Subthalamic nucleus stimulation reverses mediofrontal influence over decision threshold

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Supplemental Material

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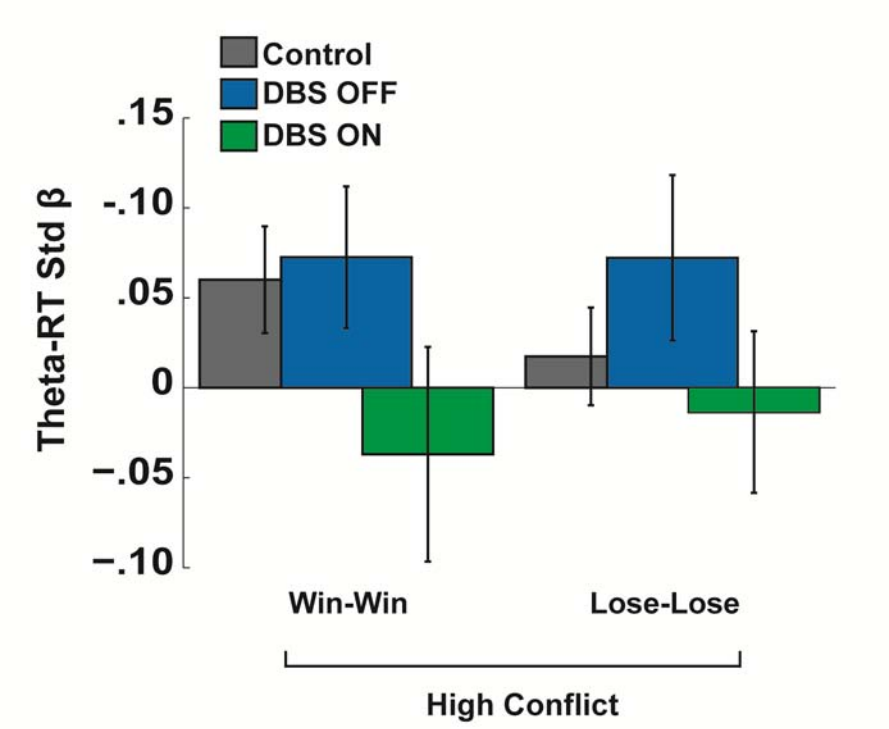
Results



Supplemental Figure 1. DBS ON/OFF Study: High conflict condition split by valence. Both win-win and lose-lose conditions demonstrated positive theta-RT regression weights in Control and OFF DBS conditions and the inverse pattern ON DBS.

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EEG and Performance

To test the specificity of the cue-locked findings, low frequency power was calculated pre-response (–350 to –50ms, 3 to 4.5 Hz) and post-response (–50 to 250ms, 3 to 6 Hz). Unlike cue-locked effects reported in the main text, within-subject statistical tests of individual regression weights between peri-response theta power and reaction time did not reveal any significant main or interactive effects; either for high conflict or valenced conflict (see Supplemental Figure 2). These results are consistent with a mechanism whereby initial stimulus-response conflict evoked by the cues is reflected in mPFC theta, and leads to an increase in decision threshold via STN– but not a mechanism in which mPFC is directly associated with RT at the time of response.

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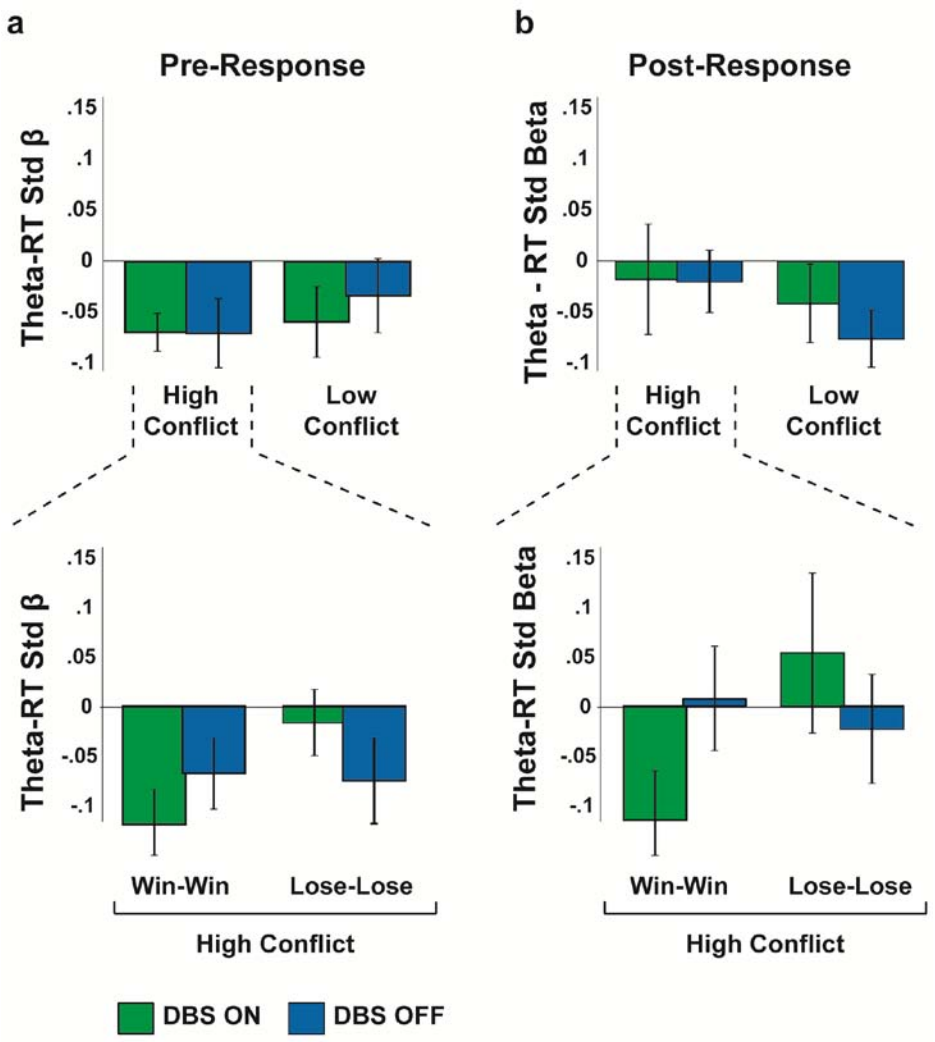

