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Expressive suppression and neural responsiveness to nonverbal affective cues

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Abstract

Optimal social functioning occasionally requires concealment of one's emotions in order to meet one's immediate goals and environmental demands. However, because emotions serve an important communicative function, their habitual suppression disrupts the flow of social exchanges and, thus, incurs significant interpersonal costs. Evidence is accruing that the disruption in social interactions, linked to habitual expressive suppression use, stems not only from intrapersonal, but also from interpersonal causes, since the suppressors' restricted affective displays reportedly inhibit their interlocutors' emotionally expressive behaviors. However, expressive suppression use is not known to lead to clinically significant social impairments. One explanation may be that over the lifespan, individuals who habitually suppress their emotions come to compensate for their interlocutors' restrained expressive behaviors by developing an increased sensitivity to nonverbal affective cues. To probe this issue, the present study used functional magnetic resonance imaging (fMRI) to scan healthy older women while they viewed silent videos of a male social target displaying nonverbal emotional behavior, together with a brief verbal description of the accompanying context, and then judged the target's affect. As predicted, perceivers who reported greater habitual use of expressive suppression showed increased neural processing of nonverbal affective cues. This effect appeared to be coordinated in a top-down manner via cognitive control. Greater neural processing of nonverbal cues among perceivers who habitually suppress their emotions was linked to increased ventral striatum activity, suggestive of increased reward value/personal relevance ascribed to emotionally expressive nonverbal behaviors. These findings thus provide neural evidence broadly consistent with the hypothesized link between habitual use of expressive suppression and compensatory development of increased responsiveness to nonverbal affective cues, while also suggesting one explanation for the suppressors' poorer cognitive performance in social situations. Moreover, our results point to a potential neural mechanism supporting the development and perpetuation of expressive suppression as an emotion regulation strategy.

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The unadulterated experience and expression of affective states sometimes impedes optimal functioning. On those occasions, people tend to use a variety of strategies to alter when and how they experience and express their emotions (Gross, 1998). Expressive suppression is a commonly used affect regulatory strategy, which is intended to stifle external affective displays, after the internal emotional response to an evocative episode has already been generated (Gross & John, 2003).

Despite its effectiveness in reducing emotionally expressive behavior, habitual use of suppression as an emotion regulation strategy incurs significant costs in both affective and cognitive well-being, such as higher negative affect and lower life satisfaction (Gross & John, 2003; John & Gross, 2004). Indeed, further testifying to the malign consequences of chronic expressive suppression use are clinical findings suggesting that it is one of the emotion regulation strategies commonly used by individuals diagnosed with depression or anxiety-related disorders (Aldao, Nolen-Hoeksema, & Schweizer, 2010).

Beyond the intrapersonal realm, there is evidence that habitual expressive suppression use also impedes optimal interpersonal functioning, as it is associated with lower levels of social support and less satisfying relationships with one’s peers (English & John, 2013; English, John, Srivastava & Gross, 2012; Gross & John, 2003; Srivastava, Tamir, McGonigal, John, & Gross, 2009). Because emotions serve a communicative function, their suppression presumably introduces a sense of affective separation between the self and other social actors (English & John, 2013; English, John, & Gross, 2013; Srivastava et al., 2009). As such, suppressors tend to be perceived as being more distracted and less responsive during social interactions, and, thus, less desirable as potential companions (Butler et al., 2003; English & John, 2013; English et al., 2013).

Intriguingly, recent studies indicate that the poor social functioning outcomes, linked to habitual expressive suppression use, stem not only from the aforementioned intrapersonal causes, but may be also due to interpersonal factors. Specifically, a recent investigation provided evidence that interlocutors of individuals who had been asked to suppress their emotions demonstrated themselves impoverished emotionally expressive behaviors (Butler, Gross, & Barnard, 2014). Thus, it seems that not only the suppressors, but also their interlocutors, contribute to an emotionally “drier” interpersonal environment and, thus, impoverished social exchanges.

However, despite the well-documented association between chronic expressive suppression and poor interpersonal functioning (English & John, 2013; English et al., 2013; Gross & Jon, 2003; Srivastava et al., 2009), a strong link between expressive suppression use and clinically significant impairments in social functioning, specifically, has not been established. One reason may be that over the lifespan, individuals who habitually engage in expressive suppression come to compensate for the emotionally impoverished environment that they and their interlocutors create (cf. Butler et al., 2014) by developing an increased sensitivity to nonverbal affective cues.

A link between chronic expressive suppression use and increased sensitivity to the emotional states of *others* would dovetail nicely with a sizeable body of research documenting a significant association between expressive suppression and increased sensitivity to *one's own* internal states. Indeed, there is evidence that although suppressors demonstrate poorer memory for the factual details associated with affectively laden episodes (Egloff, Schmukle, Burns, & Schwerdtfeger, 2006; Richards & Gross, 2000, 2006), they tend to show superior memory for the emotions they experienced during those episodes (Richards, Butler, & Gross, 2003). Moreover, suppressors are reportedly more likely to allow their currently experienced mood states to impact their decision making (e.g., evaluation of commercial products, which are unrelated to the suppressors' current affective state, Hess, Beale, & Miles, 2010), in line with the conjecture that habitual use of expressive suppression may render inner states particularly salient. Indeed, compatible with this line of reasoning and with the notion of use-dependent brain plasticity (Kleim, Barbay, & Nudo, 1998; Kleim et al., 2002), a recent study documented a significant positive association between habitual use of expressive suppression and volume of the anterior insula, a brain region that is critically involved in inner state awareness (Giuliani, Drabant, Bhatnagar, & Gross, 2011).

