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Authors

Patterson, Tara K
Lenartowicz, Agatha
Berkman, Elliot T
[et al.](#)

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Putting the brakes on the brakes: negative emotion disrupts cognitive control network functioning and alters subsequent stopping ability

Tara K. Patterson¹  · Agatha Lenartowicz² · Elliot T. Berkman³ · Danni Ji¹ · Russell A. Poldrack⁴ · Barbara J. Knowlton¹

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Abstract The ability to inhibit unwanted responses is critical for effective control of behavior, and inhibition failures can have disastrous consequences in real-world situations. Here, we examined how prior exposure to negative emotional stimuli affects the response-stopping network. Participants performed the stop-signal task, which relies on inhibitory control processes, after they viewed blocks of either negatively emotional or neutral images. In Experiment 1, we found that neural activity was reduced following negative image viewing. When participants were required to inhibit responding after neutral image viewing, we observed activation consistent with previous studies using the stop-signal task. However, when participants were required to inhibit responding after negative image viewing, we observed reductions in the activation of ventrolateral prefrontal cortex, dorsolateral prefrontal cortex, medial frontal cortex, and parietal cortex. Furthermore, analysis of neural connectivity during stop-signal task blocks indicated that across participants, emotion-induced changes in behavioral performance were associated with

changes in functional connectivity, such that greater behavioral impairment after negative image viewing was associated with greater weakening of connectivity. In Experiment 2, we collected behavioral data from a larger sample of participants and found that stopping performance was impaired after negative image viewing, as seen in longer stop-signal reaction times. The present results demonstrate that negative emotional events can prospectively disrupt the neural network supporting response inhibition.

Keywords Cognitive control · Emotion · Functional connectivity · Mood · Prefrontal cortex · Neural network

Introduction

Of the many effects that emotion can have on cognition, one of the most consequential is the detrimental effect of emotion on self-control. Failure to stop an inappropriate response can have disastrous consequences in real-world situations such as driving, yet the effect of emotion on the ability to control such errors is not well understood, particularly at the neural level. Several prior studies (De Houwer and Tibboel 2010; Hartikainen et al. 2012; Kalanthroff et al. 2013; Lindstrom and Bohlin 2012; Pessoa et al. 2012; Rebetz et al. 2015; Verbruggen and De Houwer 2007; Yu et al. 2012) have shown that emotional or threat-relevant stimuli can have deleterious effects on the performance of an ongoing response inhibition task. For example, Verbruggen and De Houwer (2007) presented emotional images to participants while they performed the stop-signal task, and found that response and stopping latencies were impaired. Such evidence has been interpreted as support for the hypothesis that emotional stimuli disrupt ongoing cognitively controlled activities by attracting attention away

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✉ Tara K. Patterson
tkpatterson@ucla.edu

- ¹ Department of Psychology, University of California, Los Angeles, Los Angeles, CA, USA
- ² Semel Neuropsychiatric Institute, University of California, Los Angeles, Los Angeles, CA, USA
- ³ Department of Psychology, University of Oregon, Eugene, OR, USA
- ⁴ Department of Psychology, Stanford University, Stanford, CA, USA

from the ongoing central task. However, negative emotional stimuli need not be immediately present to impair top-down control, suggesting the presence of another mechanism that lingers after stimulus offset. For instance, driving by a distressing car accident could impair one's ability to respond to a detour sign down the road. Therefore, in the present pair of experiments, we sought to investigate how prior emotional experience affects performance of a subsequent response inhibition task, completed when emotional stimuli are no longer present. The presence of a response inhibition deficit in the absence of concurrent negative stimuli would be evidence that negative affect can create a persistent impairment to top-down control.

We employed the stop-signal task (Logan 1994; Logan and Cowan 1984) to measure response inhibition. In this task, participants make speeded responses to a continuous stream of stimuli (e.g., visually presented arrows) but are instructed to attempt to inhibit their responses on a small percentage of trials in which a stop signal (e.g., an infrequent auditory cue) is presented after the go stimulus. The latency of the stop signal relative to the participant's reaction time distribution allows one to estimate the duration of the inhibitory process and thus quantify response inhibition, using a model that treats the inhibition process as a race between stop and go processes. Whether the response is withheld depends on which process is completed first. The resulting estimate of the duration of the stopping process is called the stop-signal reaction time (SSRT). A shorter SSRT suggests that the stop process is more efficient and can be completed even after the go process is closer to being completed. A longer SSRT means that the stop process is less efficient, in that it must be initiated soon after the go process begins in order to be effective.

In Experiment 1, we collected fMRI data as participants alternated between viewing blocks of images (negative or neutral) and performing the stop-signal task. Research using the stop-signal paradigm has demonstrated that successful response inhibition appears to rely critically on the ventrolateral prefrontal cortex (inferior frontal gyrus, IFG), especially in the right hemisphere (Aron et al. 2003; Chambers et al. 2006; for review, see Aron et al. 2004, 2014). Other regions that appear to contribute to response inhibition include dorsolateral prefrontal cortex, medial frontal cortex, parietal cortex, and the basal ganglia (for review, see Chambers et al. 2009; Verbruggen and Logan 2008b). We predicted that experiencing negative emotion prior to performance of the stop-signal task would disrupt activity and connectivity in this network of brain regions. In Experiment 2, we collected behavioral data from a larger sample of subjects performing the stop-signal task after inducing negative emotion as in Experiment 1. This experiment was designed to investigate the behavioral consequences of experiencing negative emotion prior to performance of the

stop-signal task. We hypothesized that if emotion prospectively interferes with response inhibition by altering top-down control, we would observe increased SSRT following negative image viewing.

Experiment 1

Method

Participants

A total of 19 people participated in the experiment. One person failed to complete the experiment, yielding a sample size of 18 people (7 women, 11 men, $M_{\text{age}} = 21.28$ years, $SD_{\text{age}} = 3.95$ years). Participants were recruited from the University of California, Los Angeles (UCLA) community. Study procedures were approved by the Institutional Review Board at UCLA, and all participants provided written record of informed consent.

