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Interactions between cognition and motivation during response inhibition

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Abstract

A growing number of studies have investigated how motivation interacts with particular cognitive functions, including attention, working memory, and other executive functions. In these studies, the emphasis has been on understanding how motivation impacts brain regions that contribute to improving behavioral performance. Less is understood about how positive incentives may actually impair behavioral performance. Here, we were interested in investigating a situation in which reward would be potentially deleterious to behavioral performance. Specifically, we hypothesized that rewarding participants for correct *going* would impair *stopping* performance. Critically, we hypothesized that the effects on inhibition would be specific, namely, not simply attributable to a speeding-up of reaction time during *go* trials. To investigate the interaction between inhibition and motivation, participants performed a stop-signal task during two conditions, namely, during a neutral, control condition and during a rewarded condition during which they were rewarded for correct *go* performance. Behaviorally, participants exhibited longer stop-signal reaction times during the reward relative to the control condition, indicating that it was harder to inhibit their responses during the former condition. Neuroimaging findings revealed that a host of brain regions were

involved in stop-signal inhibition, as indexed via the contrast of successful and unsuccessful stop trials. Critically, a subset of these regions, which included the right inferior frontal gyrus, the left precentral gyrus, and bilateral putamen, exhibited significant inhibition by condition interactions, demonstrating that cognitive and motivational signals interact in the brain during inhibitory control.

Keywords: Motivation; fMRI; Response inhibition; Stop-signal

Article Outline

Human behavioral flexibility depends on a set of so-called executive control functions that are engaged when non-habitual behaviors are required. Human behavior is also shaped by motivational factors, which are closely tied to reward and punishment. A growing number of studies have investigated how motivation interacts with particular cognitive functions, including attention, working memory, and other executive functions ([Engelmann et al., 2009], [Locke and Braver, 2008], [Mohanty et al., 2008] and [Small et al., 2005]). In these studies, the emphasis has been on understanding how motivation impacts brain regions and contributes to improving behavioral performance ([Braver et al., 2007] and [Pessoa, 2009]).

Less is understood about how positive incentives may actually impair cognitive performance. Such knowledge is of importance, however, because diminished behavioral control is a central feature of many clinical and non-clinical groups, including impulsive individuals, ADHD, OCD, and drug abuse populations ([Chambers et al., 2009] and [Li and Sinha, 2008]). In particular, the latter appears to be linked to alterations in processes that are involved in optimizing behavioral responses (Garavan & Stout, 2005).

Inhibiting a prepotent response has been investigated both behaviorally, with monkey physiology, and with human ERPs and fMRI by using go/no-go and stop-signal tasks. Inhibition is believed to involve "control regions" in prefrontal cortex ([Aron et al., 2007b] and [Chambers et al., 2009]). In particular, the inferior frontal cortex (IFC), especially on the right hemisphere, is thought to be centrally involved in this function (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003). Other frontal regions, including the pre-supplementary motor area (pre-SMA), anterior cingulate cortex (ACC), superior/medial frontal gyrus, and precentral gyrus, also have been implicated in response inhibition ([Floden and Stuss, 2006], [Li et al., 2006], [Nachev et al., 2007] and [Picton et al., 2007]). Subcortical regions, including the caudate, putamen, and the subthalamic nucleus, appear to be important, too ([Aron et al., 2007a], [Aron and Poldrack, 2006] and [Li et al., 2008]).

Response inhibition is known to be compromised in, for instance, chronic cocaine users (Hester & Garavan, 2004) and impulsive individuals (Logan, Schachar, & Tannock, 1997), consistent with the notion that it interacts with motivational factors. However, the explicit effect of motivation on inhibition remains largely unexplored and little is known about its neural basis. Here, we were interested in investigating a situation in which reward would be potentially deleterious to behavioral performance. Specifically, we hypothesized that rewarding participants for correct *going* would impair *stopping* performance. Critically, we hypothesized that the effects on inhibition would be specific, namely, not simply attributable to a speeding-up of reaction time during *go* trials. To probe the neural correlates of the interaction between inhibition and motivation, participants performed a stop-signal task under two conditions during functional magnetic resonance imaging (fMRI). During the *reward* condition, participants were rewarded for correct *go* performance; no explicit incentive was associated with stopping performance. During the control condition, no incentives were administered. We anticipated that the stop-signal reaction time (SSRT), a measure of the time course of inhibition, would be increased during the reward relative to the control condition. Critically, we expected that this behavioral interaction would be paralleled by changes in evoked responses across brain regions involved in response inhibition. In particular, we predicted that differential responses evoked to successful and unsuccessful stop trials would be *reduced* during the rewarded vs. control condition, consistent with the notion that stop-task inhibition was harder during the former condition.

