

An fMRI investigation of the impact of interracial contact on executive function

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We investigated whether individual differences in racial bias among white participants predict the recruitment, and potential depletion, of executive attentional resources during contact with black individuals. White individuals completed an unobtrusive measure of racial bias, then interacted with a black individual, and finally completed an ostensibly unrelated Stroop color-naming test. In a separate functional magnetic resonance imaging (fMRI) session, subjects were presented with unfamiliar black male faces, and the activity of brain regions thought to be critical to executive control was assessed. We found that racial bias predicted activity in right dorsolateral prefrontal cortex (DLPFC) in response to black faces. Furthermore, activity in this region predicted Stroop interference after an actual interracial interaction, and it statistically mediated the relation between racial bias and Stroop interference. These results are consistent with a resource depletion account of the temporary executive dysfunction seen in racially biased individuals after interracial contact.

Daily life requires regular contact with individuals from different demographic groups. Recent research suggests that brief interactions with people from different racial groups can be disquieting and, sometimes, even psychologically threatening^{1,2}. In addition to being awkward, interracial interactions have been found to impair performance on tasks requiring response inhibition, especially for individuals who harbor relatively high levels of racial bias³. Specifically, the extent to which white individuals reveal bias on an unobtrusive measure of racial attitudes predicts the interference they exhibit on the Stroop color-naming task after interacting with black, but not white, individuals.

This study examined one putative mechanism for the impact of interracial contact on executive function; namely, resource depletion. This theory is based on the proposition that executive attention is a limited, renewable resource that can be depleted temporarily^{4,5}. Performing a task that requires executive control impairs performance on subsequent tasks that tap the same resource^{4–6}. How does this relate to interracial interactions? Considerable behavioral research attests to the recruitment of central executive processes to combat the expression of stereotypes and negative attitudes that often come to mind automatically and unintentionally^{7–9}. Moreover, previous research shows that white individuals with higher levels of racial bias are particularly likely to activate negative stereotypes automatically upon exposure to black faces¹⁰. According to resource depletion, therefore, executive control after interracial interactions should be disrupted in proportion to individuals' engagement of executive control processes, such as response inhibition¹¹, during the interaction.

Given the focus of the proposed resource depletion model on the mediating role of executive control, we based the present investigation on emerging literature in cognitive neuroscience that has identified a complex circuit of brain structures—consisting, in part, of dorsolateral prefrontal cortex (DLPFC) and anterior cingulate cortex (ACC)^{12–19}—that supports executive control. Specifically, research suggests that DLPFC functions to maintain an attentional set by modulating activity within posterior processing systems in a manner that favors the selection of task-relevant processes^{16,20,21} (but see ref. 22), whereas the ACC monitors for the presence of conditions in which control may be necessary, as in the conflict between intentional and pre-potent responses^{12,13,23}. Furthermore, recent imaging and patient research suggests that executive function in humans is likely to involve both ventral and dorsolateral PFC regions in both hemispheres^{24–32}. The right middle frontal gyrus of DLPFC, for instance, has been associated with response inhibition in the go/no-go task^{16,18,33,34}, as well as the inhibition of imitative behavior³⁵.

Because it is not yet feasible to measure brain activity during actual face-to-face interracial interactions, we used fMRI to assess neural activity in response to photographs of unfamiliar, black faces as a proxy. That is, neural activity during the display of photographs was expected to reflect meaningful aspects of the cognitive processes engaged during an interracial interaction. Specifically, we investigated individual differences in the activity of both left and right lateral PFC, as well as ACC, in response to photographs of black faces, compared to photographs of white faces. In accordance with the proposed mechanism, we found that activity in lateral PFC and ACC varied sys-

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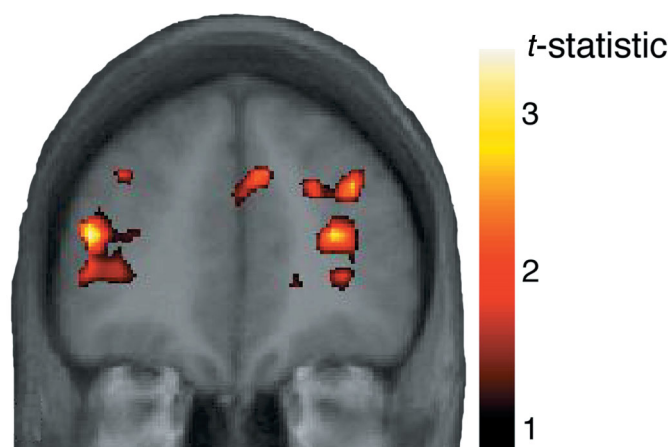


