Correction

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Correction for "Patterns of neural activity associated with honest and dishonest moral decisions," by Joshua D. Greene and Joseph M. Paxton, which appeared in issue 30, July 28, 2009, of *Proc Natl Acad Sci USA* (106:12506–12511;first published July 21, 2009, 10.1073/pnas.0900152106).

The editor wishes to note that the conflict of interest footnote should have included the following, "Marcus E. Raichle is a member of the governance board for the Law and Neuroscience project with the John D. and Catherine T. MacArthur Foundation, which provided funding for this work."

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Patterns of neural activity associated with honest and dishonest moral decisions

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What makes people behave honestly when confronted with opportunities for dishonest gain? Research on the interplay between controlled and automatic processes in decision making suggests 2 hypotheses: According to the "Will" hypothesis, honesty results from the active resistance of temptation, comparable to the controlled cognitive processes that enable the delay of reward. According to the "Grace" hypothesis, honesty results from the absence of temptation, consistent with research emphasizing the determination of behavior by the presence or absence of automatic processes. To test these hypotheses, we examined neural activity in individuals confronted with opportunities for dishonest gain. Subjects undergoing functional magnetic resonance imaging (fMRI) gained money by accurately predicting the outcomes of computerized coin-flips. In some trials, subjects recorded their predictions in advance. In other trials, subjects were rewarded based on self-reported accuracy, allowing them to gain money dishonestly by lying about the accuracy of their predictions. Many subjects behaved dishonestly, as indicated by improbable levels of "accuracy." Our findings support the Grace hypothesis. Individuals who behaved honestly exhibited no additional control-related activity (or other kind of activity) when choosing to behave honestly, as compared with a control condition in which there was no opportunity for dishonest gain. In contrast, individuals who behaved dishonestly exhibited increased activity in control-related regions of prefrontal cortex, both when choosing to behave dishonestly and on occasions when they refrained from dishonesty. Levels of activity in these regions correlated with the frequency of dishonesty in individuals.

dishonesty | fMRI | honesty | lie detection | moral judgment

R ecent research in moral psychology/neuroscience has focused on the respective roles of automatic and controlled processes in moral judgment (1, 2), particularly in the context of hypothetical dilemmas involving life-and-death tradeoffs ("trolley problems") (3–11). Comparably little is known about the cognitive processes that generate honest and dishonest behavior (12, 13), and the neural bases of choices to behave honestly or dishonestly have, to our knowledge, never been studied specifically. Though there is much recent research on brain-based lie detection (14), subjects in these experiments are instructed to lie, and therefore their behavior is not genuinely dishonest.* Moreover, studies examining instructed lies do not examine the *choice* to lie.

The present study uses fMRI (functional magnetic resonance imaging) and a behavioral design inspired by research on moral hypocrisy (15) to examine the neural bases of honest and dishonest choices. More specifically, this study tests 2 competing hypotheses concerning the cognitive nature of honesty. According to the "Will" hypothesis, honesty results from the active resistance of temptation, comparable to the controlled cognitive processes that enable individuals to delay gratification (16, 17). According to the "Grace" hypothesis, honesty results from the absence of temptation, consistent with research emphasizing the determination of behavior by the presence or absence of automatic processes (1, 18). These hypotheses make competing predictions concerning the engagement of prefrontal structures associated with cognitive control (19–23) in honest individuals as they choose to refrain from dishonest behavior.

Subjects undergoing fMRI attempted to predict the outcomes of random computerized coin-flips and were financially rewarded for accuracy and punished for inaccuracy. In the No Opportunity condition, subjects recorded their predictions in advance, denying them the opportunity to cheat by lying about their accuracy. In the Opportunity condition, subjects made their predictions privately and were rewarded based on their selfreported accuracy, affording them the opportunity to cheat. (Fig. 1) We used a cover story to justify our giving subjects obvious opportunities for dishonest gain. This study was presented as a study of paranormal abilities to "predict the future," aimed at testing the hypotheses that people are better able to predict the future when their predictions are (i) private and (ii) financially incentivized. Thus, subjects were implicitly led to believe, first, that the opportunity for dishonest gain was a known but unintended by-product of the experiment's design and, second, that they were expected to behave honestly. We note that in employing this cover story, subjects were deceived about the experimenters' interests, but not about the economic structure of the task.

Thirty-five subjects were classified as honest, dishonest, or ambiguous based on self-reported accuracy in the Opportunity condition (Fig. 2). We emphasize that these labels describe these subjects' present behavior only and that we make no claims concerning their more general behavioral tendencies. Fourteen subjects reporting improbably high levels of accuracy at the individual level (one-tailed binomial test, P < 0.001), 69% or higher, were classified as dishonest (M "accuracy" = 84%). This conservative threshold was used to ensure an adequate number of cheat trials per dishonest subject. The 14 lowest-accuracy subjects (M accuracy = 52%) were classified as honest. This was the largest group of subjects exhibiting no significant evidence of cheating at the group level (486/926 trials, P > 0.05). Measures were taken to exclude dishonest subjects who disguised their cheating by underreporting accuracy for relatively low-value Opportunity trials. The remaining 7 subjects (M = 62%) were classified as ambiguous. (See Methods and supporting information (SI) Text for further discussion of subject classifications/ exclusions.)