Supplemental Figure 2. DBS ON/OFF study: standardized theta-RT regression weights (mean +/– SEM). No significant main or interaction effects were found. (a) Pre-response. (b) Post-response.

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Control Group and Replication of General Effects

In order to demonstrate that these EEG-threshold effects are a natural feature of human cognitive architecture and are not specific to Parkinson's patients, we replicated the major findings of the manuscript with two separate samples of participants. Since the data from the two control groups did not differ from each other (accuracy P's>.25, theta-RT regression weight P's>.70), we combined them into a single group for comparison with DBS ON and OFF conditions. Here we report the data from each group individually.

First, we gathered a new sample of 15 healthy senior participants (10 female). Pilot testing indicated that the effects of conflict on the relationship between theta and RT described in the main text were robust when high conflict conditions were chosen to induce sufficient difficulty (so that accuracy rates in high conflict trials were in the same range as those described for Parkinson's patients). Accordingly, the task was the same as the task in the main text, except it was made slightly harder by changing the 100%/0% condition to 87.5%/12.5% reward. There were no differences between these healthy seniors and Parkinson's patients in mean age (both groups: M=65, $p > .60$) or high conflict accuracy (DBS ON P=.61, OFF P=.76). EEG was gathered in a Brown University laboratory using a Pegasus EEG system (.02-100HZ, 500Hz sampling rate) and a similar 64-channel cap. All EEG post-processing procedures were identical to the analyses in the main text. There was a significant difference between high and low conflict conditions ($t(14)=2.4$, $p=.03$) in theta power-RT regression weights, see Supplemental Figure 3b.

The above findings show that the theta-RT relationships are not just a feature of

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Parkinson's disease, yet is unknown if they specifically related to older age. To address this question, we also replicated these effects in college students using data taken from a previous publication[1]. In this investigation, N=50 college students performed a reinforcement learning and choice conflict task with yet more difficult reinforcement contingencies (again to match difficulty across groups). As in prior investigations[2,3], high conflict choices were taken from test phase stimulus pairs with the closest reinforcement values (80%/70%, 70/60%, 20/30%, 30%/40%), whereas low conflict choices were taken from stimulus pairs that were distant in conflict (80%/20%, 80%/30%, 70%/20%, 70%,30%). Neither high nor low conflict accuracies were significantly different than Parkinson's patients ON (p's >.37) or OFF (p's > .24) DBS. EEG was collected in a laboratory at the University of Arizona using a similar setup as the experiment in the main text. All EEG post-processing procedures were identical to the analyses in the main text. The high conflict theta-RT regression weight was significantly above zero, $t(49)=2.21$, $p=.03$ and the low conflict theta-RT regression weight was significantly below zero $t(49)=2.51$, $p=.015$; these were, of course, significantly different from each other $t(49)=3.09$, $p<.01$, see Supplemental Figure 3b.

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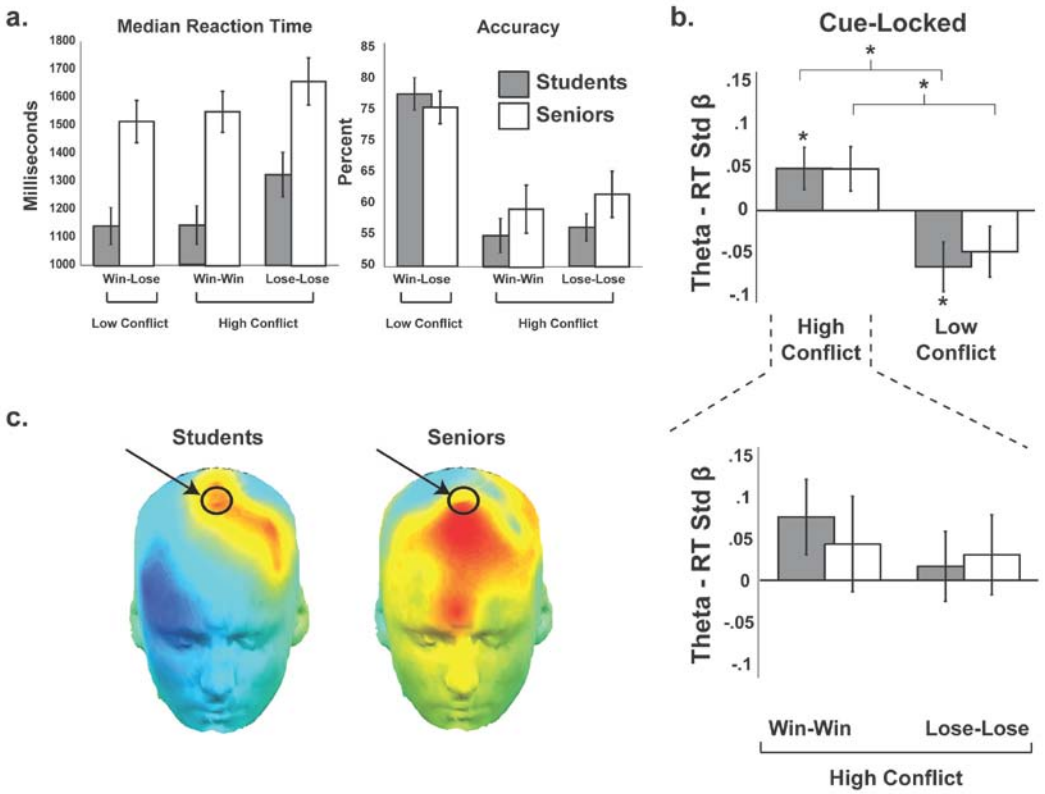