1. Methods

1.1. Subjects

Thirty-five volunteers (22 ± 3 years old; 19 females) participated in the study, which was approved by the Institutional Review Board of Indiana University, Bloomington. Subjects were recruited based on responses to flyers posted on different message boards at the Bloomington campus. All subjects were in good health with no past history of psychiatric or neurological disease as assessed by a brief neuropsychiatric interview (MINI) (Sheehan et al., 1998). All participants had normal or corrected-to-normal vision and were free of medications. All participants gave informed written consent. One participant's data were removed from the analysis because of unusually poor performance on *go* trials (70% correct).

1.2. Stimuli and behavioral task

Response inhibition, which requires cancelling an intended action, has been investigated both behaviorally, with monkey physiology, and with human ERPs and fMRI by using go/no-go

([Casey et al., 1997], [Eimer, 1993] and [Kalaska and Crammond, 1995]) and stop-signal ([Aron et al., 2007b], [Boucher et al., 2007], [Logan, 1994] and [Logan and Cowan, 1984]) tasks. We employed a stop-signal paradigm to investigate the effects of motivation on response inhibition (Fig. 1). We used a simple choice-reaction time task, which included both *go* and *stop* trials. Each *go* trial started with the presentation of a simple shape stimulus and participants were asked to indicate “circle” or “square” via button-press on an MR-compatible response box by using the index or middle finger of their right hand. Participants were instructed to respond as soon as possible during the presentation of the shape stimulus (trials with reaction time longer than 1 s were treated as incorrect trials). Following the visual stimulus, subjects viewed a blank screen for 1000 ms. *Stop* trials were identical to *go* trials, except that a brief tone (duration 300 ms) was played after a variable stop-signal delay (SSD) relative to the onset of the *go* stimulus, which indicated that participants should withhold their response. The SSD was adjusted dynamically throughout the experiment, such that if the participant successfully inhibited their response on a *stop* trial, the SSD was increased by 50 ms on a subsequent *stop* trial, and if the participant failed to inhibit their response, the SSD was reduced by 50 ms on a subsequent *stop* trial ([Logan et al., 1997] and [Rubia et al., 2003]). This staircasing procedure ensured that the participants were successfully inhibiting their response on approximately 50% of the *stop* trials. Participants were instructed to respond as quickly and accurately as possible and were asked to inhibit their response upon hearing a tone that followed the initial shape stimulus. They were also told that sometimes it might not be possible to successfully inhibit their response and that, in such cases, they should simply continue performing the task. Overall, the importance of going and stopping was stressed equally. Participants performed a short practice run (approximately 4 min) during the initial anatomical scan (see below) to familiarize themselves with the task.

Full-size image (27K)
High-quality image (117K)

Fig. 1. Stop-signal task paradigm. During *go* trials (84%) subjects responded to the *go* signal (circle or square?), whereas during *stop* trials (16%) they were instructed to withhold the response upon hearing an auditory *stop*-signal. The *stop*-signal followed the *go* stimulus after a variable-length delay (stop-signal delay: SSD), which was updated based on a staircase procedure that maintained behavioral performance at approximately 50% correct.

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Each participant performed four runs of the stop-signal task under the control (no reward) condition and another four runs under the reward condition in an alternating fashion (the order was counterbalanced across participants). The type of run was indicated at the beginning of the run via the presentation of an instruction screen. Separate staircases were used to adjust the SSD during control and reward runs. The initial value of the SSD was set to 250 ms in both staircases. Each run comprised a total of 150 trials, out of which there were 126 (84%)

go trials and 24 (16%) *stop* trials. *Go* and *stop* trials contained circle and square shape stimuli in equal proportion.

Reward and control runs contained the same proportion of *go* and *stop* trials except that participants had a chance of winning money based on their performance on *go* trials during reward runs. Specifically, participants were told the following: "During the reward runs of the experiment, each correct answer on *go* trials will have a potential of winning $1. At the end of each reward run, the program will pick 5 *go* trials at random and based on your performance on those trials you will be rewarded. The amount awarded will be displayed after each reward run. Overall, you will have the chance of winning an extra $20 based on your performance in the four reward runs". They were also clearly informed that there was no reward associated with *stop* trials in this experiment. At the end of the experiment, each participant's base pay ($25) was potentially increased as outlined above and the total amount was paid immediately in cash.

1.3. MR data acquisition

MR data were collected using a 3 Tesla Siemens TRIO scanner (Siemens Medical Systems, Erlangen, Germany). Each scanning session began with a high-resolution MPRAGE anatomical scan (TR = 1900 ms, TE = 4.15 ms, TI = 1100 ms, 1 mm isotropic voxels, 256 mm field of view). Subsequently, in each functional run, 153 EPI volumes were acquired with a TR of 2000 and TE of 25 ms. Each volume consisted of 34 axial-slices with a thickness of 3.8 mm and an in-plane resolution of 3.8 mm × 3.8 mm (240 mm field of view).