Figure 1 Statistical activation map of black faces > white faces contrast, showing regions in right and left middle frontal gyri, as well as right anterior cingulate cortex. See **Table 1** for coordinates.

tematically as a function of scores on a measure of racial bias. Furthermore, we found that individual differences in brain activity in lateral PFC and ACC in response to black faces predicted Stroop performance after interracial contact. Lateral PFC activity was found to statistically mediate the relation between racial bias and Stroop impairment after interracial, but not same-race, dyadic interactions.

Experiment 1

Our first experiment focused on the neural activity in regions implicated in executive control, and its correlations with individual differences in racial bias, as well as differences in performance on a behavioral task of response inhibition after interracial contact. The primary question was whether neural activity in brain regions known for their participation in cognitive control mediates the relation between racial attitude bias and inhibitory task performance after interracial contact.

RESULTS

Session 1

Preliminary analyses revealed that racial bias scores ranged from +65 ms to +390 ms (mean = 249) and Stroop interference scores ranged from -29 ms to +212 ms (mean = 85). In replication of our previous work³, individuals with greater bias revealed greater impairment on the Stroop task than individuals with lower bias, $r_{13} = 0.67$, $P < 0.01$.

Session 2

Correct responses in the spatial location task during the fMRI session were at ceiling for both black and white faces, and there were no differences in mean RTs (mean = 466.2 ms and 441.7 ms, respectively; $t_{14} = 1.18$, $P > 0.25$). Initial results revealed that BOLD signal intensi-

ties were significantly greater in response to black faces compared to white faces ($P < 0.005$ corrected, see **Table 1**) in several PFC regions. Significant activations were revealed in regions of both right and left lateral PFC, as well as in the ACC (**Fig. 1**). These findings suggest that, as a group, participants engaged cognitive control brain regions to a greater extent upon exposure to faces of black males compared to faces of white males, despite the fact that the task did not explicitly require cognitive control.

Recall, however, that our primary interest was not in differences between activity in response to black compared to white faces; instead, we were interested in the relations among neural activity, racial bias and Stroop impairment after interracial contact. Specifically, the present work examined whether neural activity in response to black faces in brain regions implicated in cognitive control statistically mediates the relation between racial bias and Stroop impairment after interracial contact. Three sets of analyses are required in order to establish statistical mediation³⁶. Analyses must address the following: (i) whether racial bias predicts activity in lateral PFC and ACC during the presentation of black faces (ii) whether activity in these regions during the presentation of black faces predicts inhibitory task performance after interracial contact; and (iii) if the correlation between racial bias and Stroop impairment is reduced when the variance associated with the proposed mediator (*i.e.*, neural activity) is accounted for.

To consider these conditions of mediation, we conducted region of interest (ROI) analyses for the brain regions that revealed significant activation in our black compared to white contrast (**Table 1**). Specifically, we extracted the mean percent signal change associated with the presentation of black faces compared to baseline, and white faces compared to baseline, in each of these regions, for each participant, and then examined their correlations with participants' IAT and Stroop scores. One-tailed significance levels are reported for the correlations reflecting our *a priori* hypotheses.

Correlations between racial bias and neural activity

Results revealed that racial bias scores predicted signal intensities in response to black faces within a region of the ACC extending into right medial frontal gyrus (BA 32; x, y, z : 6, 39, 33; $r = 0.44$, $P = 0.05$). Furthermore, neural activity in the right middle frontal gyrus of DLPFC (BA 9; x, y, z : 39, 48, 27) was significantly correlated with IAT scores ($r = 0.53$, $P < 0.05$). These regions within the right ACC and right DLPFC were relatively more active, upon