Supplemental Figure 3. Replication study in two different groups. A) Students and seniors had similar accuracies to each other and to the Parkinson's patients in the main text. B) Both groups had greater regression weights for high compared to low conflict. In the students, each averaged regression weight was significantly different than zero. C) Topomaps (+/– .05 std β) of the high-low conflict theta-RT regression weights demonstrate the mid-frontal focus of this effect. The electrode of interest (FCz) in the main analyses is indicated here.

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Hierarchical Bayesian Drift Diffusion Model

Markov-Chain Monte-Carlo estimation of the hierarchical DDM was performed using our recently developed HDDM software (https://github.com/hddm-devs/hddm/)[4] and PyMC (http://code.google.com/p/pymc)[5]. Bayesian inference was performed to derive posterior probability densities by using the likelihood function for the drift-diffusion model[6]. Each DDM parameter for each subject and condition was modeled to be distributed according to a normal (or truncated normal, depending on the bounds of parameter intervals) distribution centered around the group mean with group variance. Priors for group means and variances for each parameter and condition were non-informative (i.e. uniform over wide interval, allowing the parameters to describe the data without a priori assumptions). This typical hierarchical pattern of parameter estimation among groups and individuals[7,8] optimizes the tradeoff between random and fixed effect models of individual differences, such that fits to individual subjects are constrained by the group distribution, but can vary from this distribution to the extent that their data are sufficiently diagnostic.

Statistical analysis of effects used to test our hypotheses was performed on the mean group posteriors. In the case of effect distributions (which describe the impact of one variable (e.g., theta) on the change in a parameter (e.g., threshold)), there were convergence problems leading to difficulty in confidently estimating effect strength in each individual subject, likely due to the low number of trials for each subject and condition and theta values. Thus, for all effect distributions reported here, we directly estimated the group mean without allowing for individual differences within the group, in which case all chains converged. All other

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distributions (e.g. intercept in overall decision threshold) allowed for individual differences within the group in their posterior distributions. Note, however, that models which allowed for individual differences in effect strengths showed the same pattern as those described in the main paper, but we are most confident in the current analyses where all chains converged.

Diffusion analysis was performed with different models and different effect-coding, but robustly revealed the same qualitative pattern. The Deviance Information Criterion (DIC) was used for model comparison, where lower DIC values favor models with highest likelihood and least number of parameters[9]. To test whether behavioral-EEG effects were better accounted for by other decision variables, we included an alternative model in which mPFC theta modulated drift rate (and where this relationship could change as a function of DBS). This model produced a worse fit and there were no significant effects of theta or DBS on drift rate. This result is consistent with the observation that patients ON DBS were more likely to respond faster during suboptimal rather than optimal choices, consistent with a reduced threshold but not faster drift rate (in which they would respond faster but more accurately).

Inclusion of additional parameters allowing for inter-trial variability in other parameters (starting point and non-decision time) did not converge. These models did, however, show the same robust pattern of results as reported for the model with only inter-trial variability in drift. Similar effects to those reported in the main text were found if the overall threshold ‘a’ and e_dbs terms were also allowed to vary by conflict condition (in addition to the effect of mPFC theta on threshold as a function of conflict), but these extra parameters did not improve model fit as assessed by DIC. In sum, irrespective of the exact formulation of the model, the reported effects

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of theta and DBS status on decision threshold were very robust.

In addition to the hypothesis tests using probability mass reported in the main paper, we performed significance testing by computing the Bayes-factor (BF). The BF as it is used here is a likelihood ratio between the posterior and prior density. This ratio provides a measure for the degree to which we should change our belief away from the prior hypothesis, based on observing the data[10,11]. The BF was computed via the Savage-Dickey density ratio, which is the likelihood provided by a prior over the expected parameter range divided by the computed posterior at the a point of interest (e.g. to test if an effect is different from zero we would divide the posterior density from the prior density at x=0, giving the Bayes factor for the evidence against the null). The expected parameter range was chosen to be uniform in the interval [0, 0.3] reflecting our prior hypotheses regarding theta and DBS influences on threshold, with 0.3 reflecting the upper bound on our expected change in threshold as a function of theta. Best fitting parameter estimates of our three datasets for the main DDM parameters are reported in Supplemental Table 1. Effect strengths and Bayes Factors (BF) are reported in Supplemental Tables 2 and 3. These results complement those provided by the P value estimates in the main text. The theta*conflict interaction term reported in the main text is shared between age-matched controls and college students as model fits were objectively better when these were considered a single group of controls, compared with a model in which these groups were assigned different parameter distributions. Nevertheless, the effect of conflict*theta was significant in the college students alone, demonstrating that the effect is robust with sufficient sample sizes (N=50) in healthy controls. The age-matched controls (N=15) alone showed the same directional effect, but did not

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reach significance (note however, that the theta-RT regression weights were significant in these participants alone, as well as in the college students).

As expected given their increased difficulty, high-conflict trials (WW and LL) were associated with decreased drift-rates relative to low-conflict trials (WL). Analyses of the effect of theta on threshold were found controlling for these overall drift-rate differences; thus these results confirm the notion that drift rate changes are not sufficient to account for slower high-conflict RT distributions but that an increased threshold is required as well. Finally, in addition to modulating the relationship between mPFC and threshold, there was also a significant main effect of DBS (e_{dbs}) on decision threshold under high ($P=0.035$) and low conflict ($P<0.001$), such that thresholds were greater OFF than ON DBS.