1.4. Behavioral data analysis

The SSD was adjusted dynamically to yield an inhibition success rate of approximately 50%. The stop-signal reaction time, which provides an estimate of the "inhibitory reaction time", was calculated by subtracting the average SSD from the median RT during correct *go* trials, following the race model (Logan & Cowan, 1984). The calculation of SSRT was performed separately for control and reward runs.

1.5. General fMRI data analysis

Pre-processing of the data was done using tools from the AFNI software package (Cox, 1996) (http://afni.nimh.nih.gov.ezproxy.is.cuni.cz/afni). The first 3 volumes of each functional run were discarded to account for equilibration effects. The remaining volumes were slice-time corrected using Fourier interpolation such that all slices were realigned to the first slice to account for the timing offset between slices (via program *3dTshift*). Six-parameter rigid-body motion correction within and across runs was performed using Fourier interpolation (Cox & Jesmanowicz, 1999) such that all volumes were spatially registered to the volume acquired closest in time to the particular subject's high-resolution anatomy (via program *3dvolreg*). To normalize the functional data to Talairach space (Talairach & Tournoux, 1988), initially each subject's high-resolution MPRAGE anatomical volume was spatially registered to the TT_N27 template (in Talairach space) using a 12-parameter affine transformation (Jenkinson & Smith, 2001); the same transformation was applied to the functional data (via program *@auto_tlrc*). All volumes were spatially smoothed using a Gaussian filter with a full-width at half maximum of 7.6 mm (i.e., two times the voxel dimension; via program *3dmerge*). Finally, the signal intensity of each voxel was scaled to a mean of 100.

1.6. Voxelwise analysis

Each participant's fMRI data were analyzed by deconvolving the responses of three main event types with shifted delta (i.e., stick) functions (starting at the onset of the shape stimulus): successful stop trials (succ), unsuccessful stop trials (unsucc), and a nuisance event type that included all incorrect *go* trials. Constant, linear, and quadratic terms were included for each run separately (as covariates of no interest) to model the baseline and drifts of the MR signal. Correct *go* trials were not modeled explicitly and constituted the implicit baseline in the model. This type of baseline condition has been used successfully in several fMRI studies of the stop-signal task ([Chamberlain et al., 2009], [Rubia et al., 2003] and [Rubia et al., 2007]). Therefore, all parameters estimates reported in this study are with respect to correct *go* trials as a baseline. Because a hemodynamic shape was not assumed in our analysis, as an index of response strength, we employed the maximum of the estimated responses at times 4 and 6 s following trial onset.

A central goal of the voxelwise analyses was to determine regions of interest (see below). However, for completeness, a voxelwise analysis was also performed and followed the same 2 inhibition (succ, unsucc) × 2 condition (reward, control) repeated-measures ANOVA that was employed in the region of interest analysis.

1.7. Region of interest analysis

To maximize statistical power, we focused our analysis on a set of regions of interest (ROIs) that were robustly activated by our task. ROIs were defined based on the main effect of inhibition (i.e., succ vs. unsucc trials pooled over control and reward conditions) at a p value of .05, corrected for multiple comparisons according to a false discovery rate procedure (Genovese, Lazar, & Nichols, 2002). We adopted this selection criterion to determine ROIs because it was statistically independent of the central goal of our analysis, namely, to probe inhibition by condition interactions (see below) ([Kriegeskorte et al., 2009] and [Vul et al., 2009]). Individual ROIs were drawn using a sphere of 5-mm radius centered at peak voxel of each cluster (at the group level). A representative time series for the ROI was then defined by averaging across all the voxels.

As in the voxelwise analysis, as an index of response strength, we employed the maximum of the estimated responses at times 4 and 6 s following trial onset. This procedure was applied for all ROIs, except the right inferior frontal gyrus, because the responses in this region appeared to be slightly shifted in time (see Fig. 2A). For this region, the maximum of the estimated responses at times 6 and 8 s was employed as the index of response strength. Note that this procedure did not change our results as employing the maximum of the estimated responses at times 4 and 6 s following trial onset also revealed an interaction between inhibition and motivation ($p < .05$; see below).

Full-size image (101K)
High-quality image (639K)

Fig. 2. Average deconvolved responses (relative to correct *go* trials) as a function of trial type in the right inferior frontal gyrus (R IFG; A), left inferior frontal gyrus (L IFG; C), and left precentral gyrus (E). Average stop trial differential activation as a function of condition in the right IFG (B), left IFG (D), and left precentral sulcus (F). The brain insets indicate the position of the ROIs. Error bars indicate standard within-subject errors (Loftus and Masson, 1994). C: control; R: reward; succ: successful stop trial; unsucc: unsuccessful stop trial.