As noted above, the Will and Grace hypotheses make competing predictions concerning the neural activity of honest individuals when they choose to refrain from dishonest behavior. More specifically, these hypotheses make competing predictions concerning the following comparison within the honest group:

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^{*}In one study (40), subjects were instructed by a second experimenter to deceive the first experimenter. This deception, though described as "dishonest," involves neither temptation nor, in our estimation, morally questionable behavior.

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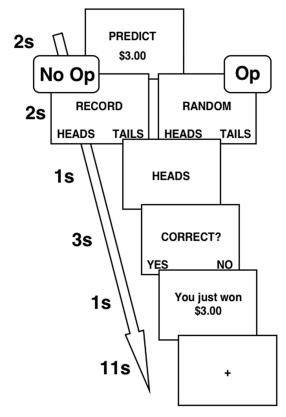


Fig. 1. Task sequence: The subject (1) observes the trial's monetary value and privately predicts the outcome of the upcoming coin flip, (2) records this prediction by pressing 1 of 2 buttons (No Opportunity condition) or presses one of these buttons randomly (Opportunity condition), (3) observes the outcome of the coin flip, (4) indicates whether the prediction was accurate, (5) observes the amount of money won/lost based on the recorded prediction (No Opportunity) or the reported accuracy (Opportunity), and (6) waits for the next trial. Op, opportunity. Button presses in response to screen 2 in the Opportunity condition and screen 4 in the No Opportunity condition control for motor activity.

Opportunity Loss trials (in which the subject lost money because s/he chose not to cheat) vs. No-Opportunity Loss trials (in which the subject lost money and could do nothing about it). According to the Will hypothesis, forgoing an opportunity for dishonest gain requires the active resistance of temptation. Thus, the Will hypothesis predicts that, in the honest group, the Opportunity

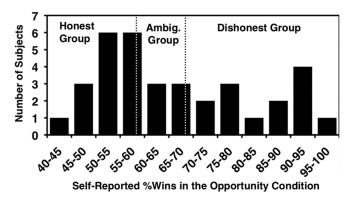


Fig. 2. Distribution of self-reported percent Wins in the Opportunity condition. Subjects were classified into 3 groups based on the probability that they behaved dishonestly. Mean percent Wins in the No Opportunity condition was 50%. See Table 1 for reaction time data.

Table 1. Reaction time data

Group	Condition	<i>M</i> (SD) RT, ms
Honest	Op Win	519 (195)
	Op Loss	556 (215)
	No-Op Win	520 (152)
	No-Op Loss	580 (215)
Ambiguous	Op Win	511 (229)
	Op Loss	585 (324)
	No-Op Win	507 (208)
	No-Op Loss	548 (307)
Dishonest	Op Win	527 (218)
	Op Loss	800 (298)
	No-Op Win	504 (164)
	No-Op Loss	611 (274)

Op, opportunity; RT, reaction time.

Loss trials (relative to No-Opportunity Loss trials) will preferentially engage brain regions associated with response conflict, cognitive control, and/or response inhibition. Such regions include the anterior cingulate cortex (ACC) (19, 20), the dorsolateral prefrontal cortex (DLPFC) (20, 21, 23), and the ventrolateral prefrontal cortex (VLFPC) (22, 24, 25). For convenience we refer to these regions as the "control network," but our use of this label does not imply a one-to-one mapping of structure to function. (See *SI Text* for further discussion.) According to the Grace hypothesis, honest behavior follows from the absence of temptation, implying no need to actively resist temptation when the opportunity for dishonest gain is present. Thus, the Grace hypothesis, in its strongest form, predicts that honest individuals will exhibit no additional control-related activity when they choose to refrain from dishonest behavior. Both of these hypotheses also make competing predictions concerning reaction time (RT). The Will hypothesis predicts that honest individuals will exhibit increased RTs when they choose to refrain from dishonest behavior, reflecting the engagement of additional controlled cognitive processes in actively resisting temptation. In contrast, the Grace hypothesis, in its strongest form, predicts that honest individuals will exhibit no difference in RT between Opportunity Loss trials and No-Opportunity Loss trials.