Documenting a link between habitual expressive suppression use and increased sensitivity to the affective states of others would have the potential to illuminate the determinants of the poorer cognitive performance, evidenced by suppressors, particularly in social situations (Richards et al., 2003; Richards & Gross, 2006). Indeed, if increased sensitivity to nonverbal affective cues depends upon deployment of cognitive control resources, then the suppressors' preferential processing of nonverbal affective information in social situations may be partly to blame for their reduced processing of emotionally unrelated information (Richards et al., 2003; Richards & Gross, 2006). Such an account would complement existing theory and research that the suppressors' perpetual monitoring of their own internal states diminishes the amount of cognitive resources that suppressors have available during social encounters (cf. Giuliani et al., 2011).

Moreover, showing a link between chronic expressive suppression use and increased sensitivity to nonverbal affective information may pave the way for investigations on the factors that may reinforce the use of suppression as a preferred emotion regulation strategy, despite its adverse socioaffective consequences (e.g., Gross & John, 2003). It is noteworthy that of all the aspects of an emotional response, it is behavioral expression that constitutes the focus of suppressors' regulatory efforts (Gross & John, 2003). Furthermore, as documented above, of all the aspects of a personal episode, it is the emotions and emotionally expressive behaviors that suppressors recall best (Richards et al., 2003). It is thus plausible that for individuals who habitually engage in expressive suppression (relative to those who do not), nonverbal emotional information carries greater personal relevance and, as such, preferential processing of such information may be reinforced through mechanisms linking processing of self-relevant information to reward-like neurobehavioral responses (Grady, Grigg, & Ng, 2012; Grigg & Grady, 2010).

1.2 Current Research

The present study sought to test three interrelated predictions regarding the effect of habitual expressive suppression use on sensitivity to nonverbal affective behavior. First, we tested whether social perceivers who report greater expressive suppression use would show neural activity patterns suggestive of preferential processing of the nonverbal affective behaviors, rather than the verbal contextual information. Second, we probed whether the suppressors' predicted preferential neural processing of nonverbal cues would be supported by cognitive control processes, a mechanism that may account for the suppressors' poorer cognitive performance in social situations (i.e., because their cognitive resources are invested in processing nonverbal cues). Third, we tested whether preferential neural processing of nonverbal cues among perceivers who tend to suppress their emotions is particularly self-relevant and is, thus, linked to activation in neural reward centers, an effect that may explain the perpetuation of expressive suppression as an emotion regulation strategy.

To test our predictions, we used fMRI to scan healthy older women, who varied in their self-reported use of expressive suppression, while they viewed silent videos of a male social target, who displayed nonverbal emotional behavior. The social target's silent nonverbal video was accompanied by a brief verbal description of the context, in which the respective behavior occurred and perceivers were asked to judge the target's affect. Because existing literature suggests that expressive suppression use impacts nonverbal affective behavior (cf. Gross & John, 2003) and because we sought to test the generalizability of our findings across social targets varying in emotional behavior expressivity, each perceiver was presented with two social targets: one who reported high and a second who reported low expressive suppression use. We opted to focus on an elderly sample of perceivers because we reasoned that it would be the long-term habitual use of expressive suppression, and, thus, long-term exposure to other social actors' restricted expressive behaviors (cf. Butler et al., 2014) that would lead to the development of heightened sensitivity to the nonverbal affective cues. We only tested women due to evidence of significant sex differences in both emotional experience and functional brain anatomy (Caeyenberghs & Leemans, 2014; Tomasi & Volkow, 2012; Wager, Phan, Liberzon, & Taylor, 2003), which could have thus interfered with the detection of our hypothesized effects.

To investigate the predicted effect of expressive suppression use on sensitivity to nonverbal behavior, we employed partial least squares (i.e., PLS, Krishnan et al., 2011), a powerful multivariate technique, sensitive enough to use with sample sizes such as ours (or even smaller, cf. McIntosh & Lobaugh, 2004). PLS can identify in an unconstrained, data-driven manner whole-brain patterns of activity that robustly differentiate distinct experimental conditions as a function of individual differences variables (behavioral PLS). Thus, we used behavioral-PLS to investigate whether perceivers who report greater expressive suppression use would demonstrate brain activity patterns reflective of greater processing of nonverbal (rather than verbal) information across all scrutinized social targets.

To test our hypothesis that the suppressors' preferential processing of nonverbal information draws upon cognitive control resources, we capitalized on existing evidence that a so-called frontoparietal control network (FPC), encompassing the lateral PFC, the anterior part of the inferior parietal lobule (IPL), medial superior PFC, and the anterior insula, coordinates optimal cognitive performance by virtue of its flexible functional coupling with task-relevant regions (Cole et al., 2013; Spreng et al., 2010). Thus, we tested whether greater FPC recruitment would predict the pattern of preferential neural processing of nonverbal cues, hypothesized to typify higher suppression perceivers.