Procedure

Participants alternated between two tasks, image viewing and stop signal (Fig. 1). Stimuli for the image-viewing task were selected from the International Affective Picture System (IAPS; Lang et al. 2008), a standardized set of images normalized for affective valence (1 = low positive valence, 9 = high positive valence) and arousal (1 = low arousal, 9 = high arousal). Images presented in the neutral condition had an average valence rating of $M = 4.64$ ($SD = 0.20$) and an average arousal rating of $M = 2.96$ ($SD = 0.59$). Images presented in the negative condition had an average valence rating of $M = 1.70$ ($SD = 0.17$) and an average arousal rating of $M = 6.66$ ($SD = 0.40$). Images were presented in blocks of five. All five images within the block were of the same type (neutral or negative). Images were presented for 7 s each, and after each image, participants were prompted to rate their level of distress on a scale of 0–9 (0 = no distress, 9 = extreme distress). The interval between images was 1 s.

Following each block of the image-viewing task, participants performed one block of the stop-signal task. Participants were instructed to make responses indicating the direction of left- and right-facing arrows (go trials), but were asked to inhibit this response on a subset of trials when the arrow was presented along with an auditory cue (stop trials). Each stop-signal task block contained 54 trials (38 go trials and 16 stop trials). Trials began with 0.5 s of fixation followed by the arrow stimulus. The response window for indicating arrow direction was 1 s. The intertrial interval varied according to a continuous exponential distribution with mean of 1 s, and a range of 0.5–4 s. Stop trials

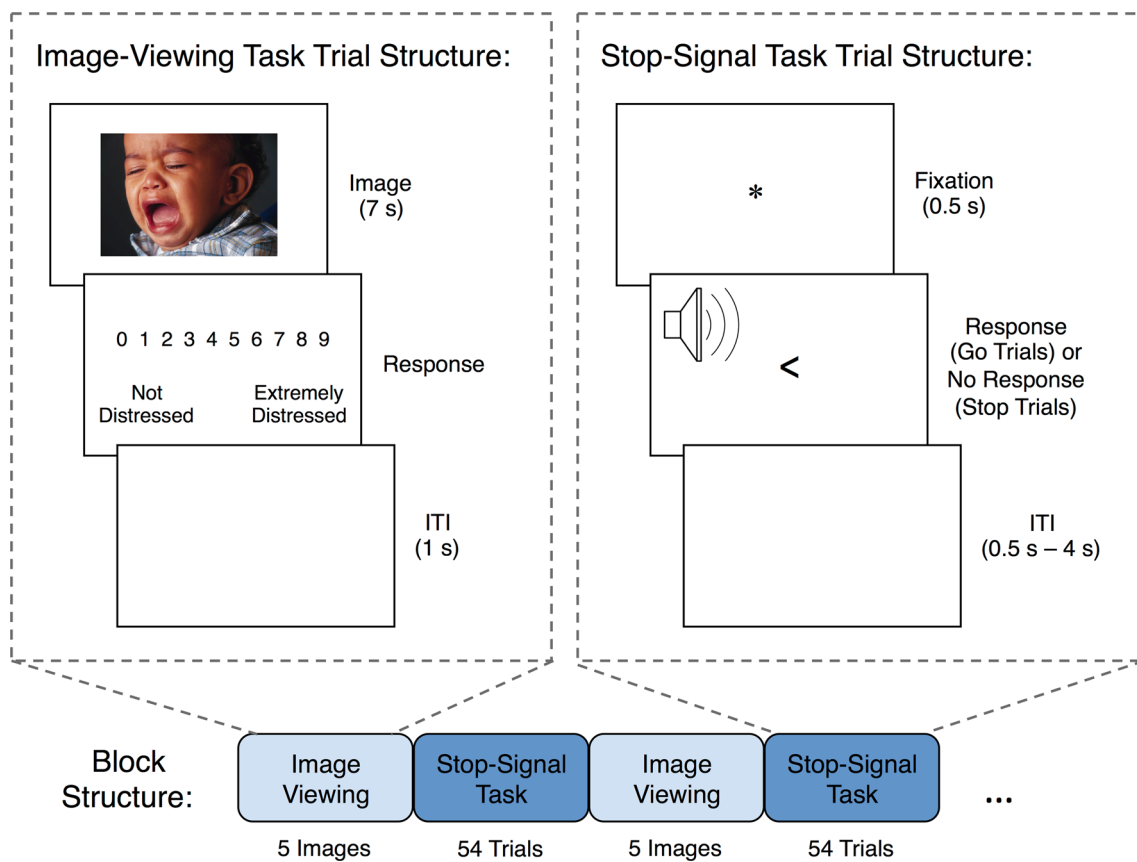


Fig. 1 Schematic of task structure. Participants alternated between viewing images and performing the stop-signal task. In the image-viewing task, participants viewed either five neutral or five negative images, giving self-reports of distress on a scale of 0–9 after each

image. In the stop-signal task, participants made button responses indicating the direction of left- and right-facing arrows, but were asked to inhibit their motor response when the arrow was presented along with an auditory cue. *ITI* intertrial interval

were pseudo-randomly distributed throughout the block, with the constraint that no more than three consecutive stop trials were allowed. Following procedures described in Lenartowicz et al. (2011), we employed two staircases to vary the onset of the auditory cue relative to the onset of the arrow (stop-signal delay, SSD), ensuring the probability of successful inhibition converged to 50%. SSRT was calculated using the quantile method (Band et al. 2003).

The experimental session began with a training phase, during which participants practiced the stop-signal task. During the testing phase, we acquired four runs of fMRI data. Stimulus presentation was implemented in MATLAB, and responses were recorded with an MRI-compatible button box. Each of the four runs of the testing phase consisted of two blocks of image viewing (one negative, one neutral), alternating with two blocks of the stop-signal task. Images were not repeated within the experiment. Runs containing poor behavioral performance (stop-task accuracy < 20% or go-task accuracy < 80%) were excluded from the analysis (total of three runs). Participants were scanned with a 3-T Siemens Trio MRI system.