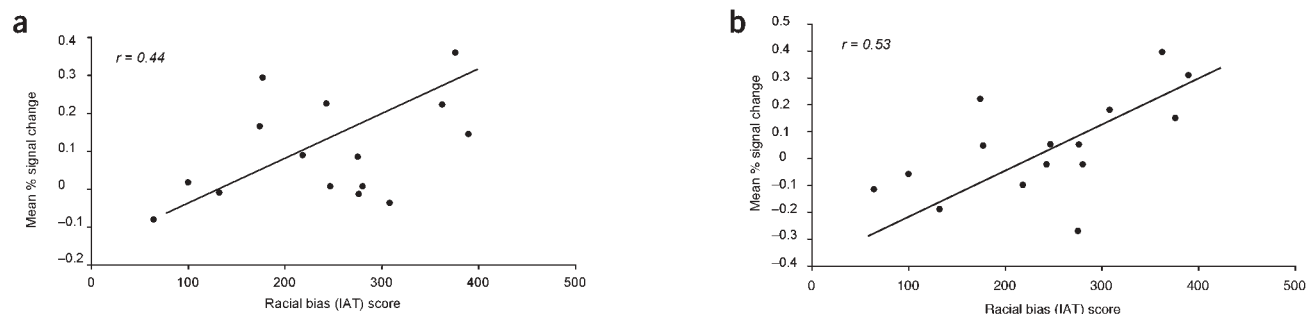


Figure 2 Scatterplots of significant correlations between racial bias and neural activity. (a) Right anterior cingulate (6, 39, 33); (b) right middle frontal gyrus of DLPFC (39, 48, 27).

exposure to black faces, for individuals with higher racial bias scores (Fig. 2a,b). Importantly, neither signal intensities in right DLPFC, nor those in this region of ACC, in response to white faces, reliably predicted IAT scores ($r = 0.22$ (DLPFC) and 0.17 (ACC); both $P > 0.40$). No other significant correlations between neural activity and IAT scores emerged (all $r < 0.30$).

Correlations between neural activity and inhibitory performance

We tested whether the neural activity in response to viewing black faces in the ROIs that showed significant correlations with IAT scores (*i.e.*, right middle frontal and right ACC) also predicted individuals' post-interaction Stroop performance. Results revealed that activity in the right middle frontal gyrus predicted Stroop interference after the interracial interaction (Fig. 3; $r = 0.69$, $P < 0.01$), as did right ACC activity ($r = 0.47$, $P < 0.05$). Thus, both right DLPFC and ACC activity in response to black faces correlated with individuals' Stroop impairment after a face-to-face interracial interaction. Activity in response to viewing white faces in these regions did not reliably predict Stroop impairment ($r = 0.29$ (DLPFC) and 0.03 (ACC), respectively). Consistent with resource depletion, these findings indicate that individual differences in the neural response to black faces in brain regions specifically implicated in the efficient inhibition of pre-potent responses^{16,18,33–35} reliably predict individual differences in impairment on a task that requires the inhibition of pre-potent responses.

Tests of mediation

We conducted regression tests of mediation³⁶ on the neural activity in response to black faces of the right middle frontal gyrus ROI (BA 9; 39, 48, 27) and the right ACC ROI (BA 32; 6, 39, 33). We used the neural activity to black faces compared to baseline in the present analyses, as it is likely to reveal activation most similar to the experience of interacting with an unfamiliar black male. Results showed evidence of mediation by right DLPFC, but not ACC. Specifically, in a regression in which both IAT bias scores and right middle frontal activity were included as predictors of Stroop interference, neural activity remained a reliable predictor ($b = 180.6$, $P < 0.05$), and the effect of racial bias on Stroop interference decreased significantly (from $r = 0.67$ to $r = 0.50$; Sobel test $Z = 1.66$, $P < 0.05$). Consequently, the present results are consistent with the hypothesis that racial bias predicts Stroop impairment after interracial interactions because of resource depletion.

Experiment 2

Although the findings of the first experiment offered considerable evidence for the resource depletion mechanism, a comprehensive examination must consider whether neural activity in the regions identified in experiment 1 also predicts cognitive inhibitory performance after same-race interactions. We examined this question in experiment 2. Again, racial bias was expected to predict neural activity to black faces, but neural activity was not expected to predict Stroop impairment after same-race contact. Consistent with previous work³, the correlation between IAT bias and Stroop interference after same-race interactions did not approach statistical significance, $r_{13} = -0.07$, $P > 0.40$.