	Posterior mean		
Overall Parameters	PD	Seniors	Students
threshold	1.76	2.28	1.96
non-decision time	0.65	0.59	0.42
drift $rate_{LL}$	0.28	0.26	0.15
drift $rate_{WW}$	0.47	0.22	0.16
drift $rate_{WL}$	0.87	0.63	0.84
variability in drift-rate	0.4	0.56	0.56
variability in non-decision time	0.44	0.57	0.57

Supplemental Table 1. DBS ON/OFF Study: best fitting hierarchical Bayesian parameter estimations (maximum *a posteriori* values).

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Effect Parameters	Posterior mean	BF_{10}
e_{dbs} high conflict	0.093	30.53
e_{dbs} low conflict	0.082	3.42
$e_{interaction}$ high conflict	0.11	15.93
$e_{interaction}$ low conflict	–0.01	0.32
e_{theta} high conflict	–0.05	2.81
e_{theta} low conflict	–0.02	0.52

Supplemental Table 2. DBS ON/OFF Study: Best fitting hierarchical Bayesian parameter estimations and Bayes Factors of effect parameters (i.e. influence of dbs and theta on decision threshold for high and low conflict trials).

	Seniors		Students		PD Patients	
Effect Parameters	Posterior mean	BF_{10}	Posterior mean	BF_{10}	Posterior mean	BF_{10}
$e_{conflict}$	–0.03	0.47	–0.05	0.75	0.02	0.29
$e_{interaction}$	0.04	0.88	0.04	0.88	0.07	2.36
e_{theta}	–0.03	0.84	–0.04	0.54	–0.02	0.37

Supplemental Table 3. Controls: Best fitting hierarchical Bayesian parameter estimations and Bayes Factors of effect parameters (i.e. influence of conflict and theta on decision threshold).

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Fast Diffusion Modeling

In the main article we employed hierarchical Bayesian parameter estimation to characterize the relationship between mPFC theta and decision thresholds on a trial-to-trial basis, and to test whether this relationship was altered by DBS. This Bayesian method is particularly valuable when attempting to estimate parameters (and uncertainty about those parameters) at the group level, while allowing for individual differences in such parameters. Moreover, hierarchical modeling facilitates reliable estimation when the number of trials is small[7,12].

Nevertheless, we sought to confirm the basic effects of theta power and decision threshold with a more traditional (non Bayesian, non hierarchical) approach, using the *fast-dm* algorithm[13]. Due to the small numbers of trials for each subject, trials were median split into high and low theta power conditions, and thresholds were initially estimated separately for these two trial types, irrespective of conflict. Models were fit once for each subject OFF DBS and again ON DBS. When DBS was OFF, estimated decision thresholds were higher when mPFC theta power was high than low ($t(13) = 1.73$, $P = .05$ one-tailed). This relationship between threshold and theta was not found while ON DBS ($t(13) = -0.73$, n.s.). For high theta trials, estimated decision thresholds were significantly higher in patients OFF than ON DBS ($t(13) = 2.6$, $P = .01$), whereas they did not differ for low theta trials ($P > .1$). Moreover, there was a significant interaction between DBS status and theta on estimated decision threshold ($t(13) = 1.81$, $P = .046$). Because the change in decision threshold from low to high threshold was not normally distributed (Shapiro-Wilk test, $P < .01$), we also computed a non-parametric Mann-Whitney test, which also revealed a significant effect of DBS status on this change in threshold due to theta

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(z=1.63, P =.05). Importantly, no such effect of theta was found on other model parameters, such as drift rate, when these were allowed to vary as a function of theta instead of threshold in follow-up simulations. The model estimated similar drift rates for high and low theta trials, in both on and off DBS states (all P's n.s.).

To determine whether the effects of theta on decision threshold were specific to conflict, we refit the data to estimate thresholds separately for each condition, each with their own low and high theta estimates. In the absence of any main effects of theta or DBS, there was a DBS*theta interaction on decision threshold in high conflict ($F(1,13) = 5.9$, $p = .03$, two tailed), see Supplemental Figure 4. No such interaction was observed in low conflict trials (F=.03). Thus these fast-dm simulations demonstrate the same pattern of results as that observed with the hierarchical Bayesian parameter estimation. Nevertheless, we remain more confident in the hierarchical Bayesian simulations, given that these fast-dm analyses depended on a limited number of trials when dividing into low and high theta for each condition separately, and parameter estimation can be unstable in these cases. Similarly, the hierarchical analysis allowed us to more stably estimate trial-type drift-rate effects simultaneously with threshold/theta/DBS effects in a single model.

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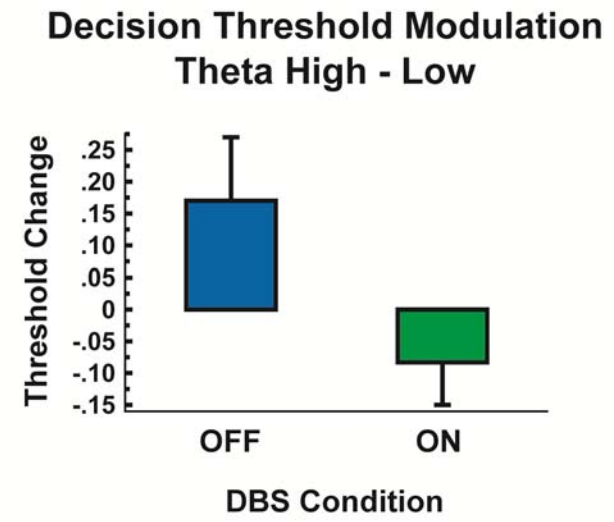

Supplemental Figure 4. DBS ON/OFF study: fast-dm model estimation of decision threshold (mean + SEM). The difference in theta power (high–low) is related to increased threshold OFF DBS but a somewhat reduced threshold ON DBS, replicating hierarchical Bayesian parameter estimation in the main text.