During each scanning run, we collected 232 functional (T2*-weighted) echo planar images (34 axial slices, slice thickness = 4 mm, matrix = 64 × 64, FOV = 192 mm, TR = 2 s, TE = 30 ms). Structural (T1-weighted) images were acquired with an MPRAGE (240 sagittal slices, slice thickness = 1 mm, matrix = 256 × 256, FOV = 256 mm, TR = 2.53 s, TE = 3.31 ms). For registration purposes, we also acquired a matched-bandwidth high-resolution scan from each participant with the same slice prescription as the functional scans (34 axial slices, slice thickness = 4 mm, matrix = 128 × 128, FOV = 192 mm).

fMRI data analysis

Data were analyzed with FMRIB Software Library version 4.1.9. The following pre-processing steps were taken: removal of non-brain tissue (Smith 2002), head motion correction with six degrees of freedom (Jenkinson et al. 2002), spatial smoothing (Gaussian kernel 5 mm FWHM), grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor, and high-pass temporal

filtering [Gaussian-weighted least-squares straight line fitting, with cutoff = 0.01 Hz ($\sigma = 50$ s) for the activity analysis and cutoff = 0.0067 Hz ($\sigma = 75$ s) for the connectivity analysis]. Functional images were registered to the matched-bandwidth images, then to the structural images, then to Montreal Neurological Institute (MNI) standard space using linear registration and FSL's MNI152 T1 $2 \times 2 \times 2$ mm template (Jenkinson et al. 2002; Jenkinson and Smith 2001). Nonlinear registration was then used to refine the registration to standard space (Andersson et al. 2007a, b). In the first-level analysis, pre-whitening was applied to correct for local autocorrelation (Woolrich et al. 2001), and the six estimated motion parameters were included to remove residual motion effects. Voxel timeseries were analyzed using general multi-level linear modeling (Beckmann et al. 2003; Woolrich et al. 2004). Statistical analysis was conducted at the group level using mixed-effects modeling with automatic outlier detection (Woolrich 2008). Statistical maps were thresholded using cluster-based correction for whole-brain multiple comparisons with a Z threshold of 2.0 and a cluster significance threshold of $p = .05$ (Worsley 2001).

We used separate models to assess brain activity and functional connectivity during the stop-signal task. For the analysis of brain activity, we modeled the image-viewing periods as blocks and the stop-signal task trials as events. Image-viewing blocks were classified as negative or neutral depending on the presented stimuli, and the three predominant stop-signal task trial types (correct go trials, correct stop trials, and failed stop trials) were classified as negative or neutral depending on the type of stimuli presented during the previous image-viewing block. Finally, erroneous go trials (incorrect button press or no button press), if any, were modeled as events, yielding a total of nine task regressors. Runs that contained no erroneous go trials were modeled with eight task regressors and one empty regressor. The waveforms for each task variable were convolved with a double-gamma hemodynamic response function, and temporal derivatives of the task variable waveforms were included to improve model fit. Our contrasts of interest included (a) comparison of successful stop trials and successful go trials after neutral image viewing; (b) comparison of successful stop trials and successful go trials after negative image viewing; and (c) the difference between the pairwise contrasts in (a) and (b) (i.e., the event type \times image type interaction).

For the analysis of functional connectivity, we used a psychophysiological interaction (PPI) model (Friston et al. 1997; O'Reilly et al. 2012). This analysis identifies regions that differ in functional connectivity with a seed region under different psychological conditions. A seed region within right IFG was selected based on its known role in successful response inhibition. We used a spherical

mask with a radius of 6 mm defined in MNI space and centered at ($x = 48, y = 16, z = 28$), a local maximum within right IFG *pars opercularis* from contrast (a) above. The seed mask was transformed into subject space, and the timeseries in the seed was extracted for each run. The PPI model included four task conditions modeled as blocks: negative image viewing, neutral image viewing, stop-signal task after negative image viewing, and stop-signal task after neutral image viewing. As in the analysis of brain activity, the task variables were convolved with a double-gamma hemodynamic response function, and temporal derivatives for the task variables were included in the model. The element-by-element products of the right IFG timeseries and the two convolved stop-signal task regressors (i.e., $SST_{neutral}$ and $SST_{negative}$) were added to the model along with the raw right IFG timeseries, and the PPI was tested as a contrast between the two interaction regressor coefficients (i.e., $SST_{neutral} \times rIFG - SST_{negative} \times rIFG$) (McLaren et al. 2012; O'Reilly et al. 2012). Individual SSRT difference scores were added to the model at the group level, in order to determine which brain regions differed in their connectivity with right IFG in a way that varied with the behavioral effect of negative image viewing.

Results and discussion

The results of our fMRI analyses are shown in Figs. 2, 3, 4, and detailed cluster characteristics are given in Tables S1–S4 in the Electronic Supplementary Material. Figure 2a shows the comparison of successful stop trials after neutral image viewing to successful go trials after neutral image viewing. Consistent with previous investigations of stopping versus going, we found clusters of activation in ventrolateral prefrontal cortex (right IFG *pars opercularis*, MNI: 48, 16, 28; right IFG *pars triangularis*, MNI: 54, 24, 0), dorsolateral prefrontal cortex (MNI: 40, 30, 38), medial frontal cortex (MNI: 10, 32, 24), lateral parietal cortex (MNI: -56, -44, 26), and the basal ganglia (MNI: 20, 10, -12). This pattern of activation confirms robust engagement of the response-stopping network during stopping after neutral image viewing. Figure 2b shows the results of the same stop versus go contrast after negative image viewing. A similar pattern of activation was found, but in general the magnitude of the activations was diminished relative to the activations elicited during stopping after neutral image viewing. To confirm this observation, we directly tested the difference between these two contrasts; i.e., we looked for regions where activity associated with stopping was significantly reduced by negative image viewing. The results of this test are shown in Fig. 2c. Consistent with our prediction of stop-signal network disruption, we observed reduced stopping activity for negative versus neutral conditions in ventrolateral prefrontal cortex (right