Correlations between racial bias and neural activity

In replication of the findings of experiment 1, planned comparisons showed that IAT scores predicted signal intensities in response to black faces in both the right ACC ($r = 0.70$, $P < 0.005$) and the right middle frontal gyrus ($r = 0.50$, $P < 0.05$). Moreover, activity in response to white faces in these regions did not correlate reliably with

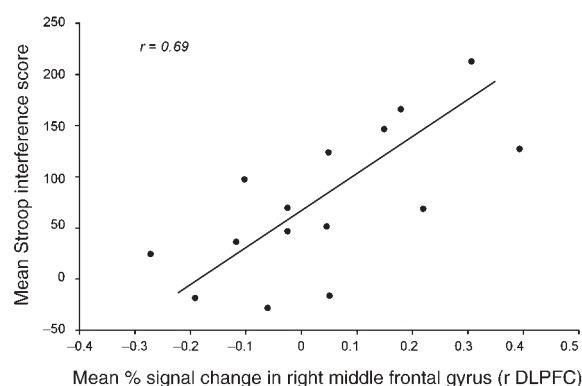


Figure 3 Stroop interference by right middle frontal gyrus activity (39, 48, 27).

IAT scores ($r = -0.13$ and 0.24 , respectively; $P > 0.05$). Thus, racial bias scores predicted the response to black faces of the same regions within right DLPFC and right ACC found in experiment 1.

Correlations between neural activity and inhibitory performance

Consistent with predictions and in contrast to experiment 1, neither right middle frontal gyrus activity, nor right ACC activity, in response to black faces, reliably predicted Stroop interference after same-race interactions ($r = -0.07$ and 0.06 , respectively; both $P > 0.40$). Thus, the present results indicate that the proposed mechanism for the impact of racial bias on inhibitory performance after interracial interactions does not generalize to same-race interactions.

Coupled with the findings of experiment 1, the present data offer considerable support for resource depletion as a viable mechanism through which interracial contact impairs executive function. Specifically, we found that racial bias predicted brain activity in a region distinctly involved in the inhibition of pre-potent responses (*i.e.*, right middle frontal gyrus of DLPFC) during the presentation of black, but not white, faces. Moreover, right middle frontal activity to black faces predicted the extent to which individuals were impaired on the Stroop task, after having interacted with a black individual during an independent testing session, but not after having interacted with a white individual. Furthermore, when both racial bias scores and activity in right middle frontal gyrus were considered in one model as predictors of Stroop interference after interracial contact, brain activity remained a reliable predictor, and the effect of racial bias was reduced—suggestive of partial mediation.

DISCUSSION

The present work considered, and found evidence for, one putative mechanism for the impact of interracial contact on inhibitory task performance. That is, our data supported resource depletion as a viable mechanism through which interracial contact temporarily impairs executive function. We used experimental behavioral data in tandem with fMRI data collected during a separate testing session to examine a theoretical model of the effect of social behavior on cognition. Social cognitive neuroscience approaches, such as this one, may soon prove useful for testing the plausibility of mechanisms that have been proposed for any number of psychological phenomena (see ref. 37 for a similar argument), as well as highlight the relevance of research in cognitive neuroscience to social behavior.

One puzzling facet of the present findings is that neural activity in the right middle frontal gyrus of DLPFC was a statistical mediator of Stroop performance after interracial contact, but activity in ACC was

Table 1 Regions showing greater activity to black faces than to white faces

Regions of peak activation in Black > White contrast						
Brain region	BA	x	y	z	Size	t-value
R anterior cingulate cortex	32	6	39	33	11	3.05
R anterior cingulate cortex	24	12	30	18	16	4.87
	24	6	18	30	19	4.52
R middle frontal gyrus	9	39	48	27	11	3.18
	9	33	57	18	17	4.31
L middle frontal gyrus	46	-45	42	15	16	4.11
	46	-39	36	24	16	3.46
R inferior frontal gyrus	10	27	63	-3	11	4.24
L/R supplementary motor area	6	0	6	48	19	5.81
R insula	—	39	9	9	13	5.09

BA, approximate Brodmann's area location. L, left; R, right; Talairach⁴⁵ coordinates of locations based on center of mass. Size, number of 3 × 3 × 3 mm voxels.

not. Although it is unclear what role each region plays in the control of pre-potent behaviors, some work suggests that DLPFC is involved in exerting control, whereas ACC is responsible for monitoring the need for control¹⁶. Consequently, the partial dissociation between these two regions found in the present work could suggest that actually engaging in cognitive control during interracial contact, rather than simply monitoring the need for control, may be primarily responsible for the subsequent executive dysfunction. As this explanation is only speculative, future research is needed.