With respect to dishonest individuals, there are at least 3 reasons to expect increased control network activity for Opportunity trials. First, research on instructed lying consistently implicates control network activity in decisions to lie (14, 26), possibly because honesty is the default response in such contexts. Second, dishonest individuals may engage cognitive control in resisting the temptation to lie, however infrequently or unsuccessfully. Third, control network activity may be engaged in the process of actively deciding whether to lie, independent of the choice made. The present study is not designed to distinguish among these processes, but may offer guidance for future research. As an alternative to all 3 of these hypotheses, one might suppose that individuals who cheat do so automatically, engaging no additional control processes. We note that this hypothesis, though analogous to the Grace hypothesis, is distinct from the Grace hypothesis because it applies to dishonest behavior rather than honest behavior.

Results

Behavioral Data. Table 1 summarizes the RT data. Here we report on planned contrasts following a 2 (group: Honest vs. Dishonest) \times 2 (condition: Opportunity vs. No Opportunity) \times 2 (outcome: Win vs. Loss) mixed-effects ANOVA with subject as a random effect using the residual maximum likelihood (REML) fitting method. We compared Opportunity Win trials, which include both honest and dishonest wins, to No-Opportunity Win

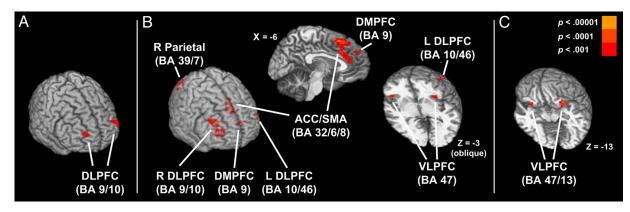


Fig. 3. Brain regions exhibiting increased activity in the Opportunity condition, as compared with the No Opportunity condition, broken down by group (honest vs. dishonest) and outcome type (win vs. loss). BA, Brodmann area. fMRI data are projected onto a reference anatomical image. (A) Increased activity in bilateral DLPFC is associated with decisions to lie (Opportunity Wins > No-Opportunity Wins) in dishonest subjects. (B) Increased activity in bilateral ACC/SMA, DLFPC, VLPFC, DMPFC, and right parietal lobe is associated with decisions to refrain from lying (Opportunity Losses > No-Opportunity Losses) in dishonest subjects. (C) Increased activity in bilateral VLPFC is associated with decisions to accept honest wins (Opportunity Wins > No-Opportunity Wins) in honest subjects. No significant effects were observed in association with decisions to refrain from lying (Opportunity Losses > No-Opportunity Losses) in honest subjects.

trials, which include only forced honest wins. Within the dishonest group there was no significant difference in RT between these 2 cells [F(1, 78) = 0.31, P = 0.58]. Within the dishonest group, Opportunity Loss trials involve "limited honesty" (i.e., decisions to refrain from dishonest behavior in individuals who are willing to behave dishonestly in the present context). The No-Opportunity Loss trials, in contrast, involve only forced losses. Within the dishonest group, there was a significant difference in RT between these 2 cells [F(1, 78) = 21.98, P < 0.0001]. This finding suggests that additional cognitive processes are engaged when dishonest subjects forgo opportunities for dishonest gain (i.e., when they engage in limited honesty). Consistent with these findings, Opportunity Loss trials were slower than Opportunity Win trials within the dishonest group [F(1, 27) = 44.30, P < 0.0001].

Within the honest group there was no significant difference in RT between Opportunity Win trials and No-Opportunity Win trials [F(1, 78) = .001, P = 0.97]. Critically, there was also no significant difference in RT between Opportunity Loss trials and No-Opportunity Loss trials [F(1, 78) = 0.03, P = 0.87]. This finding contrasts starkly with that obtained for the dishonest group and is consistent with the Grace hypothesis, suggesting that honest subjects engage no additional cognitive processes when they forgo opportunities for dishonest gain. Likewise, there was no significant difference in RT between Opportunity Win trials and Opportunity Loss trials in the honest group [F(1, 78) = 1.81, P = 0.18].

For Opportunity Win trials, there was no significant difference in RT between the honest and dishonest subjects [F(1, 58.2) =0.04, P = 0.84]. For Opportunity Loss trials, however, the dishonest subjects took longer [F(1, 58.2) = 15.27, P = 0.0002]. As these findings suggest, within the Loss trials there was a significant group × condition interaction [F(1, 26) = 8.67, P =0.007], generated by the longer RTs for Opportunity Loss trials in the dishonest group. No such interaction was observed within the Win trials [F(1, 26) = 0.75, P = 0.39].

fMRI Data. (See Table S1 for a summary of fMRI contrasts.) To identify neural activity associated with choosing to behave dishonestly, we separately analyzed the data from the dishonest group. (See following text for group comparisons.) We compared Opportunity Win trials (which include both honest and dishonest wins) to No-Opportunity Win trials (which include only honest wins). This comparison revealed increased activity bilaterally in the DLPFC for Opportunity Win trials, associating

these regions with choosing to lie (Fig. 3A and Table S1). Critically, these 2 conditions, both here and in subsequent contrasts, did not differ significantly in mean reward/punishment per trial (signed Wilcoxon rank sum, P > 0.5). Thus, the findings reported here cannot be explained in terms of differing levels of reward. The reverse contrast (No-Opportunity Wins > Opportunity Wins) yielded no significant effects.