Fig. 2 Neural activation during the stop-signal task following emotional image viewing (whole-brain analyses, $p < .05$, $Z > 2.0$). Images are in MNI space. The *three panels* show surface projections of activity related to **a** stopping after neutral image viewing, **b** stopping after negative image viewing, and **c** the difference between the two. Following negative image viewing, there was significantly decreased activation in regions known to be important for successful stopping, including the right inferior frontal gyrus

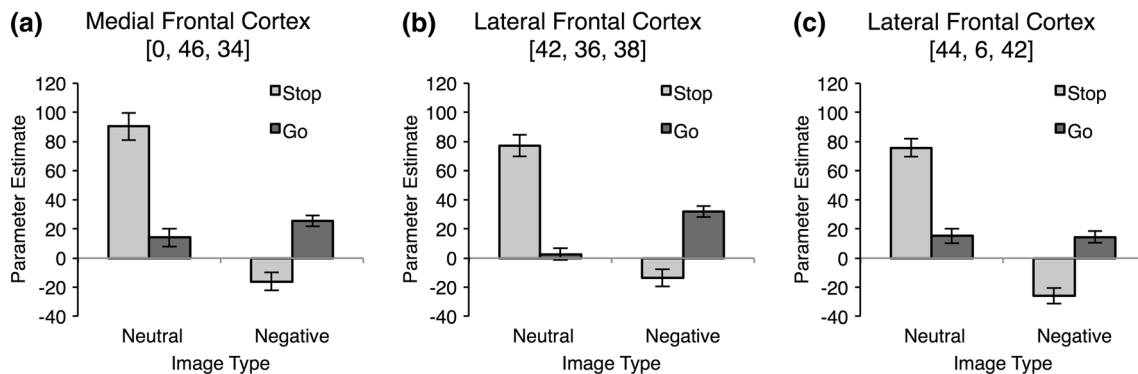
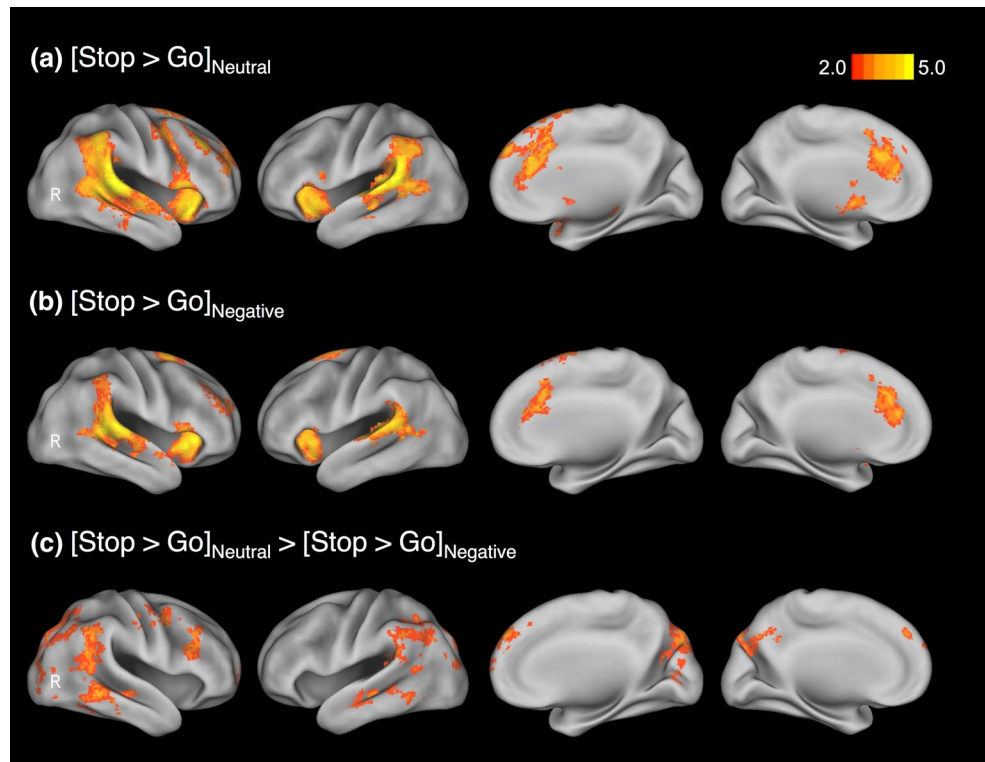