Finally, we sought to test the hypothesis that among perceivers who habitually suppress their emotions, preferential neural processing of nonverbal information is particularly self-relevant and, thus, rewarding (cf. Grady et al., 2012; Grigg & Grady, 2010). To this end, we focused on the ventral stratum (VS), a brain region involved in processing rewards (e.g., Rademacher et al., 2010; Salimpoor et al., 2013), including social rewards (e.g., positive emotional expressions, Bedi, Luan, Angstadt, & de Wit, 2009; self-relevant stimuli, Grady et al., 2012; social approval, Izuma, Saito, & Sadato, 2010; attractive faces, Liang, Zebrowitz, & Zhang, 2010). Because extant literature suggests that the left and the right VS are similarly involved in reward processing (e.g., Grady et al., 2012; Izuma et al., 2010; Rademacher et al., 2010)., we tested whether greater neural processing of nonverbal cues would predict increasingly stronger bilateral VS activity in those perceivers who report greater use of expressive suppression.

2. Method

2.1 Participants

Fifteen female participants (mean age 72.14 ± 7.09 years) were recruited from an initial sample of 52 elderly married couples who participated in a behavioral study two years prior to the scanning session. All 15 participants were screened for a history of neurological and psychiatric conditions and use of psychotropic drugs, as well as for physical conditions or bodily implants that may render their participation unsafe and provided informed consent in accordance with the regulations of the Research Ethics Board at Baycrest. One participant completed fewer than half of the fMRI trials and was thus eliminated from all analyses, leaving a final sample of l4 participants (mean age 71.69 ± 7.17 years at the time of scanning). This sample was part of a larger study and their data have been partly reported elsewhere (Petrican, Rosenbaum, & Grady, *in press*). Nevertheless, there was no overlap in the reported analyses and only minimal overlap in the data used in Petrican et al.

2.2 Expressive Suppression Measure

As a measure of the dispositional tendency to control one's emotions by not expressing them, participants completed the Emotion Regulation Questionnaire (ERQ; Gross & John, 2003), which includes a four-item expressive suppression subscale (e.g., "I control my emotions by not expressing them"). The scale, which uses a 1 (*strongly disagree*) to 7 (*strongly agree*) response format, demonstrated good psychometric qualities (Cronbach's alpha = .87; $M = 3.29$, $SD = 1.34$). The ERQ also assesses individual differences in reappraisal (e.g., "I control my emotions by changing the way I think about the situation I am in."). In our sample, habitual use of the two emotion regulation strategies was significantly positively correlated, $r(13) = .54$, $p < .05$. Consequently, to ensure that all the reported effects are specifically linked to habitual engagement in expressive suppression, rather than habitual engagement in any emotion regulation strategy, we created a residual expressive suppression score by regressing out the ERQ reappraisal score from the ERQ suppression score. This "purer" suppression score is used in all the reported analyses, including the norming study results.

2.3 fMRI Task Stimuli and Norming

The fMRI stimuli were acquired one year prior to the scanning session. Specifically, 17 married older men (mean age 73.41 ± 5.44 years at the time) provided one-sentence written descriptions and 9-point Likert-type ratings of valence (from 1 *very negative* to 9 *very positive*) of 15 positive and 15 negative personal events from the beginning of their marriage, as well as of 15 positive and 15 negative personal events from the 5 years preceding their laboratory visit. Subsequently, they were videotaped (from shoulders up), while they described each event to R.P. for about 1–2 minutes. One 10 s video segment, capturing the emotional climax of the event described, was selected from each recording (by R.P.). The sound was eliminated from all the selected segments.

To have the fMRI stimuli validated, 14 female age-matched raters (70 in total for all 17 targets), who were unacquainted with the social targets and who did not participate in the fMRI study, evaluated first the valence (from 1 *very negative* to 9 *very positive*) of each 10 s silent clip, and, subsequently, of each event description. There was good inter-rater agreement in valence ratings of both video and verbal event descriptions (Cronbach's alphas of .83 and .98, respectively). As expected, the female judges gave higher affect ratings to both the videos and the verbal descriptions associated with target-rated positive, rather than negative personal events (for target-rated positive events, mean rating of associated videos = 5.67 ± 1.10 and mean rating of associated verbal descriptions = 7.70 ± .78; for target-rated negative events, mean rating of associated videos = 4.70 ± .91 and mean rating of associated verbal descriptions = 2.71 ± 1.10). As such, across all 17 social targets, there was a significant positive correlation between the female judges' evaluations of the video and verbal description associated with a recalled event, $r(1014) = .40$, $p < .0001$.

2.3.1 fMRI Task Social Target Norming—As a manipulation check of our selected social targets, we conducted two regression analyses to verify that, in accordance with extant literature (e.g., Gross & John, 2003), the social targets' habitual use of expressive suppression would be linked to reduced nonverbal affective behavior clarity, but not emotionality of the events selected to be recounted. Results of these two analyses are described separately in the following sections.

2.3.1.1 Social target suppression use and nonverbal behavior clarity: In order to verify that the social target's expressive suppression use impacted the perceivers' evaluation of his behavior in our norming study, we conducted a multilevel regression analysis (HLM 7.01, Raudenbush, Bryk, & Congdon, 2013), predicting the perceivers' affect ratings of each of the collected nonverbal videos from the valence assigned to the video by the featured social target and the social target's expressive suppression use.