To identify neural activity associated with choosing to refrain from dishonest behavior in the dishonest group (limited honesty) we compared Opportunity Loss trials (limited honest losses) to No-Opportunity Loss trials (forced losses). This comparison revealed increased activity for Opportunity Loss trials bilaterally in the control network (Fig. 3B and Table S1). The reverse contrast yielded no significant effects. Thus, consistent with the RT data, we find that control network activity is most robustly associated not with lying, but with refraining from lying in individuals who are willing to lie in the present context (i.e., with limited honesty).

To identify neural activity associated with honest behavior, we repeated the previous analyses in the honest group. Once again, the critical test for the Will and Grace hypotheses is the comparison between Opportunity Loss trials and No-Opportunity Loss trials. Consistent with the RT data, this comparison revealed no significant effects. This null result is striking in that the same contrast (with identical power and statistical thresholds) revealed robust activation in dishonest subjects (Fig. 3B). To further explore this finding, we conducted a spatially restricted analysis using a region of interest (ROI) mask generated by the same contrast in dishonest subjects (Fig. 3B) and a dramatically reduced voxelwise threshold (P < 0.05). This contrast also yielded no significant effects. A voxelwise analysis restricted to the PFC confirmed this group \times condition interaction in the R DLPFC, ACC/SMA, and DMPFC (P < 0.05 corrected). A whole-brain analysis (Fig. S1) confirmed this interaction in the R parietal lobe (P < 0.001 uncorrected). The L DLPFC and bilateral VLPFC exhibited this interaction as well, but at lower thresholds (see Tables S1 and S2). Thus, the honest subjects, unlike the dishonest subjects, showed no sign of engaging additional control processes (or other processes) when choosing to forgo opportunities for dishonest gain. These findings support the Grace hypothesis. Critically, all 14 honest subjects stated in debriefing that they were aware of the opportunity to cheat, indicating that their honest behavior was not due to ignorance.

Comparing Opportunity Wins to No-Opportunity Wins re-

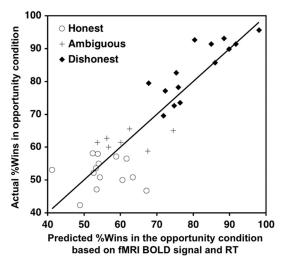


Fig. 4. A stepwise regression model accounts for the frequency of dishonest behavior in individuals (as indexed by percent Wins in the Opportunity condition) based on fMRI BOLD signal in 5 brain regions (L DLPFC, DMPFC, R parietal lobe, and bilateral VLPFC). Model $R^2 = 0.79$; Adj. $R^2 = 0.74$, r = 0.89, n = 35, P < 0.0001 (See Table S3).

vealed increased activity for Opportunity Wins bilaterally in the VLPFC and no significant effects for the reverse contrast (Fig. 3*C* and Table S1). These VLPFC regions are ventral to those identified previously. Neither the Will nor Grace hypothesis explains why honest subjects would exhibit increased VLPFC activity when choosing to *accept* honest wins.[†] We emphasize, however, that this result is not inconsistent with the Grace hypothesis, which specifically predicts the absence of additional control network activity for only those trials in which honest subjects *forgo* dishonest wins (Opportunity Loss trials).

The present findings suggest that individual differences in control network activity may be correlated with individual differences in the presence/frequency of dishonest behavior. To explore this possibility, we performed a backward stepwise multiple regression analysis using each subject's self-reported percent Wins in the Opportunity condition (an estimate of lying frequency) as the dependent variable. We initially entered into the model 18 independent neural variables for each subject, consisting of the mean percent signal change (averaged over 3 postdecision time points) in spherical ROIs corresponding to each of the 9 brain regions identified in our analyses of dishonest subjects, for both Opportunity Win and Opportunity Loss trials. We also included each subject's mean RT for Opportunity Win and Opportunity Loss trials. Following stepwise reduction, the resulting model captured 79% of the variance using 5 brain regions and 7 independent variables (Fig. 4 and Table S3).

Discussion

The behavioral and fMRI data support the Grace hypothesis over the Will hypothesis, suggesting that honest moral decisions depend more on the absence of temptation than on the active resistance of temptation. Individuals who behaved honestly showed no sign of engaging additional controlled cognitive processes when choosing to behave honestly. These individuals exhibited no additional neural activity of any kind when they chose to forgo opportunities for dishonest gain, as compared with control trials in which there was no such opportunity. We provided a more stringent test of this negative result by dramatically reducing the statistical threshold for this comparison, focusing on brain regions that exhibited effects for this comparison in dishonest subjects (Fig. 3B). This more-stringent test also revealed no effects, and further tests (group \times contrast interaction) confirmed that the honest and dishonest subjects exhibited different patterns of activity in these regions. The RT data support the Grace hypothesis as well: Honest individuals took no longer to forgo opportunities for dishonest gain than they did to report their forced losses in control trials. Dishonest individuals, in contrast, took considerably longer to forgo opportunities for dishonest gain. This convergent support for the Grace hypothesis is somewhat surprising. We conducted a survey to assess the a priori plausibility of the Will and Grace hypotheses and found that ordinary people tend to favor the Will hypothesis (See SI Text).