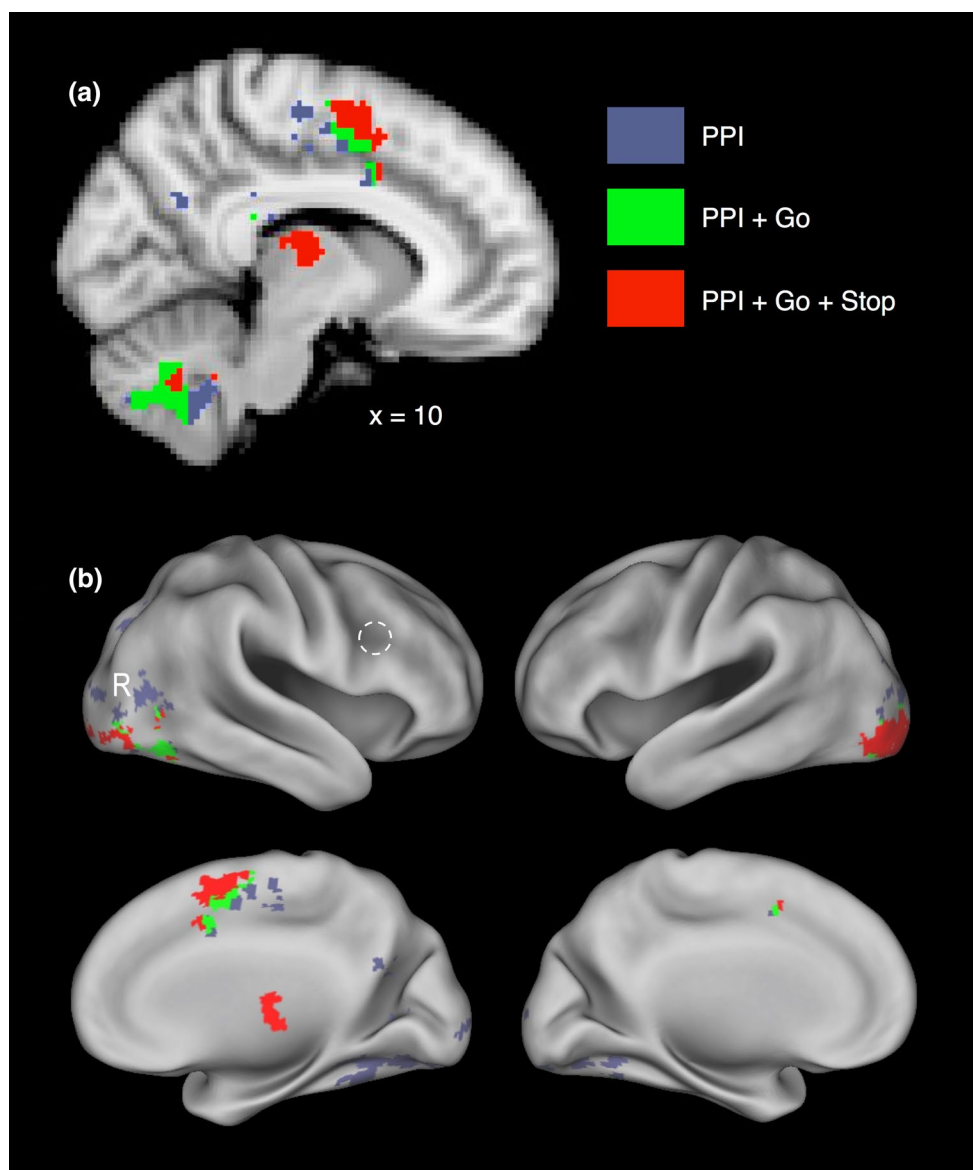
Fig. 3 Modulation of brain activity by emotion and response inhibition. The *three panels* show parameter estimates of activity extracted from the three frontal lobe clusters identified with the contrast ($[\text{Stop} > \text{Go}]_{\text{Neutral}} > [\text{Stop} > \text{Go}]_{\text{Negative}}$). **a** Medial frontal cluster centered at

[0, 46, 34]; **b** lateral frontal cluster centered at [42, 36, 38]; **c** lateral frontal cluster centered at [44, 6, 42]. Coordinates of cluster peaks are given in MNI space. See Table S3 for full anatomical extent of each cluster. *Error bars* represent standard error of the mean

IFG *pars opercularis*, MNI: 50, 18, 24; right IFG *pars triangularis*, MNI: 52, 28, 18), dorsolateral prefrontal cortex (MNI: 44, 6, 42), medial frontal cortex (MNI: 0, 46, 34), and lateral parietal cortex (MNI: 56, -48, 38). To illustrate the nature of this interaction, we extracted average parameter estimates for the four included conditions. Extracted parameter estimates for the three frontal clusters are shown in Fig. 3. As can be seen in the figure, we found a pattern of substantially reduced activity during stop trials, and modestly increased activity during go trials, following negative image viewing.

These results support the hypothesis that viewing negative images prior to performing the stop-signal task disrupts activation within regions associated with successful response inhibition that are otherwise engaged. Next we examined whether this emotion-induced disruption translated into a behaviorally significant disruption of connectivity within the response inhibition network. We used a PPI to test the hypothesis that emotion-induced increases in SSRT were correlated with emotion-induced decreases in functional connectivity of right IFG during stop-signal task blocks. At the whole-brain level, the negative interaction

Fig. 4 Emotion-induced changes in functional connectivity (whole-brain analyses, $p < .05$, $Z > 2.0$). Images are in MNI space. Sagittal slice (a) and surface projections (b) showing results of the psychophysiological interaction (PPI) analysis, in conjunction with the regions activated by go trials and regions activated by both go trials and successful stop trials. Significant clusters in the PPI analysis indicate regions that showed decreased functional connectivity with the right inferior frontal gyrus seed region (dashed white line) during stop-signal task blocks after negative image viewing compared to neutral image viewing in a way that varied with individual emotion-induced changes in stop-signal task performance



was significant in medial frontal cortex (MNI: $-6, 2, 56$), medial parietal cortex (MNI: $4, -58, 26$), occipital cortex (MNI: $-24, -90, -14$), thalamus (MNI: $18, -28, 16$), and cerebellum (MNI: $8, -62, -34$). The regions activated by this contrast, shown in Fig. 4, had weakened connectivity with right IFG following negative image viewing that, across participants, was associated with greater SSRT impairment on the stop-signal task. We next performed a set of conjunction analyses to determine whether the regions identified in the PPI analysis overlapped with portions of the stop-signal task network. For these analyses, we used masks from the neutral stop-signal task blocks. We found no overlap between the regions identified in the PPI analysis and regions activated for the contrast of successful stop trials versus go trials. We did, however, find overlap between the regions identified in the PPI analysis

and regions activated during go trials, and the majority of these voxels were active during successful stop trials as well. (There were no voxels positive for the conjunction of PPI and successful stop trials that were not also active during go trials.) As shown in the figure, voxels positive for the conjunction of PPI, go trials, and successful stop trials were located in medial frontal cortex, occipital cortex, thalamus, and cerebellum. Thus, the functional connectivity of right IFG with this set of regions was disrupted by negative emotional induction, with significant detrimental effect on SSRT.