As mentioned above, videos associated with target-rated positive (relative to target-rated negative) received more positive affect ratings from perceivers, $b = .97$, $SE = .06$, $t(1001) =$

16.64, $p < .01$, but this effect was weaker in response to targets who reported greater suppression use, $b = -.21$, $SE = .08$, $t(1001) = -2.78$, $p < .01$ (see Figure 1). Thus, as expected, perceivers in the norming study provided less differentiated affect ratings in response to the nonverbal behavior of social targets who reported greater habitual use of expressive suppression. There was no statistical evidence that this effect was driven primarily by the perceivers' evaluation of either positive or negative videos (both *p*s > .30).

2.3.1.2 Social target suppression use and personal event selection: To verify that the observed effect in the nonverbal video ratings is not due to the selection of less emotional events by targets who tend to suppress their emotions, we conducted a second multilevel regression analysis, predicting the perceivers' affect ratings of each of the collected verbal event descriptions from the valence assigned to the event by the social target who experienced it and the social target's expressive suppression use. Although target-rated positive (relative to target-rated negative) event descriptions received more positive affect ratings from perceivers, $b = 4.99$, $SE = .06$, t(995[1]) = 84.76, $p < .01$, there was no evidence that this effect was moderated by the social target's use of expressive suppression, $b = -.004$, $SE = .07$, $t(995) = -.05$, $p = .96$, indicating that the high suppression targets did not tend to choose less emotional events to describe in their videos.

Taken together, the results of the norming study gave us confidence that consistent with existing behavioral findings (e.g., Gross & John, 2003), our social targets' habitual use of expressive suppression was a significant predictor of the clarity of their emotionally expressive behavior, but not of their willingness to recount more emotionally laden personal events.

2.4 Task Trial types

The fMRI task comprised congruent multimodal and unimodal (nonverbal video or text only) trials. On multimodal trials, perceivers saw a social target's silent video and the appropriate one-sentence description, provided by the respective target (on all trials, the normed valence of the individual video coincided with the normed valence of the individual caption, i.e., positive > 5, negative < 5). The unimodal nonverbal video trials comprised the silent videos from a male target, not featured on the multimodal trials. The unimodal text trials included the one-sentence event descriptions provided by the social target featured on the unimodal nonverbal video trials.

The fMRI task featured three distinct strangers: one who was pseudo-randomly selected from the mid-range scorers on expressive suppression and who appeared only on the unimodal video trials, and two others who were featured only in the multimodal trials. The two strangers who appeared on the multimodal trials were at the upper and lower end, respectively, of the expressive suppression continuum, as determined by their self-ratings on Gross and John's (2003) Emotion Regulation Questionnaire (the social targets' self-ratings were collected in a separate behavioural session, a year prior to their videotaping session).

[1]The degrees of freedom in this analysis is smaller than the one involving the nonverbal videos because 6 of the 1020 event descriptions, provided by the 17 targets, failed to be included in the norming study due to a programming error.

2.5 Task instructions and Procedure

For the multimodal trials, perceivers were informed that the one-sentence caption provided a summary of the event described by the target and were told to use both video and text to evaluate how the social target felt when he *recalled* the respective event. For unimodal trials, perceivers were told that the social target in the silent videos was describing emotional events from his past, whereas the sentences presented in isolation represented personal events from a male target's past (the latter's identity was not specified to the participants). The participants' task was to evaluate how the social target felt when he recalled the respective event.

The fMRI task comprised 8 conditions: (1) positive video+text, featuring the low suppression target; (2) negative video+text, featuring the low suppression target; (3) positive video+text, featuring the high suppression target, (4) negative video+text, featuring the high suppression target; (5) positive text only; (6) negative text only; (7) positive video only and (8) negative video only. The different trial types were presented in a balanced manner across 12 functional runs (which comprised other trial types, cf. Petrican et al., *in press*).

A trial began with a 5-s fixation cross, followed by the 12 s presentation of a multimodal video+text pair, text alone or silent video alone. After the stimulus terminated, the question "How did this person feel?" appeared on the projector screen together with a 9-point Likert type scale. Participants were allowed 6 s to make a key press response using a bilateral response box, which had eight response buttons. Buttons 1 to 4 were assigned in order to each of the four fingers (i.e., index to pinkie) of the right hand (1 assigned to the index and 4 assigned to the pinkie), whereas buttons 6 to 9 were assigned in order to each of the four fingers (i.e., index to pinkie) of the left hand (6 assigned to the index and 9 assigned to the pinkie). While in the scanner, but prior to starting the actual scanning, participants practised key pressing on the response box to ensure that they were able to use all the assigned fingers to make the desired response. For half of the participants, the rating scale ranged from 1, *very positive* to 9, *very negative*, whereas for the remaining half, the direction of the scale was reversed (5, *neutral* was not an available response option and participants were made aware of this in the practice session outside the scanner). We introduced this control because, as already mentioned, participants used a bilateral response box to rate the stimuli, and we wanted to avoid incidental laterality effects.