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Study II – Intraoperative recording of the STN

Additional exploratory analyses with optimized frequency sensitivities in the wavelet families used for convolution did not reveal any additional effects lower than 2.5 Hz or greater than 50 Hz. Supplemental Figure 5 details intra-operative performance, with participants split between 'Better Performers and 'Worse Performers' based on pre-surgery and surgery test phase low conflict accuracies (note that one subject had too few Pre-Surgery trials to average and was left out of that condition). Better Performers had greater than chance accuracy during the training phase ($t(3)=3.72$, $P=.033$), whereas Worse Performers did not ($t(3)<1$). Supplemental Figure 6 demonstrates high conflict cue- and response-locked time-frequency plots split by valence (win-win or lose-lose). Supplemental Figure 7 details the high-low conflict contrasts for 'Better Performers' only, demonstrating a replication of the major effects from Figure 4 in the main text. Whereas this analysis provides evidence for significant low frequency power dynamics during conflict based on a *post-hoc* between-subject determination, the permutation methods used for Figure 4 in the main text provide a *data-driven* account of meaningful within- and between-subject variance.

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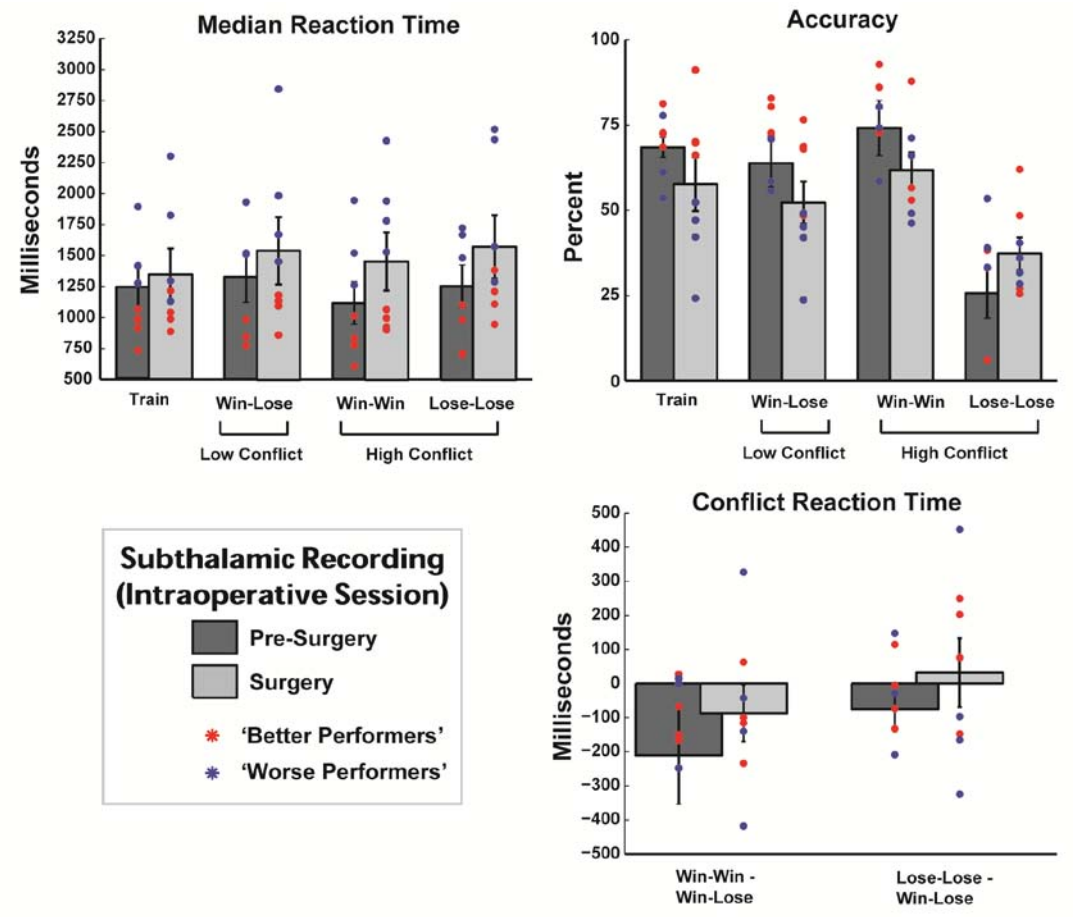

Supplemental Figure 5. Intraoperative study: performance data (mean +/– SEM) for pre-surgical session (3-5 hrs prior to surgery) and surgery.