One intriguing aspect of the present findings is the emergence of a positive correlation between racial bias scores and the recruitment of executive control regions upon exposure to black faces. Although this finding is somewhat counter-intuitive, it must be interpreted within the context of contemporary societal norms in which it is unacceptable to show prejudice. Furthermore, many individuals who generate high scores on subtle measures of racial bias endorse egalitarian values and aspire to behave in nonprejudiced ways³⁸. Coupled with previous findings that racial bias predicts the automatic activation of negative stereotypes¹⁰, our results suggest that individuals with high scores on subtle measures of racial bias may put forth additional effort to control their thoughts and behaviors in order to live up to their egalitarian, nonprejudiced values. As interracial contact becomes increasingly involuntary, therefore, the present results suggests that harboring racial bias may be maladaptive to optimal cognitive functioning.

METHODS

Experiment 1

Participants. Fifteen healthy white American undergraduates (8 female; mean age = 20.5 years), all right handed, with normal or corrected vision, provided written, informed consent to participate in this study for a combination of partial course credit and monetary compensation (\$20).

Session 1: behavioral testing. Before the fMRI session, participants were met by a white experimenter who took them to a laboratory testing room where they began a study entitled "Serial Cognition: the influence of one cognitive task on a subsequent task when there is a delay between the two." Similar to our previous study³, the first cognitive task was the implicit associations test³⁹ (IAT) that served as an unobtrusive measure of racial bias. Next, participants engaged in an ostensibly unrelated 5-min session with a black experimenter that occurred in a different testing room. During the 'delay task,' participants spent about 1 min introducing themselves, then were asked to comment on two issues, each for about 2 min (the college fraternity system and racial pro-

filings, in counterbalanced order), presumably to create stimulus materials for a different study. The black experimenter did not make any comments other than asking participants to comment on the two issues. Afterwards, participants were met by the original experimenter who took them back to the original testing room, where they performed the second 'cognitive task'—a Stroop (1935) color-naming test—which measured inhibitory performance⁴⁰.

The IAT measures automatic associations between categories (e.g., flowers, insects) and evaluations (positivity, negativity), and it has recently been used in numerous studies as a measure of subtle differences in the automatic association of social groups with evaluative categories³⁹. The IAT in the present study required participants to categorize White names, Black names, Positive words, and Negative words as quickly as possible by pressing one of two marked response keys. In one block of 40 trials, White names and Positive words shared a response key, and Black names and Negative words shared a key (White⁺/Black⁻ phase). In another block of 40 trials, the associations were reversed—white with negative, and black with positive (White⁻/Black⁺ phase). The order of these two phases was assigned to participants according to an ABBA scheme. All IAT latencies under 300 ms and over 3,000 ms were re-coded⁴¹, then mean latencies for the White⁺/Black⁻ phase were subtracted from mean latencies for the White⁻/Black⁺ phase for each participant in order to index their level of racial bias.

Thus, these IAT racial bias scores reflect the differential ease with which individuals were able to associate the white American and black American racial groups with positive concepts, compared with negative concepts. Consequently, the bias scores do not allow for the distinction between the extent to which individuals hold particularly favorable attitudes toward their own racial group, or particularly negative attitudes toward blacks, or, rather, some combination of the two. Furthermore, in addition to assessing a subtle form of racial bias that is hard to control, IAT bias scores could also reflect differences in cultural, rather than personal, beliefs about the relevant groups⁴¹, or baseline individual differences in general processing speed⁴². Thus, these scores should not be over-interpreted as perfect estimates of individuals' racial attitudes.

The Stroop task was conducted with a color-coded four-button response box. Instructions were to report the color of the font type in which a stimulus word appeared, as quickly and accurately as possible, by pressing the appropriate key on the response box. The stimulus words were either color words (e.g., "red") or strings of Xs (for control). Color names or control Xs appeared on the screen one at a time, in one of the following four colors: yellow, red, green or blue. Each word or control stimulus appeared for a maximum of 2,000 ms, preceded by a fixation cross (+). The inter-trial interval was 1,500 ms. The task consisted of 20 practice trials followed by 7 blocks of 12 trials each, for a total of 84 experimental trials. 'Incompatible' trials were those in which the color name appeared in a color other than its semantic meaning (e.g., the word "red" written in blue type). Control trials, in contrast, were those in which the string of Xs appeared in blue type. Stroop interference scores were calculated by subtracting mean latencies associated with control trials from mean latencies associated with incompatible trials.