Dishonest behavior was associated with neural activity in brain regions associated with cognitive control, including the ACC (19, 20), DLPFC (20, 21, 23), and VLPFC (22, 24, 25) (Fig. 3 A and B). Moreover, patterns of activity in these control-related regions were correlated with individual differences in the frequency of dishonest behavior (Fig. 4 and Table S3). These findings are consistent with prior research examining instructed lying (14) in associating control network activity with lying. However, in contrast to prior studies,[‡] we find that control network activity is most robustly associated, not with lying per se, but with the limited honesty of individuals who are willing to lie in the present context. It is unlikely that control network activity associated with limited honesty (Fig. 3B) is related to overcoming a default honesty response because such responses are themselves honest. However, this hypothesis may still explain the DLPFC activity observed in association with decisions to lie (Fig. 3A). Alternatively, all of the observed control network activity may reflect (often unsuccessful) attempts to resist temptation. Finally, this activity may reflect the process of actively deciding whether to lie, independent of the choice made. This may be the most parsimonious explanation, given that control network activity was observed in decisions to lie as well as decisions to refrain from lying in dishonest individuals. The fact that control network activity was more robust and widespread in association with decisions to not lie may be explained by the fact that all Opportunity Loss trials involve decisions not to lie, whereas only a minority of Opportunity Win trials involve decisions to lie because most Opportunity Win trials are won honestly. Consistent with this idea, a direct comparison of Opportunity Win to Opportunity Loss trials revealed no effects in the control network (Table S1), suggesting that the patterns of activity associated with lying and refraining from lying in dishonest individuals are not so dissimilar. Finally, we emphasize that the control network activity observed in association with limited honesty is not inconsistent with the Grace hypothesis. This is because the Grace hypothesis applies only to honest decisions in individuals who consistently behaved honestly and not to decisions reflecting limited honesty.

Although the tasks in the Opportunity and No Opportunity conditions are nearly identical, they differ at the first response stage (recording prediction vs. random button-press; see Fig. 1). Thus, one might suppose that it is this task difference, rather than processing related to dishonesty, that explains the effects observed when comparing these conditions. However, if that were so, such effects should also be observed in the honest group, but they were not. In addition, this would not explain why activity in the regions identified correlates with the frequency of dis-

[†]It is possible that this activity reflects the honest subjects' pride or self-doubt upon accepting legitimately won rewards, respectively positive and negative responses to these events. This interpretation is consistent with the implication of this region in the regulation of "self-conscious emotion" (42).

[‡]One study (41) did find increased prefrontal activity in association with the reporting of "salient truth," but the regions identified in this study appear to overlap minimally with those identified here.

honest behavior (Fig. 4). Finally, peak response time in these regions is more consistent with these effects being related to the accuracy reports (\approx 5 sec earlier) than the prediction/random responses (\approx 8 sec earlier) (27) (See Fig. S2 and related discussion in *SI Text*).

RT data are often used to identify the engagement of additional cognitive processing in task performance. We note that, here, the fMRI data complemented and/or outstripped the RT data in this capacity in at least 3 ways. First, the fMRI data revealed increased bilateral DLPFC activity in association with decisions to lie (Opportunity Win trials > No-Opportunity Win trials), whereas the RT data revealed no effect for this comparison. Second, though the RT data accounted for 27% of the individual behavioral variance, the fMRI data accounted for 79% of this variance, including all of the variance accounted for by the RT data. Finally, given that fMRI data can identify the engagement of additional cognitive processes that are not apparent in RT data, the null results observed in the fMRI data provide support for the Grace hypothesis that is complementary to, and probably stronger than, that supplied by the RT data.

Although our present focus is on the cognitive neuroscience of honesty and dishonesty, our findings and methods may be of interest to researchers studying brain-based lie detection (14), in part because the present study is arguably the first to establish a correlation between patterns of neural activity and real lying. However, the present experiment has several notable limitations that deserve attention. First, the model we have developed has not been tested on an independent sample, and therefore its probative value remains unknown. Second, our task design does not allow us to identify individual lies. Third, our findings highlight the challenge in distinguishing lying from related cognitive processes such as deciding whether to lie. Finally, it is not known whether our task is an ecologically valid model for real-world lying. For example, the neural signature of real prepared lies (28) may look different from the patterns observed in association with lying here. Bearing these limitations in mind, our findings may suggest new avenues for research on brainbased lie detection. For example, our findings suggest that interrogations aimed at eliciting indecision about whether to lie, rather than lies per se, may be more effective, provided that the goal is to assess the trustworthiness of the subject rather than the veracity of specific statements.