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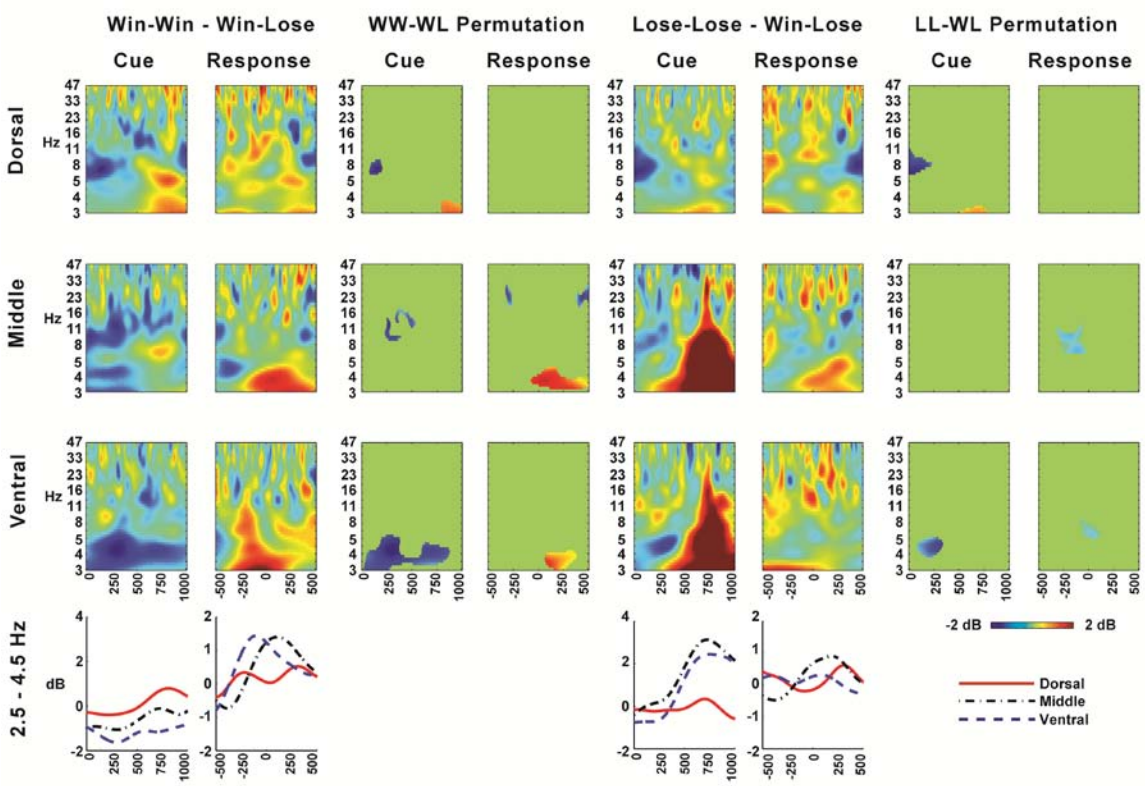

Supplemental Figure 6. Intraoperative study: high conflict trials split into valenced win-win and lose-lose conditions. Win-win trials show a similar pattern of significant post-cue and peri-reponse conflict related activity as the averaged high conflict trials (main text Figure 4). Some of these patterns are not present in the lose-lose condition, yet note the replication of a cue locked low frequency burst in the dorsal lead. Although middle and ventral leads show extremely large cue-locked LL>WL power differences, careful investigation of these trials revealed them to vary widely over trials and across participants; resulting in natural outliers that were not reliable enough to lend statistical support to these differences when averaged together.

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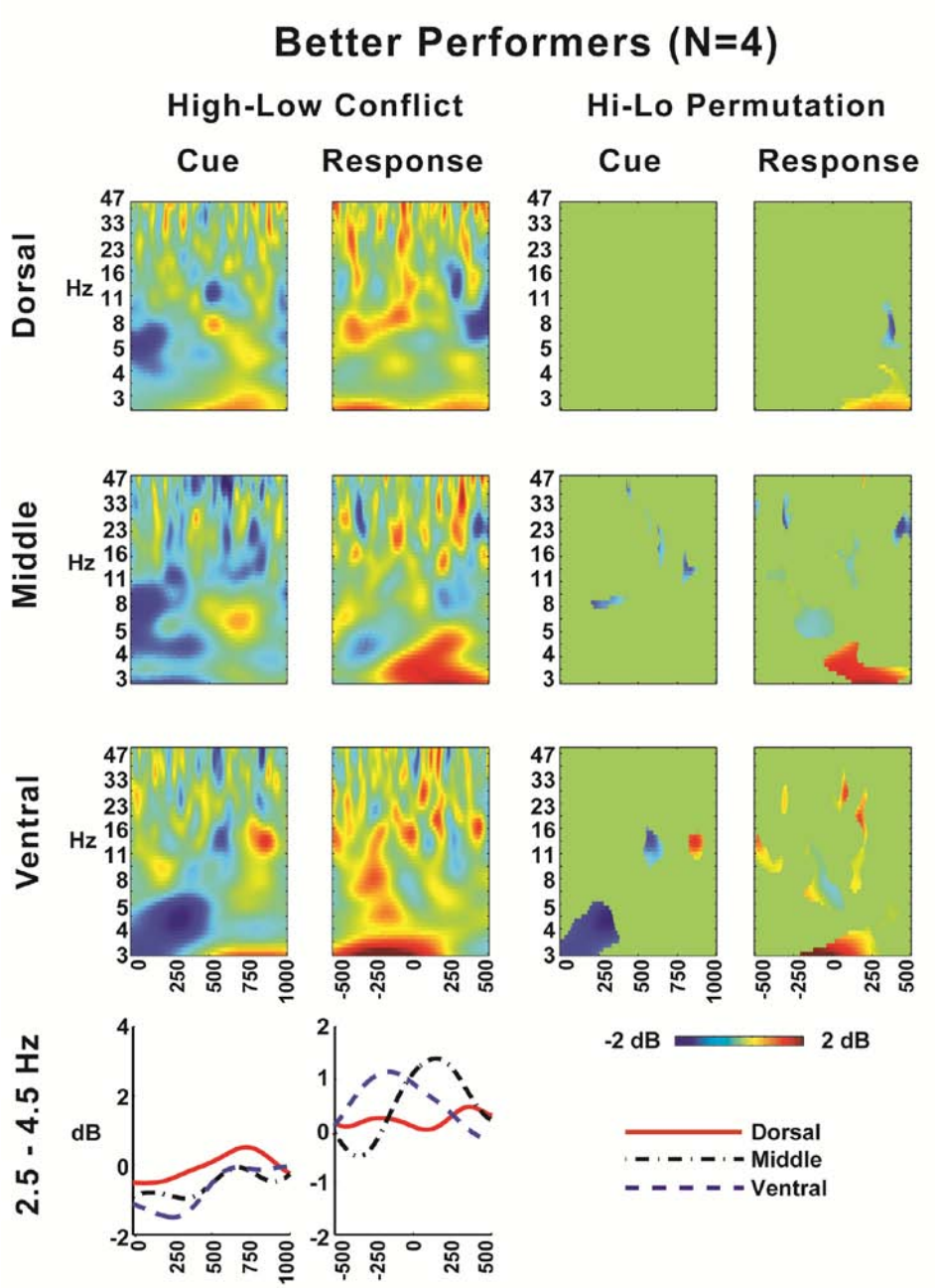