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Our main objective was to assess how the neural correlates of response inhibition were modulated by motivation. As others have suggested, to investigate the neural correlates of response inhibition in the stop-signal task, we contrasted succ and unsucc trials (e.g., [Li et al., 2006] and [Rubia et al., 2003]). Accordingly, for each ROI, response strength was submitted to a 2 inhibition (succ, unsucc) × 2 condition (reward, control) repeated-measures ANOVA. In Table 2, we report regions exhibiting an inhibition by condition interaction. To potentially maximize the behavioral effect of motivation, the control and reward conditions were administered in separate scanning runs. In addition, *go* trials were employed as an implicit baseline condition in our estimation procedure. For these reasons, our study was not optimally suited to determine the main effect of motivation per se ([Engelmann et al., 2009] and [Locke and Braver, 2008]); we thus do not report this main effect.

2. Results

2.1. Behavioral results

Behavioral results are summarized in Table 1. A small improvement in behavioral accuracy was observed for *go* performance. *Go* error rate was 2.3% during the control condition and 1.5% during the reward condition ($p < .01$; Wilcoxon signed rank test). However, no significant differences were observed in the case of reaction time (control: 487.1 ms; reward: 484.0 ms; $t(33) = .71$, $p = .48$). As expected, because of the staircasing procedure, *stop* performance was approximately 50% correct during both conditions (control: 50.5%; reward: 49.1%; $t(33) = .83$, $p = .41$). Critically, SSRT was longer during the reward (213.2 ms) relative to the control condition (192.6 ms) [$t(33) = 2.78$, $p < 0.01$], revealing that it was harder to inhibit the behavioral response during the former condition. Finally, during both conditions, the reaction time of unsucc trials was faster than those of correct *go* trials (control: $t(33) = 2.75$, $p < .01$; reward: $t(33) = 6.63$, $p < .001$), in line with predictions of the race model (Logan & Cowan, 1984).

Table 1.

Behavioral performance: mean results.

	Control	Reward
Go RT (ms)[a]	487.1 ± 18.6	484.0 ± 19.12
Inhibition rate (%)	50.5 ± 0.6	49.1 ± 0.8
SSD (ms)	294.5 ± 25.8	270.7 ± 26.1[*]
SSRT (ms)	192.6 ± 11.0	213.2 ± 10.9[*]
unsucc RT (ms)	461.0 ± 17.4	471.7 ± 17.7
Go error rate (%)	2.3 ± 0.3	1.5 ± 0.2[*]

Full-size table

SSD: stop-signal delay; SSRT: stop-signal reaction time; unsucc: unsuccessful stop trial.

[a] Values reported are the mean of individual median RTs.
[*] $p < 0.01$.

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2.2. fMRI results

To maximize statistical power, interactions between motivation and inhibition were probed across a set of ROIs that were strongly engaged during response inhibition (Table 2). ROI signals were tested via a 2 inhibition (succ, unsucc) by 2 condition (control, reward) repeated-measures ANOVA. Consistent with a growing body of literature, in a voxel-based analysis, a main effect of inhibition was observed throughout parietal and frontal regions, in addition to subcortical ones (Table 2). These regions included the parietal cortex, precentral gyrus, ACC, superior frontal gyrus, middle frontal gyrus (MFG), inferior frontal gyrus (IFG), caudate, and putamen. In most of these regions, responses observed during succ trials were stronger than unsucc trials. Regions with the reverse pattern included the left anterior insula, posterior cingulate cortex, and ACC.

Table 2.

ROI analysis (peak Talairach coordinates and *F* values).

Location		***x***	***y***	***z***	**COND × INHIB, *F*(1,33)**
succ > unsucc					
Parietal					
Intraparietal sulcus	R	24	−56	55	**5.25**[*]
	L	−26	−51	54	**5.01**[*]
Inferior parietal lobe	R	35	−41	47	**4.69**[*]
Frontal					
Frontal eye field	R	28	−13	51	0.82
	L	−24	−12	51	0.97
Precentral gyrus	L	−38	−7	41	**9.71**[***]
Middle frontal gyrus	L	−28	1	49	2.44
Inferior frontal gyrus	R	47	26	19	**7.0**[**]
	L	−45	23	23	**7.09**[**]
Superior frontal gyrus	L	−13	31	46	0.11
Subcortical					
Putamen	R	21	4	3	**5.56**[*]
	L	−21	4	3	**4.83**[*]
Caudate	R	11	6	1	0.02
	L	−8	6	1	0.77
unsucc > succ					
Central sulcus	L	−36	−27	51	0.2

Location		*x*	*y*	*z*	COND × INHIB, *F*(1,33)
Posterior cingulate cortex	L	2	−25	32	2.01
Anterior insula	L	−35	18	9	0.12
Anterior cingulate cortex	R/L	1	23	31	0.03

Full-size table

succ: successful inhibition; unsucc: unsuccessful inhibition.