Several further limitations of the present study deserve attention. First, we cannot determine how many of our dishonest subjects were aware of their dishonesty (13). Some subjects spontaneously confessed in debriefing, but we did not, in this first study, probe dishonest subjects concerning their levels of selfawareness due to this topic's sensitive nature. Second, although our analyses revealed no evidence of temptation and consequent control in the honest subjects, it is not known whether these subjects experienced and willfully extinguished temptation early in the experiment. Third, although many honest subjects claimed in debriefing to have behaved honestly for moral reasons (e.g., "I was feeling moral"), we cannot here make claims concerning these subjects' motivations for behaving honestly (13). In calling these subjects "honest," we are claiming only that they engaged in no (or very little) dishonest behavior. The data, however, do not support the hypothesis that their honest behavior was actively motivated by processes present only in the Opportunity condition, such as concern with being caught. If that were so, we would expect to observe some kind of increased activity in the honest subjects for the contrast Opportunity Loss > No-Opportunity Loss, but no such activity was observed. Finally, as noted previously, it is not known whether the behavior observed here reflects stable dispositions to behave honestly or dishonestly (29-31). The present findings do suggest, however, that some individuals can, at least temporarily, achieve a state of moral grace.

Subjects. We report data from 35 healthy adults (18 females, 17 males, ages 18-58, mean age 24 years). All were right-handed, native English speakers and were screened for the absence of any history of psychiatric and neurological problems. In addition to the data drawn from these 35 subjects, data from 8 subjects were discarded for technical reasons (excessive head movement, software/hardware failures, image artifact). Data from 4 subjects were discarded due to unbalanced factors (too few self-reported losses in the Opportunity condition) as recommended by AFNI (32). Data from 4 subjects were discarded due to suspicions revealed in debriefing concerning the study's purpose. Data from one subject were discarded due to ignorance of the possibility of cheating revealed in debriefing. Data from one subject were discarded due to evidence that the subject deliberately underreported accuracy for relatively low-value Opportunity trials to disguise cheating. To ensure an adequate balance of honest and dishonest subjects, some subjects were recruited from a pool of participants who participated in pilot testing. These subjects were not debriefed before participating in the present study. (See SI Text for further discussion of subject exclusions/inclusions.) Subjects were paid \$75 by check for participating, in addition to winnings from the experimental task.

Procedures. All experimental procedures complied with guidelines of the Harvard University and Partners Healthcare IRBs. Subjects gave written informed consent and filled out the following personality/psychometric inventories: the Ten-Item Personality Measure (33), the Need for Cognition Scale (34), the Disgust Scale (Revised) (35, 36), a 3-item delayed discounting questionnaire (Greene Lab instrument), and the Positive and Negative Affect Schedule (37). Exploratory results related to these questionnaires were inconclusive and are not reported here. To support our cover story, we also had subjects complete the Paranormal Belief Scale (38). Subjects were given detailed directions and completed a minimum of 8 practice trials to ensure task competence. (See SI Text.) At this point some subjects mentioned to the experimenter that it was possible to cheat. The experimenter responded by acknowledging his awareness of that possibility, explained that the possibility of cheating was a necessary by-product of the experimental design, and encouraged the subject to follow the directions (which preclude cheating if followed).

Subjects completed a total of 210 trials as described in Fig. 1. Within the 70 Opportunity trials, the values \$3, \$4, \$5, \$6, or \$7 USD each appeared 14 times, as was the case for the 70 No Opportunity trials. (See SI Text regarding deviations.) We included an additional set of 70 low-value Opportunity trials that were worth \$0.02, \$0.10, \$0.25, \$0.35, and \$0.50 USD. Each of these values also appeared 14 times. Data from these trials were not analyzed. They were included to provide dishonest subjects with additional opportunities for "limited honesty," giving them cover for cheating in the regular (highervalue) Opportunity trials. Subjects were paid the cumulative value of their winnings/losses. Net losses were capped at \$0, and net winnings were capped at \$75 (not including participation payment). Trials appeared in random order in a series of 7 blocks of 30 trials each. Subjects' understanding of the experiment was assessed in debriefing. They were asked in an open-ended way about their thoughts and experiences during the experiment. Subsequently, subjects were informed of the true nature of the experiment and were asked whether they were aware that they could cheat. Some subjects were excluded based on their responses to these questions (See previous text and SI Text).