2.6 fMRI data acquisition and preprocessing

Images were obtained using a Siemens Trio 3T scanner (12-channel coil). Anatomical scans were acquired with a 3D MP-RAGE sequence (TR = 2 s, TE = 2.63 ms, FOV = 256 mm, 256 ×256 matrix, 1 mm isotropic voxels). Functional runs were acquired with an ep2d_pace sequence (162 volumes, TR = 2 s, TE = 30 ms, flip angle = 70°, FOV = 200 mm, 64 ×64 matrix, 30 interleaved slices of 3.12 × 3.12 mm in-plane resolution, 5 mm thick, no gap). We opted for an interleaved slice acquisition mode in order to minimize cross-talk between the slices. Because of the thickness and number of slices used, we were able to cover the whole without introducing any gap between slices. Pulse and respiration were measured during scanning. The scanning session comprised one high-resolution structural scan, followed by 12 functional task runs, each lasting 5:28 minutes.

Image preprocessing was performed with Analysis of Functional NeuroImages software (AFNI; Cox, 1996). The first three images in each run were discarded to allow the MR signal to reach steady-state equilibrium. Subsequent preprocessing consisted of correction for motion due to respiration and heart rate (Glover et al., 2000), slice timing correction, rigid-body motion correction, spatial normalization to the standard Montreal Neurological Institute (MNI)-152 template (resampling our data to 4 mm isotropic voxels), smoothing (full-width half-maximum, 8 mm), and regressing out white matter, ventricular and large blood vessel signal from each voxel time series (Grady et al., 2010).

2.7 fMRI Data Analysis

2.7.1 Whole-brain analyses—The preprocessed functional data were analyzed with partial least squares (i.e., PLS, Krishnan et al., 2011), a multivariate technique, similar to principal components analysis, that can identify whole-brain spatiotemporal patterns (latent variables; LVs) associated with different experimental conditions, either globally (task-PLS) or as a function of individual differences variables (behavioral PLS), as well as spatiotemporal patterns linked to correlated neuronal activity (seed PLS). In the present study, to test our hypotheses, we used behavioral and seed PLS analyses: a detailed description of the specific contrasts is provided in the Results section, in the section corresponding to each empirical question posed. An advantage of PLS is that the decomposition of the data matrix is performed in one analytic step, thereby circumventing the need for post-hoc correction of *p*-values due to multiple comparisons (McIntosh et al., 2004).

In all the reported analyses, the significance of each LV was determined using a permutation test with 5000 permutations (McIntosh & Lobaugh, 2004). In PLS, each brain voxel is assigned a weight, which reflects the respective voxel's contribution to a specific LV. The reliability of each voxel's contribution to a particular LV was thus tested by submitting all voxel weights to a bootstrap estimation (1000 bootstraps) of the standard errors (SEs, Efron, 1981). We opted to use 5000 permutations and 1000 bootstrap samples in order to increase the stability of the reported results (these parameters are 10 times greater than the standard ones recommended by McIntosh and Lobaugh [2004] for use in PLS analyses of neuroimaging data). Clusters of activity were identified using a weight/SE ratio ≥ 3 (the bootstrap ratio, or BSR, $p < 0.003$). For all PLS analyses, we report activity clusters containing at least 60 above-threshold adjacent voxels. The spatial extent threshold was determined employing AFNI's AlphaSim program (Cox, 1996), using 10,000 Monte Carlo simulations of whole brain data with the same scanning parameters as the present study in order to produce a Type I error probability lower than .0001. All PLS analyses focused on neural activity during the first 5 TRs (10 s) of each trial while participants were viewing the video and/or text.

2.7.2 HLM—Complementing our whole-brain PLS analyses, we also used one-level multivariate HLM analyses (HLM 7.01, Raudenbush et al., 2013) to test our predictions regarding the role of cognitive control and reward value/self-relevance in nonverbal cue processing (see Questions 2 and 3 below). For these analyses, we report the estimates obtained from the homogenous level-1 variance output. In these analyses, the expressive suppression scores were introduced as level-1 predictors of the association between the scrutinized brain variables.

3. Results

3.1 Question #1: Does the perceiver's habitual use of expressive suppression predict preferential neural processing of nonverbal (rather than verbal) emotional cues?

To test this hypothesis, we conducted a behavioural PLS analysis, comparing the brain activity patterns observed on the unimodal positive and negative video and text trials, respectively, with those observed on the positive and negative multimodal trials, as a function of perceiver suppression use. Our goal was to elucidate whether on multimodal trials, perceivers who reported greater suppression use would show whole-brain activity patterns that would be more similar to those observed on unimodal video, rather than text, trials. Such a pattern of results would imply that on video + text trials, perceivers who tend to suppress their emotions show neural markers indicative of greater processing of the information presented in the video, rather than the accompanying text. Because an initial behavioral PLS analysis had revealed no significant differences in the brain activity patterns evoked by the low versus high suppression target, we combined data from the two targets for the positive and negative multimodal trials, respectively.

Results of the behavioral-PLS analysis revealed only one significant LV ($p < .021$), which accounted for 19.64 % of the total variance in the data and distinguished activity on the unimodal text trials from activity on the unimodal video and multimodal trials as a function of the perceivers' expressive suppression scores (see Table 1 and Figure 2). Thus, in line with our hypotheses, on video + text trials, perceivers who reported greater use of expressive suppression showed whole-brain activity patterns that were similar to those observed on unimodal video trials, and different from the pattern seen for text trials. These results provide neural evidence consistent with the conjecture that, when presented with both nonverbal and verbal cues, perceivers who suppress their emotions attend preferentially to nonverbal behavioral information. Greater processing of nonverbal cues, demonstrated by higher expressive suppression perceivers on multimodal trials, was associated with greater activity in the insula, dACC, putamen and the posterior cingulate cortex. In contrast, greater processing of verbal cues, among perceivers who tend to suppress their emotions, was linked to greater activity in the angular gyrus (for a full list of regions and coordinates, see Table 1).