* Bold font: statistically significant result, $p < 0.05$.
** Bold font: statistically significant result, $p < 0.01$.
*** Bold font: statistically significant result, $p < 0.005$.

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Significant inhibition by condition interactions were observed in frontal cortex in bilateral IFG and left precentral gyrus. For instance, in the right IFG (Fig. 2A and B), succ trials evoked stronger responses relative to unsucc trials, but whereas this difference was sizeable during control trials, it was greatly reduced during the reward condition. It is also of interest that, for unsucc trials, evoked responses appeared to more steeply decline after the peak (at 6 s), while this was not the case for succ trials (especially during the control condition). In addition, the peak of the estimated response during succ trials in the control condition was slightly shifted in time, similar to that of a previous report (Rubia et al., 2003). Although an inhibition by condition interaction was also observed in the left IFG, a very different pattern of results was observed (Fig. 2C and D). Finally, the pattern observed in the left precentral gyrus was similar to that observed in the right IFG (Fig. 2E and F). Although robust responses were observed during the reward condition, comparable responses were obtained for succ and unsucc trials. During the control condition, however, succ responses were considerably larger than unsucc responses.

We also observed significant inhibition by condition interactions at parietal sites, including the right inferior parietal lobe (IPL; Fig. 3A and B) and bilateral intraparietal sulcus (IPS). In these regions, the difference between succ and unsucc trials was greater during the control relative to the reward condition. An additional inhibition by condition interaction was observed in the right (Fig. 3C and D) and left putamen (Fig. 3E and F). Finally, although the focus of our investigation involved cortical and subcortical regions that are believed to be involved in response inhibition, as a control analysis, we evaluated the data in three sensory ROIs that evoked robust responses to the auditory and visual stimuli employed in the task, namely, right and left superior temporal gyrus (STG) and early visual cortex. Across the three ROIs, no main effect of inhibition or inhibition by condition interaction was detected (Fig. 4 shows responses in STG).

Full-size image (92K)
High-quality image (577K)

Fig. 3. Average deconvolved responses (relative to correct *go* trials) as a function of trial type in the right inferior parietal lobe (R IPL; A), right putamen (C), and left putamen (E). Average stop trial differential activation as a function of condition in the right IPL (B), right putamen (D), and left putamen (F). The brain insets indicate the position of the ROIs. Error bars indicate standard within-subject errors (Loftus and Masson, 1994). C: control; R: reward; succ: successful stop trial; unsucc: unsuccessful stop trial.

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Full-size image (42K)
High-quality image (250K)

Fig. 4. Average deconvolved responses (relative to correct *go* trials) as a function of trial type in the left (A) and right (B) superior temporal gyrus (STG). No significant differences were observed. The brain insets indicate the position of the ROIs. C: control; R: reward; succ: successful stop trial; unsucc: unsuccessful stop trial.

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For completeness, we also report the results of whole-brain analyses separately for control and reward conditions, as well as inhibition by condition interaction results (Table 3). Overall, stop-signal inhibition effects were relatively weak during the reward condition, which resulted in inhibition by condition interactions across several frontal and subcortical regions believed to be involved in response inhibition (note that these activations did not survive, however, correction for multiple comparisons). Note that the *F* values reported in Table 3 (voxelwise analysis) are somewhat larger than those observed in Table 2 (ROI analysis). There are at least two reasons why the statistical values differ. For one, the ROI analysis employed a representative time series that was obtained by averaging all of the voxels inside the ROI (5-mm sphere)—which likely decreases some of the highest contributions from "peak voxels". In contrast, the voxelwise analysis reports "peak" *F* values. A related factor is that we performed our ROI inferences via a two-step procedure, by first defining the ROI based on the effect of inhibition and then testing for interaction effects on the resulting representative time series. This kind of ROI selection was used to prevent any circularity in the results of the ROI analysis that can arise from selection procedures ([Kriegeskorte et al., 2009] and [Vul et al., 2009]). Therefore, the two procedures of assessing statistical interactions (ROI and voxelwise) between reward and inhibition do not map to each other in a simple direct manner.

Table 3.

Voxelwise analysis (peak Talairach coordinates, *t*, and *F* values).