Image Acquisition. Images were acquired using a 3.0 T Siemens Magnetom Tim Trio full-body scanner at the Martinos Center for Biomedical Imaging of Massachusetts General Hospital. A high-resolution, whole-brain structural scan (1 mm isotropic voxel MPRAGE) was acquired before functional imaging. T2*-weighted functional images were acquired in 33 axial slices parallel to the AC-PC line with a 0.5-mm interslice gap, affording full-brain coverage. Images were acquired using an EPI pulse sequence, with a TR of 2,500 ms, a TE of 30 ms, a flip angle of 90, a FOV of 200 mm, and $3.0 \times 3.0 \times 5.0$ mm voxels. Four additional images included at the start of each run to allow for signal stabilization were discarded.

Image Analysis. Image preprocessing and analysis used the AFNI software package (32). Images were slice-time corrected, motion corrected, spatially smoothed using an 8-mm FWHM Gaussian filter, despiked, and normalized to percent signal change within run. fMRI data were analyzed using multiple regression at the subject level and a mixed effects ANOVA followed by planned contrasts (voxelwise uncorrected threshold P < 0.001, cluster ≥ 8) at the group level. Data were fitted using 28 "tent" regressors (piecewise linear

splines) corresponding to 7 time points (0, 2.5, +5, +7.5, +10, +12.5, +15 sec postresponse), 2 conditions (Opportunity, No Opportunity), and 2 behavioral outcomes (Win, Loss). Beta weights from time points corresponding to the decision period (+5, +7.5, and +10 sec following the appearance of screen 4)were averaged to generate 4 parametric maps for each subject, corresponding to the 4 main cells: condition (Opportunity vs. No Opportunity) imes outcome (Win vs. Loss). Individual subject data were analyzed using a general linear model that included 6 sets of motion parameters as regressors of no interest. Images were then resampled to 3.0 mm isotropic voxels and spatially normalized to the standard coordinate space of Talairach and Tournoux (39) for group analyses. Subjects were classified as honest, dishonest, or ambiguous as described in the main text (see Fig. 2). Data for honest and dishonest subjects were first separately submitted to mixed-effects ANOVAs with subject as a random effect and condition and outcome as fixed effects. For each group, the following planned contrasts were performed using a voxelwise threshold of P < 0.001 and a cluster threshold of 8 voxels using a third nearest-neighbor algorithm: Opportunity Wins vs. No-Opportunity Wins, Opportunity Losses vs. No-Opportunity Losses, Opportunity Wins vs. Opportunity Losses. To test for group differences (group \times condition interactions), we conducted voxelwise

- 1. Haidt J (2001) The emotional dog and its rational tail: A social intuitionist approach to moral judgment. *Psychol Rev* 108:814–834.
- Pizarro DA, Bloom P (2003) The intelligence of the moral intuitions: Comment on Haidt (2001). Psychol Rev 110(1):193–196; discussion 197–198.
- Ciaramelli E, Muccioli M, Ladavas E, di Pellegrino G (2007) Selective deficit in personal moral judgment following damage to ventromedial prefrontal cortex. Soc Cogn Affect Neurosci 2(2):84–92.
- Cushman F, Young L, Hauser M (2006) The role of conscious reasoning and intuition in moral judgment: Testing three principles of harm. *Psychol Sci* 17(12):1082–1089.
- Greene JD, Morelli SA, Lowenberg K, Nystrom LE, Cohen JD (2008) Cognitive load selectively interferes with utilitarian moral judgment. Cognition 107:1144–1154.
- Greene JD, Sommerville RB, Nystrom LE, Darley JM, Cohen JD (2001) An fMRI investigation of emotional engagement in moral judgment. *Science* 293(5537):2105–2108.
- J. Koenigs M, et al. (2007) Damage to the prefrontal cortex increases utilitarian moral judgements. *Nature* 446(7138):908–911.
- Mendez MF, Anderson E, Shapira JS (2005) An investigation of moral judgement in frontotemporal dementia. Cogn Behav Neurol 18(4):193–197.
- Mikhail J (2007) Universal moral grammar: Theory, evidence and the future. Trends Cogn Sci 11(4):143–152.
- Schaich Borg J, Hynes C, Van Horn J, Grafton S, Sinnott-Armstrong W (2006) Consequences, action, and intention as factors in moral judgments: An fMRI investigation. J Coan Neurosci 18(5):803–817.
- Valdesolo P, DeSteno D (2006) Manipulations of emotional context shape moral judgment. Psychol Sci 17(6):476–477.
- Kern M, Chugh D (2009) Bounded ethicality: The perils of loss framing. Psychol Sci 20:378–384.
- Mazar N, Amir O, Ariely D (2007) The dishonesty of honest people: A theory of self-concept maintenance. Social Science Research Network. Available at http:// ssrn.com/abstract=979648.
- Sip KE, Roepstorff A, McGregor W, Frith CD (2008) Detecting deception: The scope and limits. Trends Cogn Sci 12(2):48–53.
- Batson CD, Thompson ER, Seuferling G, Whitney H, Strongman JA (1999) Moral hypocrisy: Appearing moral to oneself without being so. J Pers Soc Psychol 77:525–537.
- McClure SM, Laibson DI, Loewenstein G, Cohen JD (2004) Separate neural systems value immediate and delayed monetary rewards. *Science* 306(5695):503–507.
- Metcalfe J, Mischel W (1999) A hot/cool-system analysis of delay of gratification: Dynamics of willpower. Psychol Rev 106(1):3–19.
- Bargh JA, Chartrand TL (1999) The unbearable automaticity of being. Am Psychol 54:462–479.
- Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD (2001) Conflict monitoring and cognitive control. *Psychol Rev* 108(3):624–652.
- MacDonald AW, III, Cohen JD, Stenger VA, Carter CS (2000) Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science* 288(5472):1835–1838.
- 21. Miller EK, Cohen JD (2001) An integrative theory of prefrontal cortex function. Annu Rev Neurosci 24:167–202.