The behavioral results of Experiment 1 are shown in Figs. 5, 6, and Table 1. The effect of negative image viewing on participants' self-reported ratings of distress was significant, $t(17) = 17.07$, $p < .001$, $d = 4.02$, confirming that negative image viewing successfully induced distress

Fig. 5 Self-reported distress during negative and neutral image viewing for Experiment 1 (a) and Experiment 2 (b). Distress was rated after each image-viewing trial on a scale from 0 (“not distressed”) to 9 (“extremely distressed”). In both Experiment 1 and Experiment 2, distress was significantly higher during negative image viewing, indicating that the affect manipulation was successful. Error bars represent standard error of the mean

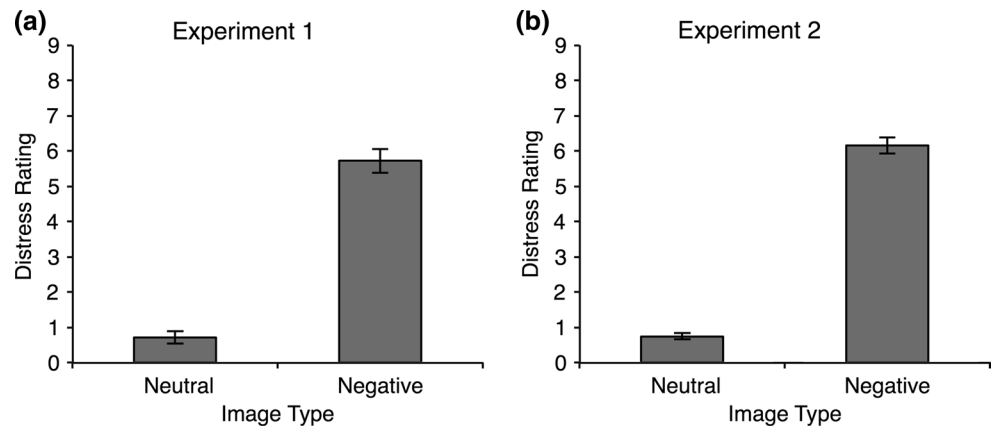


Fig. 6 Distribution of stop-signal reaction time (SSRT) difference scores for Experiment 1 (a) and Experiment 2 (b). SSRT was estimated from stop-signal task blocks that followed either negative or neutral image viewing. A positive SSRT difference score indicates slower stopping (impaired response inhibition) after negative image viewing

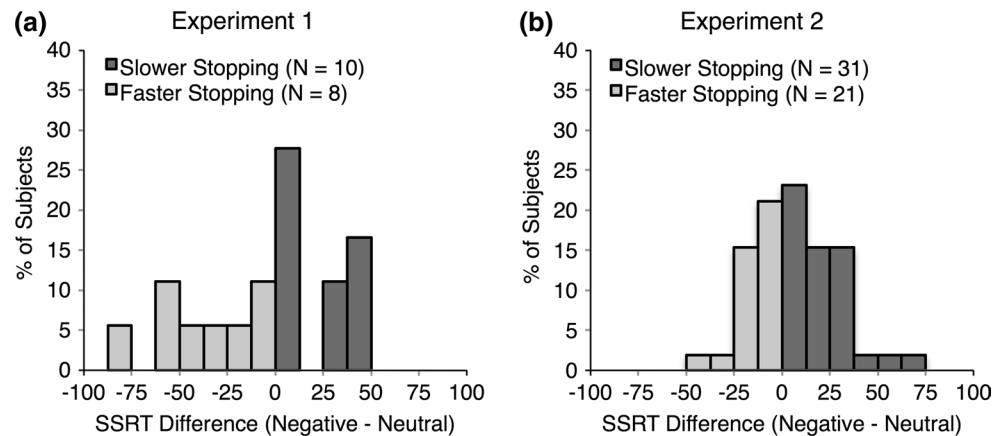


Table 1 Stop-signal task performance measures for Experiments 1 and 2

Measure	Experiment 1 ($N = 18$)		Experiment 2 ($N = 52$)	
	Neutral	Negative	Neutral	Negative
Go errors (%)	2.34 (0.56)	2.77 (0.69)	3.99 (0.49)	4.24 (0.46)
Go median RT (ms)	434.08 (16.23)	436.48 (15.64)	450.41 (8.90)	450.39 (8.65)
% Inhibition	50.55 (1.24)	50.84 (1.42)	50.03 (0.53)	49.86 (0.48)
SSD (ms)	279.14 (21.10)	285.16 (18.90)	307.57 (11.34)	299.69 (10.60)
SSRT (ms)	155.83 (13.19)	151.88 (10.11)	141.89 (6.30)	149.27 (5.79)

RT reaction time, SSD stop-signal delay, SSRT stop-signal reaction time

Standard error of the mean is shown in parentheses. Significant differences between neutral and negative ($p < .05$) are highlighted in bold

in the sample (Fig. 5a). Mean performance measures for the stop-signal task as a function of prior image-viewing block type are shown in Table 1. Successful inhibition converged to 50 %, and go trial accuracy was near ceiling. We found no significant differences between conditions on any of the stop-signal task measures (go trial error rate, go trial median RT, percent inhibition, SSD, or SSRT), smallest $p > .30$. The failure to detect an effect of negative image viewing on SSRT was not unexpected given the sample size ($N = 18$). Ten participants (55.6 %) had longer SSRT after

negative image viewing, and the median difference score (negative minus neutral) was 2.55 ms (Fig. 6a). The effect of negative image viewing on performance was therefore examined further in a larger sample in Experiment 2.

Experiment 2

The results of Experiment 1 indicated that viewing negative images increased distress and prospectively disrupted

the response-stopping network, evidenced by diminished activation during stopping events and diminished connectivity between the right IFG and other prefrontal cortical regions during stop-signal task blocks. In Experiment 2, we collected behavioral data from a larger sample of subjects to determine whether viewing negative images prior to performance of the stop-signal task can result in behavioral impairment. We predicted that negative emotion would impair the ability to stop, resulting in lengthened SSRT.