Location		**inhibition (control)**				**inhibition (reward)**			**cond × inhib**			
		x	***y***	***z***	***t*(33)**	***x***	***y***	***z***	***t*(33)**	***x***	***y***	***z***	***F*(l,33)**
succ > unsucc													
Parietal													
Intraparietal sulcus	R	26	−55	53	**3.96**[*]	23	−56	56	1.69	29	−59	47	**11.82**[U]
	L	−19	−60	48	**4.15**[*]	28	−56	53	1.54	−30	−56	54	5.05
Inferior parietal	R	36	−38	38	**4.2**	31	−39	45	1.45	29	−39	53	**12.47**[U]

Location		inhibition (control)				inhibition (reward)			cond × inhib				
		x	*y*	*z*	*t*(33)	*x*	*y*	*z*	*t*(33)	*x*	*y*	*z*	*F*(l,33)
lobe					**5**[*]								
Frontal													
Frontal eye field	R	25	−15	50	**3.87**[*]	29	−10	47	3.05	23	−13	53	1.26
	L	−22	−15	52	**4.19**[*]	−21	−16	50	3.1	25	13	55	2.6
Precentral gyrus	L	−34	−10	41	**3.60**[*]	−41	−5	41	1.03	−41	−9	41	**14.05**[U]
Middle frontal gyrus	L	−27	1	50	**4.81**[*]	−28	1	52	2.44	−28	0	49	3.35
Inferior frontal gyrus	R	49	25	17	**4.48**[*]	47	23	20	1.47	50	31	18	**14.89**[U]
	L	−47	23	25	**4.19**[*]	−43	23	20	1.78	−49	20	26	**11.27**[U]
Superior frontal gyrus	L	−9	27	49	**3.61**[*]	−19	22	53	2.76	−13	31	46	0.94
Subcortical													
Putamen	R	21	6	0	**5.18**[*]	26	3	2	3.14	23	2	2	**10.31**[U]

Location		inhibition (control)				inhibition (reward)				cond × inhib			
		x	*y*	*z*	*t*(33)	*x*	*y*	*z*	*t*(33)	*x*	*y*	*z*	*F*(1,33)
	L	−21	4	9	**5.68**[*]	−21	4	3	1.75	−18	4	7	**9.38**[U]
Caudate	R	11	5	2	2.86	11	5	3	2.82	11	6	1	0.4
	L	−12	6	2	2.89	−8	8	2	**3.52**[*]	−9	6	7	2.57
unsucc > succ													
Central sulcus	L	−37	−25	51	**3.97**[*]	37	25	51	**4.26**[*]	−37	−27	54	0.16
Posterior cingulate cortex	L	0	−25	31	**4.97**[*]	1	−22	35	2.41	2	−23	28	2.73
Anterior insula	L	−35	13	11	3.33	−35	11	5	**3.64**[*]	−28	18	10	1.05
Anterior cingulate cortex	R/L	1	17	35	**4.53**[*]	1	17	34	**3.94**[*]	1	26	34	0.28

Full-size table

succ: successful inhibition; unsucc: unsuccessful inhibition.

[*] Bold font: statistically significant result, $p < 0.05$ (false discovery rate corrected).
[U] Bold font: statistically significant result, $p < 0.005$ (uncorrected).

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3. Discussion

In this paper, we investigated the interaction between inhibition and motivation. To do so, participants performed a stop-signal task during two conditions, namely, during a neutral, control condition and during a motivated condition during which they were rewarded for correct *go* performance. Behaviorally, participants exhibited longer SSRTs during the reward relative to the control condition, indicating that it was harder to inhibit their responses during the former condition. Our neuroimaging findings revealed that a host of brain regions were involved in stop-signal inhibition, as indexed via a contrast of successful (succ) and unsuccessful (unsucc) stop trials. Critically, a subset of these regions exhibited significant inhibition by condition interactions, demonstrating that cognitive and motivational signals interact in the brain during inhibitory control.

3.1. Behavioral findings

The stop-signal task has been widely utilized in the study of response inhibition. A strength of this paradigm is that it allows the estimation of the "inhibitory reaction time" (SSRT), which is by definition, unobserved. The SSRT has been characterized in several clinical and non-clinical populations, including impulsive individuals (Logan et al., 1997), cocaine dependents ([Colzato et al., 2007], [Fillmore and Rush, 2002] and [Li et al., 2007]), and ADHD (Alderson, Rapport, & Kofler, 2007) and schizophrenia populations (Enticott, Ogloff, & Bradshaw, 2008), among others. The SSRT is remarkably stable across individuals and studies and typically averages in the range of 200–300 ms.

In the present experiment, participants exhibited longer SSRT during the rewarded (213 ms) relative to the control (193 ms) condition. At the same time, no difference between *go* RT was observed as a function of experimental condition, demonstrating the specificity of the impact of the motivational manipulation. Taken together, these results reveal that, in our task, motivation impaired inhibitory processing rather than facilitated the execution of prepotent responses; see also (Fillmore & Vogel-Sprott, 2000). In other words, during the reward condition, participants encountered difficulty inhibiting prepotent responses not because these responses were unusually fast, but instead because their inhibitory responses, which countermanded their *go* responses, were significantly slowed down.