The remaining two questions focused exclusively on the two multimodal conditions, in which the behavioral-PLS analysis provided neural evidence consistent with our hypothesis that higher suppression perceivers would attend preferentially to nonverbal (rather than verbal) emotional information. For both questions, the behavioral PLS brain scores for the positive and negative multimodal conditions were used as indices of preferential neural processing of nonverbal, rather than verbal, cues, with higher values reflecting greater neural processing of nonverbal cues.

3.2 Question #2: Does the suppressors' preferential processing of nonverbal cues depend upon cognitive control resources?

To address this question, we conducted two sets of analyses. First, we ran a seed PLS analysis to identify the components of the frontoparietal network (FPC), which is assumed to play a key role in supporting optimal cognitive performance by virtue of its flexible functional coupling with task-relevant regions (Cole et al., 2013; Spreng et al., 2010). We opted to run the seed PLS analysis in the two multimodal conditions (rather than all six conditions) because we reasoned that due to their multimodal nature, these conditions would recruit the FPC more extensively, and hence using the FPC metrics from these conditions would provide a more accurate estimate of the cognitive control resources recruited in the service of preferential processing of nonverbal, rather than verbal, information. Second, we conducted a multivariate HLM analysis to test whether the neural pattern associated with nonverbal cue processing is associated with greater engagement of the frontoparietal network and whether this link between FPC and neural activity patterns typifying nonverbal cue processing is even stronger among perceivers who habitually engage in expressive suppression. In these multivariate HLM analyses, the value of the behavioral or FPC seed PLS brain scores corresponding to the multimodal positive condition represented indicator 1, whereas the value of the behavioral or seed PLS brain scores corresponding to the multimodal negative condition represented indicator 2.

3.2.1 Seed PLS—To identify the frontoparietal network, we used an IPL seed (MNI coordinates: 48–52 44), because, of all the FPC component regions, this region has been found most consistently to show a clearly differentiated functional connectivity pattern (see Spreng et al., 2013; Nelson et al., 2010). The seed coordinates were averages derived from published studies (Andrews-Hanna et al., 2007; Campbell, Grady, Ng, & Hasher, 2012; Fox et al., 2006; Grady et al., 2010; Grady, Grigg, & Ng, 2013; Spreng et al., 2010, 2013; Vincent et al., 2008). Thus, to assess the IPL seed's functional connectivity in the two multimodal conditions, its activity was correlated with activity in all the other brain voxels, across participants (McIntosh, 1999). The analysis revealed a significant connectivity pattern ($p < .002$), consistent with the FPC (see Table 2 and Figure 3), which accounted for 67.52 % of the total variance in the data and was reliable in both multimodal conditions. The brain scores from this seed PLS analysis were used in the subsequent HLM analysis, since greater positive FPC brain scores reflected greater joint recruitment of the FPC network component regions.

3.2.2 HLM—As predicted, greater FPC engagement predicted the pattern of greater nonverbal cue processing, most strongly evidenced by higher suppression perceivers, $b = .23$, $SE = .07$, $t(25) = 3.09$, $p < .01$ (see regression 1 in Table 3), thereby implying that preferential processing of nonverbal information is implemented in a cognitively controlled manner. Moreover, there was suggestive evidence that the link between greater FPC recruitment and greater neural processing of nonverbal information is even more pronounced among perceivers who reported greater suppression use, $b = .14$, $SE = .07$, $t(25) = 1.89$, $p = .07$ (see regression 1 in Table 3), in line with our prediction that suppressors may invest greater cognitive resources towards preferential processing of nonverbal cues.

3.3 Question #3: Is the suppressors' increased processing of nonverbal cues particularly self-relevant and, thus, predictive of greater engagement of the reward-related regions?

To test whether preferential processing of nonverbal (rather than verbal) cues predicts greater recruitment of neural reward centers, we averaged the mean percent signal change in left and right VS regions in the positive and negative multimodal condition, respectively. We used the coordinates of the left and right VS regions (MNI coordinates -20 12 -4 and 20 12 -8, respectively), found by Grady et al., (2012) to be more strongly recruited by self-relevant (relative to self-irrelevant) tasks. As expected, activity in the two seeds was significantly positively correlated, $r(13) = .72$, $p < .01$, across all participants. Please note that the coordinates of the left and right VS regions are distinct from the coordinates of the insula/putamen region from the behavioral PLS analysis that was recruited by higher suppression individuals in response to unimodal video cues and video + text cues.