Method

Participants

A total of 65 people participated in the experiment. Thirteen people were excluded for poor behavioral performance (stop-task accuracy < 20 % or go-task accuracy < 80 %) or failure to complete the experiment, yielding a sample size of 52 people (23 women, 29 men, $M_{\text{age}} = 21.60$ years, $SD_{\text{age}} = 3.08$ years). Participants were recruited from the UCLA community. Study procedures were approved by the Institutional Review Board at UCLA, and all participants provided written record of informed consent.

Procedure

As in Experiment 1, participants in Experiment 2 alternated between performing the stop-signal task and viewing IAPS images (Fig. 1). In addition to the two view-only conditions used in Experiment 1, we included a reappraisal condition in which participants viewed negative images and were instructed to internally produce captions for the images. This condition was included to investigate whether the process of generating captions could attenuate the emotional response to negative image viewing. Each cycle of three image-viewing blocks contained one block from each condition (neutral, negative with reappraisal, negative without reappraisal). To minimize emotional habituation and fatigue, the neutral condition was always presented second. Although participants' ratings of distress were higher in the negative without reappraisal condition ($M = 6.21$) than the negative with reappraisal condition ($M = 6.10$), this difference did not reach statistical significance, $t(51) = 1.04$, $p = .302$. Similarly, although SSRT was longer in the negative without reappraisal condition ($M = 152.58$ ms) than the negative with reappraisal condition ($M = 145.96$ ms), this difference also did not reach statistical significance, $t(51) = 1.18$, $p = .243$. Therefore, we collapsed the data from these two conditions and refer to them in the text collectively as "negative."

Participants completed the experiment in a private testing room. Stimulus presentation was implemented in MATLAB. Stimuli were presented on a Macintosh computer,

and responses were made using the computer keyboard. The experimental session began with a training phase, during which participants practiced the stop-signal task. During the testing phase, participants completed 12 blocks of the image-viewing task alternating with 12 blocks of the stop-signal task. Images were not repeated within the experiment.

Results and discussion

As in Experiment 1, negative images were rated as significantly more distressing than neutral images, $t(51) = 23.14$, $p < .001$, $d = 3.21$ (Fig. 5b). Mean performance measures for the stop-signal task as a function of prior image block type are shown in Table 1. As in Experiment 1, successful inhibition converged to 50 % and go trial accuracy was near ceiling. Consistent with an impairing effect of negative emotion, SSRT was significantly longer in the negative condition ($M = 149.27$ ms) than the neutral condition ($M = 141.89$ ms), $t(51) = 2.38$, $p = .021$, $d = 0.33$. This 7.38-ms increase in the duration of the stopping process after negative emotion means that the stop signal would need to be processed that much sooner in order to avoid a stopping failure. In contrast, there were no differences between conditions on go trial error rate, go trial median RT, or percentage of stop trials successfully inhibited, smallest $p > .30$. The distribution of difference scores obtained in Experiment 2 was similar to the distribution obtained in Experiment 1; thirty-one participants (59.6 %) had longer SSRT after negative image viewing, and the median difference score (negative minus neutral) was 3.96 ms (Fig. 6b). The proportion of people showing slower stopping after negative image viewing did not differ between the two experiments, $\chi^2(1) = 0.09$, $p = .763$.

General discussion

We conducted two experiments to test the hypothesis that negative emotional stimuli impact subsequent control circuit integrity and ability to inhibit an ongoing behavioral response using the stop-signal task. In Experiment 1, we found that presenting negative stimuli prior to performance of the stop-signal task decreases stopping-related neural activation and decreases functional connectivity between the right IFG and other areas of the cerebral cortex and cerebellum. In Experiment 2, we found that negative emotion prolongs SSRT, meaning more time is required to successfully countermand prepotent motor responses and avoid stopping failure. Taken together, our results demonstrate that negative emotion can prospectively impair response inhibition, by a mechanism other than attentional capture. The nature of this mechanism is of interest, as it represents

a modulatory change in internal state that is consequential to top-down processes.

The results of Experiment 1 represent the first demonstration of an emotion manipulation having a prospective effect on the neural circuitry of stopping, affecting brain activity and connectivity during a subsequent response inhibition task, when emotional stimuli are no longer present. In previous experiments where emotion was found to impact neural activity during response inhibition task performance (e.g., Pawliczek et al. 2013; Sagaspe et al. 2011; Stockdale et al. 2015), emotional stimuli were presented concurrently with the inhibition task stimuli. The alternating block design employed in the present experiment, however, allowed us to make comparisons across the two emotion conditions in the absence of emotional stimulus processing effects. The brain regions where we observed reduced activation during stopping following negative image viewing—ventrolateral prefrontal cortex (right IFG *pars opercularis* and right IFG *pars triangularis*), dorsolateral prefrontal cortex, medial frontal cortex, and parietal cortex—are all regions previously shown to support response inhibition, and their reduced activation suggests disruption of the network (Chambers et al. 2009; Verbruggen and Logan 2008b). Our analysis of functional connectivity further supports this interpretation. In a PPI analysis seeded with a crucial node in the response-stopping network (right IFG *pars opercularis*), we found that negative emotion prospectively reduced connectivity between this node and other areas of cerebral cortex and cerebellum in people whose performance on the stop-signal task was impaired. Notably, there was overlap between the set of regions showing reduced connectivity with right IFG after negative image viewing and the set of regions active during stop and go trials. Overall, these results indicate that negative emotion has persistent effects on control circuit integrity. It is possible that these effects occur via the monoamine system, as pharmacological manipulations that inhibit monoamine reuptake have been shown to increase activation of right IFG during stop-signal task inhibition (Chamberlain et al. 2009).