analyses over the PFC (defined anatomically by AFNI) using a voxelwise threshold of P < 0.05 and a cluster threshold of 199 voxels, corresponding to a corrected threshold of P < 0.05 (algorithm from AFNI AlphaSim). We also tested for these interactions using whole-brain and ROI-based analyses (see Tables S1 and S2). To minimize the biased selection of voxels for our individual differences regression analysis, we replaced our functionally defined ROIs (Fig. 3 A and B) with spherical ROIs (radius 8 mm) centered on the centers of mass of the original ROIs. (Method suggested by Robert Cox, February 20, 2009.)

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- Elliott R, Dolan RJ, Frith CD (2000) Dissociable functions in the medial and lateral orbitofrontal cortex: Evidence from human neuroimaging studies. *Cereb Cortex* 10(3):308–317.
- Koechlin E, Ody C, Kouneiher F (2003) The architecture of cognitive control in the human prefrontal cortex. *Science* 302(5648):1181–1185.
- Beer J, Knight R, D'Esposito M (2006) Controlling the integration of emotion and cognition. *Psychol Sci* 17(5):448–453.
- Eisenberger NI, Lieberman MD, Williams KD (2003) Does rejection hurt? An FMRI study of social exclusion. Science 302(5643):290–292.
- Spence SA, et al. (2001) Behavioural and functional anatomical correlates of deception in humans. *Neuroreport* 12(13):2849–2853.
- Huettel S, Song A, McCarthy G (2004) Functional Magnetic Resonance Imaging (Sinauer, Sunderland, MA).
- Ganis G, Kosslyn SM, Stose S, Thompson WL, Yurgelun-Todd DA (2003) Neural correlates of different types of deception: An fMRI investigation. *Cereb Cortex* 13(8):830–836.
- Doris JM (2002) Lack of Character: Personality and Moral Behavior (Cambridge Univ Press, Cambridge).
- Harman G (1999) Moral philosophy meets social psychology: Virtue ethics and the fundamental attribution error. Proc Aristotelian Soc 99:315–331.
- 31. Ross L, Nisbett RE (1991) The Person and the Situation (McGraw-Hill, New York).
- Cox RW (1996) AFNI: Software for analysis and visualization of functional magnetic resonance images. Comput Biomed Res 29:162–173.
- Gosling SD, Rentfrow PJ, Swann WB (2003) A very brief measure of the Big Five personality domains. J Res Pers 37:504–528.
- Cacioppo J, Petty R, Kao C (1984) The efficient assessment of need for cognition. J Pers Assess 48:306–307.
- Rozin P, Haidt J, McCauley C, Dunlop L, Ashmore M (1999) Individual differences in disgust sensitivity: Comparisons and evaluations of paper-and-pencil versus behavioral measures. J Res Pers 33:330–351.
- 36. Olatunji BO, et al. (2007) The Disgust Scale: Item analysis, factor structure, and suggestions for refinement. *Psychol Assess* 19(3):281–297.
- Watson D, Clark LA, Tellegen A (1988) Development and validation of brief measures of positive and negative affect: The PANAS scales. J Pers Soc Psychol 54(6):1063–1070.
- Tobacyk JJ, Milford G (1983) Belief in paranormal phenomena: Assessment instrument development and implications for personality functioning. J Pers Soc Psychol 44:1029– 1037.
- 39. Talairach J, Tournoux P (1988) A Co-Planar Stereotaxic Atlas of the Human Brain (Thieme, New York).
- Abe N, Suzuki M, Mori E, Itoh M, Fujii T (2007) Deceiving others: Distinct neural responses of the prefrontal cortex and amygdala in simple fabrication and deception with social interactions. J Cogn Neurosci 19(2):287–295.
- 41. Langleben DD, et al. (2005) Telling truth from lie in individual subjects with fast event-related fMRI. *Hum Brain Mapp* 26(4):262–272.
- Beer JS, Heerey EA, Keltner D, Scabini D, Knight RT (2003) The regulatory function of self-conscious emotion: Insights from patients with orbitofrontal damage. J Pers Soc Psychol 85(4):594–604.