Session 2: fMRI testing. No less than 2 weeks after participating in the first session, all 15 participants came to the MRI facility for an ostensibly unrelated study examining the "perception of spatial location." Participants were contacted by a different experimenter from those associated with session 1, and no reference to the previous session was made.

Stimuli and apparatus. Thirty-two digitized color images of different black and white young adults, each bearing a neutral expression, were used as stimuli⁴³. Photographs were taken in full-face frontal view. Each face was then standardized for brightness and contrast, then centered in the image frame such that the eyes always appeared in the same place.

Imaging data acquisition. Scanning involved blocked presentation of faces. Experimental blocks (25 s each) alternated with baseline blocks that consisted of a blank screen with a central fixation point (10 s each). During each experimental block, 12 faces (different individuals of the same race) were presented one at a time for 2 s each, on either the right or left side of fixation. A total of 12 experimental blocks (6 of each race) and 14 baseline blocks were acquired. A total of 176 image volumes were used for analyses. Participants were instructed

to fixate centrally and to indicate whether the face appeared on the right or left of the screen by pressing a button in the corresponding hand. Target photographs appeared on each side of the screen an equal number of times within each experimental block, and presentation order was randomized.

Gradient-echo echoplanar MR images were acquired using a 1.5-tesla GE Signa System. A quadrature birdcage head coil was used for RF transmission and reception. In each of 25 non-contiguous planes parallel to the anterior-posterior commissure, 112 T2*-weighted MR images depicting BOLD contrast were acquired with TE 35 ms, TR 2,500 ms, flip angle 90°, slice thickness 4.5 mm and skip slice 1 mm. Head movement was limited by foam padding within the head coil. For each subject, anatomical images were acquired using a high-resolution 3-D spoiled gradient recovery sequence (SPGR; 124 sagittal slices, TE = 3 ms, TR = 7.7 ms, flip angle = 15°, IR prep time = 315 ms, FOV = 24, voxel size = 1 × 1 × 1.2 mm).

fMRI data analysis. For each functional run, data were preprocessed to remove sources of noise and artifact. Using SPM99 (Wellcome Department of Cognitive Neurology), data were then realigned within and across runs to correct for head movement, and coregistered with each participant's anatomical data. The resulting images were then transformed into a standard anatomical space with a cubic (3 × 3 × 3 mm) voxel size. The images were further smoothed using an isotropic Gaussian filter of 6 mm FWHM and corrected for global activity by proportional scaling. The different stimulation conditions (black or white faces, and baseline) were then modeled as boxcar functions, convolved with a hemodynamic response function. To identify the regions with significant BOLD changes to the two race conditions, statistics were computed on a voxel-by-voxel basis, using the general linear model⁴⁴. These individual results were then submitted to a second-level, random-effects group analysis to create mean *t*-images (thresholded at *P* < 0.005 corrected, minimal cluster size of 10 voxels). To conduct the ROI analyses, an automated peak-search algorithm identified the location of peak activations in each region based on *t*-value and cluster size.

Experiment 2

Participants. Fifteen healthy white American undergraduates (8 female; mean age = 19.8 years), all right handed, with normal or corrected vision, provided written, informed consent to participate in this study for a combination of partial course credit and monetary compensation (\$20).

Session 1: behavioral testing. The procedure for the behavioral testing session was identical to that reported in experiment 1, however, participants engaged in an interaction with a white, rather than with a black, experimenter during the delay period. Preliminary analyses revealed that IAT scores ranged from +78 ms to +428 ms (mean = 274) and interference scores ranged from −63 ms to +296 ms (mean = 81).

Session 2: fMRI testing. The procedures of the fMRI session were identical to those in experiment 1. Preliminary analyses revealed that correct responses in the spatial location task were at ceiling for both black and white faces, but the mean RTs for black faces were significantly slower than for white faces (*M* = 554.6 and 498.7, respectively; *t*₁₄ = 6.10, *P* < 0.0005). Consequently, time on task was controlled for in all subsequent analyses.