Supplemental Figure 7. Intraoperative study: high and low conflict contrasts for 'Better Performers' only.

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Discussion

As predicted, the data clearly show that mPFC theta activity is special in high relative to low conflict conditions, as only theta in the former condition was associated with increased decision threshold and RT slowing. Previous investigations of mPFC theta have suggested that signals of error[14], punishment[1], and conflict[15,16] are communicated to lateral PFC via transiently synchronous theta phase relations for instantiation of cognitive control. Future investigations could probe if this phenomenon is involved in recruiting the inferior frontal gyrus of the lateral PFC for inhibitory control; and if both of these areas communicate with the STN via synchronous phase relations. In contrast, low conflict theta power in this investigation may simply reflect a generic evaluative process that does not require the initiation of cortico-striatal network adaptation, similar to previous postulations we have made to theta occurring to correct responses and feedback[1,14,15].

Although patients showed RT slowing for lose-lose trials, consistent with prior data, this investigation did not replicate a previous finding of general RT slowing during win-win trials when in control participants or patients OFF DBS[2]. This difference may reflect the simplified nature of the task used here, where win/win reflected 100% vs. 75% choices, and the previous task involved subtler differences in value (i.e. 80% vs. 70%), none of which were a simple choice like the 100% condition. However, as discussed in the main text and in previous studies[2,17], there are two competing factors in the win-win conditions. In the absence of any conflict-induced slowing, win-win conditions are expected to elicit *faster* RTs, because there is greater overall positive value which leads to a greater likelihood that one of the responses is

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facilitated. We posit that the STN counteracts this tendency to impulsively respond quickly in the face of competing actions with positive value. The net effect may be RT slowing if the STN effect dominates over the positive value effect, but they may also cancel out (indeed there are individual differences in healthy participants in the degree to which they show slowing in win-win conflict scenarios[17]). In contrast, in lose-lose conditions, negative value slows responding, and this is exacerbated by STN mechanisms associated with decision conflict. Both BG models and humans show greater conflict-induced slowing for lose-lose than win-win conditions (see supplement of Frank et al.[2] and Ratcliff & Frank[17]).

Within the STN, increased beta power has been described in Parkinson's patients[18] and in rats lesioned with 6-OHDA[19,20]. This phenomenon is thought to hinder natural functioning of the STN, since reductions in beta power (~12-35 Hz, sometimes termed beta blocking or desynchronization) are commonly associated with action preparation and execution in the STN[21,22], with greater power reductions correlating with faster RTs[23]. While Figure 4 in the main text clearly demonstrates STN beta power suppression prior to and following each response, conflict-related differences were not apparent in the beta band. Although other studies have found increases in gamma (> 50Hz) activity in the STN during movement[22], we did not find any other condition-wide effects outside the high delta / low theta band in exploratory analyses.

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Age	Sex	PD Stage	Years Dx	Meds	UPDRS: ON	UPDRS: OFF	Ed	NAART	MMSE	VoltageR	FreqR	VoltageL	FreqL
74	M	4	16	2	5	27	1	22	28	3.6	135	3.1	185
73	M	3	10	3	12	38.5	4	43	30	3	160	3	160
69	M	3	14	1,2	4.5	12	4	39	29	4.1	185	4.3	185
65	M	4	7	1,2,2,4	2.5	10.5	2	21	30	2.6	145	2.6	145
74	M	4	25	1,2	16	16	3	25	24	3.5	185	2.6	145
77	M	4	15	1	47	39	3	47	22	3.9	100	3.7	100
63	F	2.5	13	1,2,4	21.5	no data	2	48	27	3.7	135	2	145
58	M	2.5	18	1,4	40	49.5	1	23	28	2.6	185	1.8	185
57	M	2	8	1,2,4	5	37.5	4	55	26	2.8	160	2.4	185
46	M	1.5	8	1,4	0.5	22.5	3	37	30	2.1	170	2.4	185
62	M	2	11	1	2	38.5	3	19	30	3.3	185	3.2	185
54	M	2	10	1,1,2,4	7.5	12	2	34	26	3.6	145	4	185
68	M	4	18	1,2,3,4	15	31.5	4	33	28	3.5	130	3	130
75	F	3	10	1,2	6	14.5	3	49	29	3.4	135	3.6	135

Meds 1=Carbidopa / Levodopa 2=D2 Agonist 3=1+2+Persisting Med 4=Other

Ed: 1=HS or GED 2=Some College 3=Bachelor's 4=Higher Ed (Master's +)

Supplemental Table 4. Demographic information for participants in the ON/OFF stimulation study. UPDRS: United Parkinson's Disease Rating Scale; ED= Education; NAART=North American Adult Reading Test; MMSE=Mini Mental State Exam; Voltage and frequencies of stimulation on right (R) and left (L) STN

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Age	Sex	PD Stage	Years Dx	Surgery Meds
66	F	3	6	none
67	F	4	10	1,2,3
62	F	2	5	2,3
53	M	3	3	3
68	F	3	5	none
62	F	3	4	1,2,3
71	M	4	no data	1,2,3
69	M	4	20	1,2,3

1=Fentanyl 2=Midazolam 3=Propofol

Supplemental Table 5. Demographic information for patients in the intraoperative study. All patients were free of their normal Parkinson's medication during surgery; however some patients had surgery-specific medications.