We subsequently conducted a multivariate HLM analysis predicting the averaged mean percent signal change in the VS from the behavioral PLS brain scores in the positive and negative multimodal condition, respectively, as a function of the perceivers' expressive suppression scores. In these analyses, the value of the behavioral PLS brain scores and mean VS activity corresponding to the multimodal positive condition represented indicator 1, whereas the value of the behavioral PLS brain scores and mean VS activity corresponding to the multimodal negative condition represented indicator 2. The mean activity level in the VS was used as the outcome variable because we hypothesized that in the two multimodal conditions, it is greater neural processing of non-verbal cues (as revealed by the behavioral PLS brain scores) that is associated with differential reward value/personal significance among higher (versus lower) expressive suppression perceivers and is thus predictive of VS engagement. Results of this analysis supported our hypothesis, since among perceivers who reported greater expressive suppression use, greater neural processing of nonverbal cues predicted greater mean activity levels in the VS, $b = .007$, $SE = .003$, $t(25) = 2.80$, $p = .01$ (see regression 2 in Table 3).

4. Discussion

Individuals who habitually engage in expressive suppression reportedly reside in a rather impoverished affective environment, which is due not only to their own muted affective expression, but also to the apparently inhibitory effect that their own restricted emotional behavior exerts over those who interact with them (Butler et al., 2014). Nevertheless, expressive suppression is not known to lead to clinical impairments in social functioning. Consequently, in the present study, we set out to test the hypothesis that this may be partly due to the fact that individuals who report greater use of expressive suppression as an emotion regulation strategy develop compensatory mechanisms that would render them more sensitive to behavioral displays of emotion and, thus, enable them to cope with their interlocutors' restrained affectively expressive behavior.

As predicted, during a task that featured congruent nonverbal and verbal emotional cues, individuals who reported greater habitual engagement in expressive suppression demonstrated neural activity patterns suggestive of preferential processing of nonverbal (rather than verbal) emotional cues in the multimodal trials. Specifically, suppressors' greater processing of nonverbal cues was linked to increased activity in brain areas underlying interoceptive awareness and resonance with the visceral states of others (i.e., insula, dACC, cf. Giuliani et al., 2011; Zaki & Ochsner, 2012), affective responses to both positive and negative stimuli (i.e., putamen, cf. Philips et al., 2003; Surguladze et al., 2005), as well as areas involved in judging one's own emotions, as well as the emotions of others based on visual stimuli (i.e., posterior cingulate cortex, Ochsner et al., 2004; Zaki et al., 2010). Of note, as predicted, we also found evidence that the neural pattern of increased nonverbal cue processing, most strongly expressed among suppressors, is coordinated via frontoparietal cognitive control areas. Thus, because preferential neural processing of nonverbal cues was linked to recruitment of neural networks involved in cognitive control, particularly among suppressors, this effect may provide an explanation for the suppressors' reduced processing of emotion-unrelated information (Richardson et al., 2003; Richardson & Gross, 2006). Finally, we also gathered evidence suggestive of the potential neural mechanisms that may help perpetuate habitual use of expressive suppression despite its adverse socioemotional consequences (English & John, 2013; English, John, & Gross, 2013; Gross & John, 2003; Srivastava et al., 2009). Consistent with previous findings of increased VS recruitment in response to personally significant stimuli (Grady et al., 2012), we found that with increasing perceiver scores on expressive suppression, greater neural processing of nonverbal cues triggered greater VS activity, arguably reflecting the increased reward value/ personal significance of nonverbal cues among suppressors.

The present findings carry several significant implications for research on the neuro-affective processing patterns exhibited by individuals who habitually restrain their emotionally expressive behaviors, as well as on the determinants of chronic engagement in expressive suppression. First, the findings shed some light on the larger-scale neural circuitry recruited by suppressors in response to nonverbal affective cues and, as such, suggest venues of future inquiry with regards to the patterns of socio-emotional responding that typify individuals who tend to suppress their emotions. Indeed, the regions recruited by suppressors in response to nonverbal cues appear to be aligned with two larger scale networks: the salience network (SN) (i.e., insula, putamen, dACC, Seeley et al., 2007) and the default mode (DMN) core subsystem (i.e.., PCC). The SN is presumably recruited in response to sensory information that is associated with potent internal state (e.g., autonomic, visceral, hedonic) markers and is thus particularly relevant to the experiencer (Seeley et al., 2007). In the context of our study, suppressors' recruitment of SN regions in response to nonverbal affective cues is consistent with the interpretation that habitual expressive suppression use enhances the salience not only of *one's own* internal states (cf. Giuliani et al., 2011), but also of the nonverbal affective behavior of *other* social actors.

Complementarily, suppressors' recruitment of one of the two DMN core subsystem components, uniquely involved in self-referential processing (Andrews-Hanna et al., 2010), in response to nonverbal cues opens potential explanations for the link between expressive suppression and mood disorders (cf. Aldao et al., 2010). Specifically, in our study, the unimodal video and multimodal video + text trials constitute the closest approximation of real-life social situations. The observed pattern of increased DMN core subsystem recruitment, demonstrated by suppressors on these trials, raise the possibility that in real life, interpersonal encounters may trigger among suppressors the pattern of self-referential ruminative thinking that has been linked to both depression and anxiety-related disorders (Nolen-Hoeksema, 2000). Future studies that would include assessments of ruminative thinking and habitual expressive suppression use as well as recording of brain activity during social interactions are needed to shed light on whether social situations constitute a core domain underlying the link between habitual expressive suppression use and mood-related psychopathology (Aldao et al., 2010).