Analyses for experiment 2 were limited to the ROIs from experiment 1 that were found to correlate positively with IAT bias and post-contact Stroop performance. Specifically, the mean percent signal changes from baseline to black faces and to white faces in the right middle frontal ROI (BA 9; 39, 48, 27) and the right ACC ROI (BA 32; 6, 39, 33) examined in experiment 1 were extracted. These mean percent signal changes were then used in mediation analyses, similar to those conducted in experiment 1. Such a procedure provides a conservative test of whether the patterns that emerged in experiment 1 would also be revealed in experiment 2, when participants engaged in same-race, rather than interracial, contact.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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- Blascovich, J., Mendes, W.B., Hunter, S.B., Lickel, B. & Kowai-Bell, N. Perceiver threat in social interactions with stigmatized others. *J. Pers. Soc. Psychol.* **80**, 253–267 (2001).
- Devine, P.G. & Vasquez, K.A. The rocky road to positive intergroup relations. In *Confronting Racism. The Problem and the Response* (eds. Eberhardt, J.L. & Fiske, S.T.) 234–262 (Sage, California, 1998).
- Richeson, J.A. & Shelton, J.N. When prejudice does not pay. Effects of interracial contact on executive function. *Psychol. Sci.* **14**, 287–290 (2003).
- Baumeister, R.F., Muraven, M. & Tice, D.M. Ego depletion: a resource model of volition, self-regulation, and controlled processing. *Soc. Cogn.* **8**, 130–150 (2000).
- Engle, R.W., Conway, A.R.A., Tuholski, S.W. & Shisler, R.J. A resource account of inhibition. *Psychol. Sci.* **6**, 122–125 (1995).
- Vohs, K.D. & Heatherton, T.F. Self-regulatory failure: a resource-depletion approach. *Psychol. Sci.* **11**, 249–254 (2000).
- Devine, P.G. Stereotypes and prejudice: their automatic and controlled components. *J. Pers. Soc. Psychol.* **56**, 5–18 (1989).
- Shelton, J.N. Interpersonal concerns in social encounters between majority and minority group members. *Group. Process. Intergroup Relat.* **6**, 171–186 (2003).
- von Hippel, W., Silver, L.A. & Lynch, M.E. Stereotyping against your will: the role of inhibitory ability in stereotyping and prejudice among the elderly. *Pers. Soc. Psychol. Bull.* **26**, 523–532 (2000).
- Lepore, L. & Brown, R. Category and stereotype activation: Is prejudice inevitable? *J. Pers. Soc. Psychol.* **72**, 275–287 (1997).
- Shallice, T. & Burgess, P. Supervisory control of action and thought selection. In *Attention: Selection, Awareness and Control* (eds. Baddeley, A. & Weiskrantz, L.) 171–187 (Clarendon, Oxford, 1993).
- Carter, C.S. *et al.* Anterior cingulate cortex error detection and the online monitoring of performance. *Science* **280**, 747–749 (1998).
- Cohen, J.D., Botvinick, M. & Carter, C.S. Anterior cingulate and prefrontal cortex: who's in control? *Nat. Neurosci.* **3**, 421–423 (2000).
- Dehaene, S., Posner, M.I. & Tucker, D.M. Localization of a neural system for error detection and compensation. *Psychol. Sci.* **5**, 303–305 (1994).
- Miller, E.K. & Cohen, J.D. An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* **24**, 167–202 (2001).
- MacDonald, A.W., Cohen, J.D., Stenger, V.A. & Carter, C.S. Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science* **288**, 1835–1838 (2000).
- Kane, M.J. & Engle, R.W. The role of prefrontal cortex in working memory capacity, executive attention, and general fluid intelligence: an individual-differences perspective. *Psychonom. Bull. Rev.* **9**, 637–671 (2002).
- Smith, E.E. & Jonides, J. Storage and executive processes in the frontal lobes. *Science* **283**, 1657–1661 (1999).
- Milham, M.P., Banich, M.T., Claus, E.D. & Cohen, N.J. Practice-related effects demonstrate complementary roles of anterior cingulate and prefrontal cortices in attentional control. *Neuroimage* **18**, 483–493 (2003).
- Banich, M.T. *et al.* Prefrontal regions play a predominant role in imposing an attentional “set”: evidence from fMRI. *Cogn. Brain Res.* **10**, 1–9 (2000).
- Kimberg, D.Y. & Farah, M.J. A unified account of cognitive impairments following frontal lobe damage: the role of working memory in complex organized behavior. *J. Exp. Psychol. Gen.* **122**, 411–482 (1993).
- Fuster, J.M. Proceedings of the human cerebral cortex: from gene to structure and function. *Brain Res. Bull.* **52**, 331–336 (2000).
- Gehring, W.J. & Knight, R.T. Prefrontal-cingulate interactions in action monitoring. *Nat. Neurosci.* **3**, 516–520 (2000).
- Chee, M.W.L., Sriram, N., Soon, C.S. & Lee, K.M. Dorsolateral prefrontal cortex and the implicit association of concepts and attributes. *Neuroreport* **11**, 135–140 (1999).
- Leung, H.C., Skudlarski, P., Gatenby, J.C., Peterson, B.S. & Gore, J.C. An event-related functional MRI study of the Stroop color word interference task. *Cereb. Cortex* **10**, 552–560 (2000).
- Garavan, H., Ross, T.J. & Stein, E.A. Right hemispheric dominance of inhibitory control. *Proc. Natl. Acad. Sci. USA* **96**, 8301–8306 (1999).
- Garavan, H., Ross, T.J., Murphy, K., Roche, R.A.P. & Stein, E.A. Dissociable executive functions in the dynamic control of behavior: Inhibition, error detection and correction. *Neuroimage* **17**, 1820–1829 (2002).
- Bunge, S.A., Ochsner, K.N., Desmond, J.E., Glover, G.H. & Gabrieli, J.D.E. Prefrontal regions involved in keeping information in and out of mind. *Brain* **124**, 2074–2086 (2001).
- de Zubicaray, G.I., Andrew, C., Zelaya, F.O., Williams, S.C.R. & Sumanior, C. Motor response suppression and the prepotent tendency to respond: a parametric fMRI study. *Neuropsychologia* **38**, 1280–1291 (2000).
- Braver, T.S. *et al.* A parametric study of prefrontal cortex involvement in human working memory. *Neuroimage* **5**, 49–62 (1997).
- Hazeltine, E., Poldrack, R. & Gabrieli, J.D.E. Neural activation during response competition. *J. Cogn. Neurosci.* **12** (Suppl. 2), 118–129 (2000).
- Konishi, S. *et al.* No-go dominant brain activity in human inferior prefrontal cortex