The behavioral effect of negative emotion on SSRT reported in Experiment 2 is consistent with previous reports of emotional stimuli impairing response inhibition (De Houwer and Tibboel 2010; Hartikainen et al. 2012; Kalan-throff et al. 2013; Lindstrom and Bohlin 2012; Pessoa et al. 2012; Rebetz et al. 2015; Verbruggen and De Houwer 2007; Yu et al. 2012). However, unlike these previous findings, the results reported here cannot be accounted for by attentional capture, because we induced negative emotion prior to measuring response inhibition. To our knowledge, in only two previous experiments was negative mood induced prior to the performance of a response inhibition task, and both of these studies found no difference between

the negative and neutral conditions (Chepenik et al. 2007; Smallwood et al. 2009). One possible reason these previous studies failed to observe an effect is that their emotional stimuli induced sadness, whereas the emotional stimuli we used had negative valence and were also high in arousal (Lang et al. 2008), suggesting a possible dissociation between affect and arousal in their effects on control networks. A second difference between these experiments and our own is that Chepenik et al. (2007) and Smallwood et al. (2009) employed the go/no-go task, whereas our experiments were conducted with the stop-signal task. Although both the go/no-go task and the stop-signal task measure response inhibition, they differ in a number of ways that could interact with emotion. For example, in the go/no-go task, mappings between stimuli and responses are consistent (some stimuli elicit go responses and some elicit no-go responses), and these mappings can become automatic and relatively undemanding of cognitive resources with practice. In contrast, in the stop-signal task the same stimulus could elicit a go or a stop response depending on whether the stop signal is presented; because of this, response inhibition cannot become automatic and thus would consistently demand cognitive resources (Verbruggen and Logan 2008a).

Although our findings cannot be explained by the capture of attention by external emotional stimuli, it is indeed possible that our emotion manipulation increased internal distraction, such as through the creation of distressing episodic memories that were recalled during the subsequent stop-signal task blocks. One way that future research might address this possibility is by inducing negative mood that does not create specific memories. An alternative approach would be to use a decoding method such as multi-voxel pattern analysis to investigate the extent to which the episodic memory traces created during negative image viewing are re-activated during performance of the stop-signal task.

Both the changes in brain activity observed in Experiment 1 and the behavioral impairment observed in Experiment 2 are consistent with a resource competition model, although other models are also feasible. By this view, executive functions are proposed to share a common resource pool; emotion is thought to interfere with top-down control by consuming resources from this common pool (e.g., Pessoa 2009). One example of a resource is shared neural circuitry; when different executive processes rely on the same neural circuits, they may at times be in competition with each other. If the demands of competing processes exceed the availability of prefrontal cortex-dependent resources, top-down control may be compromised and prepotent responses, such as button pressing in response to frequent go stimuli, may be more likely to determine behavior. Although our experiments did not address what specific

processes may be competing for resources, one possibility consistent with our fMRI results is that in the negative condition, resources are reallocated to emotion regulation. While somewhat different constituent neural activations have been reported for emotion regulation versus response inhibition, these systems have also been shown to overlap in critical regions such as the right IFG, suggesting that there is at least some shared neural processing (Berkman et al. 2009; Cohen et al. 2013; Tabibnia et al. 2011). A second possibility is that after viewing negative stimuli, prefrontal cortex-dependent resources that would normally be allocated to response inhibition are recruited for threat detection. In support of this interpretation, a review of aversive conditioning studies indicated that several prefrontal regions involved in response inhibition, including medial frontal cortex and right lateral frontal cortex, are also activated by stimuli that have been previously paired with an aversive unconditioned stimulus (Pessoa 2009). This overlap in circuitry suggests that response inhibition and detection of potential threat may draw on the same resource pool.

One limitation of the present study is that because we used emotional stimuli that were previously rated as both negatively valenced and highly arousing, we cannot say which of these attributes is required to produce the observed effects. Both have been shown to facilitate visual processing (e.g., Lane et al. 1999) and subsequent memory (e.g., Ochsner 2000), and both have the capacity to disrupt top-down processes (Vuilleumier 2005). Arousal, however, has been shown to reorient attention (Anderson 2005) and increase physiological responses (Dan-Glauser and Gross 2011) for both positively and negatively valenced stimuli, suggesting that arousal has an effect that is independent of valence. Future research with a wider range of stimuli will be required to determine whether the effects we observed are attributable to valence, arousal, or a combination of these factors.

A second limitation of this study is that a behavioral effect of negative emotion on SSRT was only obtained in Experiment 2, not in Experiment 1. Experiments 1 and 2 had substantially different sample sizes, giving Experiment 2 greater statistical power. Given the small size of the effect observed in Experiment 2 (7.38 ms, $d = 0.33$), it is likely that Experiment 1 was underpowered to detect this effect. Another difference between Experiments 1 and 2 was that in Experiment 2, participants were asked to perform a caption generation task during half of the negative image-viewing blocks. Although this manipulation did not have a significant effect on ratings of distress or SSRT, it is possible that the addition of this task contributed to the difference in behavioral results between Experiment 1 and Experiment 2. For example, we likely obtained better estimates of SSRT in Experiment 2 due to the increased number of trials in the negative condition.

Although the effect of negative emotion on SSRT observed in the present study was small, it is important to note that even a modest increase in SSRT means an increase in the probability of a failure to stop, which can have dire consequences in many real-world situations such as driving or combat. A 7.38-ms increase in estimated stopping duration means that a stop signal (e.g., detection of a pedestrian or bystander) must be processed that much sooner to avoid a potentially catastrophic failure to stop. Furthermore, the stimuli used here to induce negative mood were relatively mild and non-complex compared to emotional stimuli experienced in the real world, so it is likely that greater effects on response inhibition would occur with more intense mood states. Finally, the construct of response inhibition, when broadly defined, encompasses not only the ability to suppress a prepotent motor response, but also stimulus–response habits and higher-order, non-motor responses such as thoughts. The interference, even to a modest degree, of negative emotion with inhibitory control at the motor level, therefore, suggests that the effects of emotion on cognitive control may have a farther reach than previously supposed. Possible directions for future research include investigating how long the observed effects persist and whether the observed effects are specific to negative emotion.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Informed consent was obtained from all individual participants included in the study.

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