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References

1 Cavanagh, J. F., Frank, M. J., Klein, T. J. & Allen, J. J. B. Frontal theta links prediction errors to behavioral adaptation in reinforcement learning. *NeuroImage* **49**, 3198-3209 (2010).

2 Frank, M. J., Samanta, J., Moustafa, A. A. & Sherman, S. J. Hold your horses: impulsivity, deep brain stimulation, and medication in parkinsonism. *Science* **318**, 1309-1312, doi:1146157 [pii] 10.1126/science.1146157 (2007).

3 Frank, M. J., Woroch, B. S. & Curran, T. Error-related negativity predicts reinforcement learning and conflict biases. *Neuron* **47**, 495-501, doi:S0896-6273(05)00526-X [pii] 10.1016/j.neuron.2005.06.020 (2005).

4 Wiecki, T. V., Sofer, I. & Frank, M. J. HDDM: Hierarchical Bayesian drift diffusion modeling in Python. (in prep).

5 Patil, A., Huard, D. & Fonnesbeck, C. J. PyMC: Bayesian Stochastic Modelling in Python. *Journal of Statistical Software* **35**, 1-81 (2010).

6 Navarro, D. J. & Fuss, I. G. Fast and accurate calculations for first-passage times in Wiener diffusion models. *Journal of Mathematical Psychology* **53**, 222-230 (2009).

7 Lee, M. D., Fuss, I. & Navarro, D. J. in *Advances in Neural Information Processing Systems* (eds B. Scholkopf, J. Platt, & T. Hoffman) 809-815 (MIT Press, Cambridge, MA, 2007).

8 Wetzels, R., Vandekerckhove, J., Tuerlinckx, F. & Wagenmakers, E. J. Bayesian parameter estimation in the Expectancy Valence model of the Iowa gambling task. *Journal of Mathematical Psychology* **54**, 14-27 (2010).

9 Gelman, A. *Bayesian data analysis*. 2nd edn, (Chapman & Hall/CRC, 2004).

10 Good, I. J. in *Bayesian Statistics* Vol. 2 (eds J.M. Bernardo, M.H. DeGroot, D.V. Lindley, & A.F.M. Smith) 249-269 (Elsevier, New York, 1985).

11 Jeffreys, H. *Theory of probability*. 3d edn, (Clarendon Press, 1961).

12 Vandekerckhove, J., Tuerlinckx, F. & Lee, M. D. Hierarchical diffusion models for two-choice response time. *Psychological Methods* (in press).

13 Voss, A. & Voss, J. A Fast Numerical Algorithm for the Estimation of Diffusion-Model Parameters. *Journal of Mathematical Psychology* **52**, 1-9 (2008).

14 Cavanagh, J. F., Cohen, M. X. & Allen, J. J. Prelude to and resolution of an error: EEG phase synchrony reveals cognitive control dynamics during action monitoring. *J Neurosci* **29**, 98-105, doi:29/1/98 [pii] 10.1523/JNEUROSCI.4137-08.2009 (2009).

15 Cohen, M. X. & Cavanagh, J. F. Single-trial regression elucidates the role of prefrontal theta oscillations in response conflict. *Frontiers in Psychology* **2**, 1-12 (2011).

16 Hanslmayr, S. *et al.* The electrophysiological dynamics of interference during the Stroop task. *J Cogn Neurosci* **20**, 215-225, doi:10.1162/jocn.2008.20020 (2008).

17 Ratcliff, R. & Frank, M. J. Reinforcement-based decision making in corticostriatal circuits: mutual constraints by neurocomputational and diffusion models. (submitted).
18 Kuhn, A. A. *et al.* High-frequency stimulation of the subthalamic nucleus suppresses oscillatory beta activity in patients with Parkinson's disease in parallel with improvement in motor performance. *J Neurosci* **28**, 6165-6173, doi:28/24/6165 [pii] 10.1523/JNEUROSCI.0282-08.2008 (2008).
19 Mallet, N. *et al.* Parkinsonian beta oscillations in the external globus pallidus and their relationship with subthalamic nucleus activity. *J Neurosci* **28**, 14245-14258, doi:28/52/14245 [pii] 10.1523/JNEUROSCI.4199-08.2008 (2008).
20 Mallet, N. *et al.* Disrupted dopamine transmission and the emergence of exaggerated beta oscillations in subthalamic nucleus and cerebral cortex. *J Neurosci* **28**, 4795-4806, doi:28/18/4795 [pii] 10.1523/JNEUROSCI.0123-08.2008 (2008).
21 Gaynor, L. M. *et al.* Suppression of beta oscillations in the subthalamic nucleus following cortical stimulation in humans. *Eur J Neurosci* **28**, 1686-1695, doi:EJN6363 [pii] 10.1111/j.1460-9568.2008.06363.x (2008).
22 Kempf, F. *et al.* Modulation by dopamine of human basal ganglia involvement in feedback control of movement. *Curr Biol* **17**, R587-589, doi:S0960-9822(07)01506-0 [pii] 10.1016/j.cub.2007.06.010 (2007).
23 Williams, D. *et al.* The relationship between oscillatory activity and motor reaction time in the parkinsonian subthalamic nucleus. *Eur J Neurosci* **21**, 249-258, doi:EJN3817 [pii] 10.1111/j.1460-9568.2004.03817.x (2005).