3.2. Neuroimaging findings

Previous neuroimaging studies of response inhibition have identified a network of brain regions believed to be engaged by inhibitory processes. Important nodes are thought to include the superior frontal gyrus (Li et al., 2006) and the IFC, possibly extending into the anterior insula (Aron, 2007). Lesion and transcranial magnetic stimulation studies converge on the suggestion that the right IFC is a critical locus in inhibitory control ([Aron et al., 2003] and [Chambers et al., 2006]). Although, in general, neuroimaging studies report a set of parietal, frontal, and subcortical sites believed to be involved in response inhibition, the emphasis on specific brain regions has depended on the type of index used to identify the neural correlates of inhibition. In particular, two strategies can be highlighted. One approach has contrasted succ trials to *go* trials ([Aron and Poldrack, 2006] and [Xue et al., 2008]), whereas a second strategy has contrasted succ vs. unsucc trials ([Li et al., 2006]

and [Rubia et al., 2003]). While both approaches have contributed to our understanding of the neural basis of executive control during stop-signal inhibition, we opted for the latter strategy as both trial types are matched along several important dimensions of interest. In particular, the contrast of succ and *go* trials is unmatched for stimulus frequency and potential "oddball" effects. The rationale for contrasting succ trials to *go* trials is, at times, that the outcome on a *stop* trial (successful or unsuccessful) depends mainly on the speed of the *go* process (e.g., [Aron and Poldrack, 2006] and [Leung and Cai, 2007]). However, according to the race model (Logan & Cowan, 1984), the outcome of a *stop* trial depends on the relative finishing times of both the *go* and *stop* processes. Accordingly, even during trials with no change in the speed of the *go* process, variability in *stop* processing will lead to, at times, the *go* process winning the race if it finishes before the *stop* process. Furthermore, when the *go* process is faster (as in unsucc trials), it may lead to weaker *stop* responses because central resources may be shared between *go* and *stop* processes (Boehler et al., 2009). Note that the latter point does not violate the independence assumption of the race model, because the race model is not a process model. In other words, it only describes the finishing times of *go* and *stop* processes and does not specify the exact nature of the underlying mechanisms ([Logan, 1994] and [Verbruggen and Logan, 2008]). Nevertheless, we do not claim that the contrast of succ vs. unsucc trials perfectly isolates purely inhibitory processes, as differences in attention may also contribute to the associated differential responses (see below).

An important challenge when studying the contributions of motivation to evoked brain responses is to disentangle specific effects of motivation from relatively *unspecific* effects of arousal or effort. Accordingly, in the present experiment, *stop* trials occurred infrequently within a rapid stream of *go* trials, which were blocked according to condition. In this manner, any changes to the *go* process were explicitly incorporated into the baseline, as stop-task inhibition was indexed via the contrast of succ and unsucc trials. This contrast revealed a network of brain regions that largely overlapped with that reported in other studies. In particular, the right IFG exhibited stronger evoked responses during succ vs. unsucc trials, a result that has been observed in several ([Chamberlain et al., 2009], [Li et al., 2006], [Rubia et al., 2003] and [Rubia et al., 2007]), but not all (Aron & Poldrack, 2006), studies in the literature. As stated, the succ vs. unsucc contrast used in the present study may not entirely isolate inhibitory processes engaged by the stop-signal task. In particular, this contrast may include potential differences in attention, as "low" attentional engagement may be associated with unsuccessful inhibition while "high" attentional engagement may be associated with successful inhibition. Consistent with this notion, a recent MEG study by Boehler et al. (2009) revealed that fluctuations of sensory processing linked to both *go* and *stop* stimuli impact inhibitory performance during the stop-signal task. Furthermore, given the role of the right IFC in attentional mechanisms (Corbetta & Shulman, 2002), the succ vs. unsucc contrast may also engage this region during the stop-signal task for reasons that are more attentional than inhibitory; similar considerations apply to other regions of the "attentional network".

Because longer SSRTs were observed during the rewarded condition, based on findings reporting *reduced* prefrontal engagement in inhibitory control in ADHD ([Aron et al., 2007b], [Dimoska et al., 2003], [Rubia et al., 1999] and [Tamm et al., 2004]), schizophrenia (Rubia et al., 2001), and cocaine dependence (Li et al., 2007), we expected reduced inhibitory-related responses in brain regions involved in inhibition during the motivation condition of our task relative to control. Consistent with this notion, succ vs. unsucc differential responses observed in the right IFG were reduced during rewarded trials.

Although the right IFC is more consistently reported to be involved in response inhibition, the IFC on the left hemisphere has been reported to exhibit differential succ vs. unsucc responses ([Li et al., 2006] and [Rubia et al., 2007]) and has been found to be important for response inhibition based on a recent lesion study (Swick, Ashley, & Turken, 2008). In the present study, a different interaction pattern of results was observed in the left IFG. Relative to the *go* baseline, *stop*-related responses were negative. Interestingly, during the control condition, succ trials evoked a larger response (i.e., less negative) than unsucc trials, and this difference decreased during the motivated condition. It thus appears that the left IFG is engaged by both *go* and *stop* processes and that motivation reduces differential responses.

