making.

In addition to the dlPFC, the amygdala and the ACC were also more active during decision-making if participants had already made an investment. The amygdala is well-known for its role in emotion, particularly in fear processing (LeDoux, 2000), but is also associated with framing effects in decision-making (de Martino et al., 2006). Increased activation of the ACC has mainly been related to cognitive and emotional conflict processing (Botvinick et al., 1999; Etkin et al., 2006). Thus, the higher activity of the amygdala and ACC in low- and high prior investment trials suggests that the decision whether to continue or stop a project in which resources have been invested involves an emotional conflict.

Our behavioral findings show that, when the expected value of a decision option was relatively low, the sunk cost effect was stronger if participants had previously made a high investment than if they had made a low investment; for high expected value options, however, there was no sunk cost effect and no differences between low- and high-prior investment trials. Our fMRI data showed that both the increases in dlPFC, ACC, and amygdala activity and the decrease in vmPFC activity during decision-making were more pronounced after high than after low investments. These findings indicate that the strength of the sunk cost effect depends on the amount that has already been invested. Higher prior investments may increase the activation of the 'don't waste rule', represented in the dlPFC, and thus reduce vmPFC activity and expected value-based choice.

Finally, it is important to note that our fMRI analyses did not distinguish between trials in which participants decided to invest and trials in which participants decided not to invest. Such a distinction was not feasible because participants' investment decisions were confounded with the expected value of a decision alternative and with the amount of prior investments. Furthermore, for a separate analysis of trials in which participants invested and those in which participants did not invest for each of the costs × probability of success × prior investment trial types, the number of trials was too low. The decision-independent analysis implicates that our data show the influence of prior investments on expected value coding rather than the impact of previous investments on actual decisions. Some evidence for the relevance of the effects of prior investments on actual decision-making, however, comes from our correlational analyses showing that alterations in vmPFC activation are associated with actual sunk cost behavior. The fact that the fMRI data show mainly prior investment effects on expected value coding may also account for the finding that the differences between low- and high-prior investment trials appeared to be somewhat stronger at the brain level than at the behavioral level, where such differences occurred only for projects with low expected value. Alternatively, the stronger differences between low- and high-prior investment trials at the brain level may also be due to a differential sensitivity of brain and behavioral data to influences of prior investments.

In conclusion, although a heuristic such as "past investments predict future benefits" may be useful in many everyday decisions (Gigerenzer and Goldstein, 1996), the overgeneralization of this heuristic is maladaptive and may promote a tendency to throw good money after bad (Arkes and Ayton, 1999). The present findings demonstrate how the biasing influence of past investments on decision-making is represented in the human brain. In particular, our findings show that prior investments increase the activity of the dlPFC and, in parallel, reduce the activity of the vmPFC when making a decision, which may render human decision-making irrational.

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Conflict of Interest

The authors report no conflicts of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2014.04.036.

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