- revealed by functional magnetic resonance imaging. *Eur. J. Neurosci.* **3**, 1209–1213 (1998).
33. Casey, B.J. *et al.* A developmental functional MRI study of prefrontal activation during performance of a go-no-go task. *J. Cogn. Neurosci.* **9**, 835–847 (1997).
 34. Kawashima, R. *et al.* Functional anatomy of go/no-go discrimination and response selection—a PET study in man. *Brain Res.* **728**, 79–89 (1996).
 35. Brass, M., Zysset, S. & von Craamon, D.Y. The inhibition of imitative response tendencies. *Neuroimage* **14**, 1416–1423 (2001).
 36. Baron, R.M. & Kenny, D.A. The moderator-mediator variable distinction in social psychological research: conceptual, strategic and statistical considerations. *J. Pers. Soc. Psychol.* **51**, 1173–1182 (1986).
 37. Gray, J.R., Chabris, C.F. & Braver, T.S. Neural mechanisms of general fluid intelligence. *Nat. Neurosci.* **6**, 316–322 (2003).
 38. Crandall, C.S., Eshleman, A. & O'Brien, L. Social norms and the expression and suppression of prejudice: the struggle for internalization. *J. Pers. Soc. Psychol.* **82**, 359–378 (2002).
 39. Greenwald, A.G., McGhee, D.E. & Schwartz, J.L.K. Measuring individual differences in implicit cognition: the implicit association task. *J. Pers. Soc. Psychol.* **74**, 1464–1480 (1998).
 40. Stroop, J.R. Studies of interference in serial verbal reactions. *J. Exp. Psychol.* **18**, 643–662 (1935).
 41. Karpinski, A. & Hilton, J.L. Attitudes and the Implicit Association Test. *J. Pers. Soc. Psychol.* **81**, 774–778 (2001).
 42. De Houwer, J. A structural and process analysis of the Implicit Association Test. *J. Exp. Soc. Psychol.* **37**, 443–451 (2001).
 43. Golby, A.J., Gabrieli, J.D.E., Chiao, J.Y. & Eberhardt, J.L. Differential responses in the fusiform region to same-race and other-race faces. *Nat. Neurosci.* **4**, 845–850 (2001).
 44. Friston, K.J., Jezzard, P. & Turner, R. Analysis of functional MRI time-series. *Hum. Brain Mapp.* **1**, 153–171 (1994).
 45. Talairach, P. & Tournoux, J. *A Stereotactic Coplanar Atlas of the Human Brain* (Thieme, New York, 1988).