Other brain regions that exhibited significant stop-signal inhibition by motivation interactions included the left precentral gyrus, regions in parietal cortex, and bilateral putamen. The precentral gyrus in involved in carrying out stimulus-response associations (Brass, Wenke, Spengler, & Waszak, 2009) and has been suggested to be a key "inhibitory motor area" (Li et al., 2006). Here, we show that whereas a robust differential response succ vs. unsucc was observed during the control condition, this difference was reduced during the reward condition. Although neuroimaging studies of both go/no-go and stop-signal tasks have identified sites in parietal cortex, their precise role in inhibition is less well understood. For instance, Li et al. (2006) did not observe differential activation in parietal cortex when succ and unsucc trials were contrasted. In the present study, the right IPL exhibited stronger responses for succ vs. unsucc trials, as well as a significant inhibition by motivation interaction (the latter was observed in the IPS, too). Given the important contribution of the parietal cortex to attentional processes ([Corbetta and Shulman, 2002] and Kastner and Ungerleider, 2000 S. Kastner and L.G. Ungerleider, Mechanisms of visual attention in the human cortex, *Annual Review of Neuroscience* **23** (2000), pp. 315–341. View Record in Scopus | Cited By in Scopus (529)[Kastner and Ungerleider, 2000]), it is possible that, during the reward condition, participants paid increased attention to the *go* stimulus. Fewer attentional resources may have then been available to process the *stop* stimulus, thereby impairing overall inhibitory performance—leading to an increase in SSRT (Pessoa, 2009). This interpretation is consistent with the MEG study cited above in which successful inhibition was accompanied by attenuated sensory processing of the *go* stimulus (Boehler et al., 2009) and, more generally, with the notion that *go* and *stop* may share processing resources—which in the present case may have been redistributed between *go* and *stop* processes given the motivational manipulation. Finally, the putamen has been implicated both in response inhibition ([Chambers et al., 2009] and [Eagle and Robbins, 2003]) and motivation (Schultz, 2000). The present findings provide further support not only for its role in these two processes but, critically, for the putamen's involvement during the *interaction* of cognitive inhibitory operations and motivational processes.

The pattern of main effects and interactions we observed in this study was specific to cortical and subcortical regions previously implicated in response inhibition and were not observed in additional ROIs that were likely engaged by the sensory stimuli (visual and auditory) employed in this task. These ROIs were engaged to a similar extent during all trial types.

In the present study, like others in the past, we employed the contrast of succ vs. unsucc trials to probe the neural correlates of stop-signal response inhibition. As reviewed above, an inhibition by condition statistical interaction was observed in several brain regions, a pattern of results that was paralleled by an increase in SSRT during the reward condition. Inspection of the results in Fig. 2 illustrates that differential succ vs. unsucc responses were in some cases sharply reduced during the reward condition (e.g., for the right IFG). Despite this pattern of fMRI results, the staircase procedure was still able to maintain successful performance at about 50% correct—albeit with a slowed SSRT. Therefore, if the contrast of succ vs. unsucc trials is to be considered a valid index of response inhibition, collectively, our results suggest that response inhibition should not be viewed as the product of only regions exhibiting inhibition by condition interactions (e.g., right IFG), but also regions that exhibited a main effect of inhibition but no significant statistical interaction (e.g., caudate). In other words, the concerted activation across a network of regions, some of which were affected by the motivational manipulation employed here, is likely needed for the generation of the countermanding motor commands required during stop-signal response inhibition.

Although our study clearly revealed an interaction between rewarding *go* behavior and stop-task inhibition in several cortical and subcortical regions previously implicated in response inhibition, we were not able to investigate these interactions at a more mechanistic level because the *go* trials were used as an implicit baseline. In other words, the current study identified some of the sites whereby motivation and stop-task inhibition interact, but left unanswered important questions. For instance, the sites identified here may receive inputs

from other regions that *integrate* motivation and inhibition, a possibility that should be addressed in future studies. In this context, techniques such as dynamic causal modeling (Friston, Harrison, & Penny, 2003) and other forms of computational modeling may provide invaluable tools to probe these questions at a more mechanistic level.

A growing literature has documented that impairments in response inhibition in clinical populations is linked to reduced activation in prefrontal cortex. For instance, adolescents with ADHD exhibited reduced activation in the IFC during an inhibitory task (Rubia, Smith, Brammer, Toone, & Taylor, 2005). We showed here that a similar pattern of results is observed when participants are rewarded for their *go* performance during a stop-signal task. Our results thus demonstrate that, under specific circumstances, positive incentives are capable of impairing behavioral performance. Future studies are needed to probe how motivational manipulations of the type employed here affect inhibitory circuits in clinical populations that are known to exhibit compromised behavioral control.

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