It is worth noting that recruitment of both SN and DMN core subsystem regions in response to unimodal nonverbal and multimodal cues was linked to recruitment of cognitive control areas in the FPC, implying that both sensitivity to emotional arousal cues and self-referential processing are implemented in a goal-directed manner. These findings raise the possibility that exposure to social situations may evoke self-other comparison processes among suppressors, in which other social actors' inner states, as implied through their nonverbal behaviors, are compared against self-related standards of appropriate emotion experience and expression. The fact that co-recruitment of FPC, SN and core DMN areas was linked to activity in the VS further implies the personal relevance of the aforementioned self-other comparison processes among suppressors. More broadly, this pattern of results underscores the importance of identifying family environments and peer relationships that may reinforce strict standards of appropriate emotion experience and expression rather than encouraging acknowledgment of the unadulterated emotional experience. Longitudinal studies assessing characteristics of one's social environment, together with neurobehavioral responses and evaluations of self-relevance for stimuli varying along the external/expressive versus the internal/experiential axes, are needed to shed light on these issues.

Our results also carry significant implications for behavioral research on the link between expressive suppression and affect processing. Specifically, our finding that preferential use of expressive suppression as an emotion regulation strategy is linked to neural markers of preferential processing of nonverbal affective cues ought to be integrated with recent reports on the adverse effects of instructed expressive suppression on emotion recognition accuracy (Schneider, Hempel, & Lynch, 2013). If chronic use of expressive suppression has similar adverse effects on affective cue labeling, then it would imply that individuals who habitually suppress their emotions may find themselves in a very challenging position in social circumstances. Specifically, they may be particularly sensitive to the underlying emotional arousal (as implied by our observed neural activity patterns), but unable to label it with the "correct" emotion category and, thus, less likely to enact an appropriate response. Interestingly, our present findings point to a potential mechanism that could account for the suppressors' affect labeling difficulties. To the extent that their cognitive resources are invested in processing the emotional arousal-relevant nonverbal cues displayed by another during an affective episode, they may be left with too few resources to process the diagnostic emotion category information required for affect labeling. It is further plausible that the ensuing cognitive depletion/overload may explain why suppressors are perceived as distracted and less responsive during affectively laden social interactions (Butler et al., 2003, 2014). To test the viability of our hypotheses, future studies are needed to probe the effect of chronic expressive suppression use on emotion recognition, as well as the potential joint roles of available cognitive control resources and heightened sensitivity to arousal-related versus emotion category-related nonverbal cues in the link between expressive suppression and poor socioemotional functioning.

Interestingly, Schneider and colleagues' (2013) aforementioned findings on the adverse effects of instructed expressive suppression for affect recognition offer an alternative interpretation. Specifically, the Schneider et al. study included only younger adults, whereas ours focused on older adults. Thus, instead of a discrepancy between responsiveness to emotional arousal and affect recognition as a function of expressive suppression use (as we implied above), there may be an age-related effect on the link between suppression use and nonverbal affective cue processing skills (perhaps both sensitive to emotional arousal and affect recognition). Thus, whereas in younger adulthood habitual expressive suppression use is linked to poorer emotion processing skills, the opposite effect emerges in later adulthood (as implied by the results of our behavioral PLS analysis showing a link between suppression use and greater neural processing of nonverbal cues on multimodal trials). This may be because, over the lifespan, people who suppress their emotions tend to compensate for the impoverished interpersonal climate created by their own expressive habits (cf. Butler et al., 2014). In light of our finding that suppressors' increased neural processing of nonverbal affective cues is linked to the recruitment of cognitive control areas, it is possible that in older adulthood, habitual expressive suppression use may be a risk factor for exacerbating the already well-documented age-related deficits on cognitive task performance (Craik & Salthouse, 2007). Future research is needed to test this hypothesis.

Promising as they may be, our present findings warrant additional empirical probing. First, because our sample included only elderly female participants, future studies need to verify that our findings generalize to males, as well as to younger individuals of either gender. Second, our research has a correlational design, which precludes any strong causal claims regarding the reported effects. Future studies incorporating a manipulation of the emotion regulation strategy used (e.g., expressive suppression vs. reappraisal) and of the perceived personal relevance of expressive aspects of emotional responses, as well as assessment of the associated brain activity patterns, may elucidate the causal direction of the effects we reported. Third, to test our hypotheses regarding the influence of expressive suppression on the processing of nonverbal emotional cues, we focused on brain activity patterns recorded during a social cognition task, which presented simultaneously congruent nonverbal and verbal cues. We reasoned that such a task would be appropriate for detecting any biases towards attending preferentially to the nonverbal affective cues, rather than the verbal contextual information. Nevertheless, additional research is warranted to evaluate the generalizability of our findings across a wider range of tasks.

Notwithstanding these potential limitations, our present study provided compelling and novel evidence indicating that individuals who habitually engage in expressive suppression demonstrate neural activity patterns suggestive of greater processing to nonverbal (rather than verbal) emotional stimuli. Importantly, this effect appears to be dependent upon cognitive control resources, a link that may explain the previously documented cognitive effects seen in suppressors in social situations. Finally, we also have identified a potential neural mechanism that may account for the development and perpetuation of habitual expressive suppression use and may prove useful in designing potential interventions to alleviate the maladaptive consequences of restraining one's emotionally expressive behaviors.

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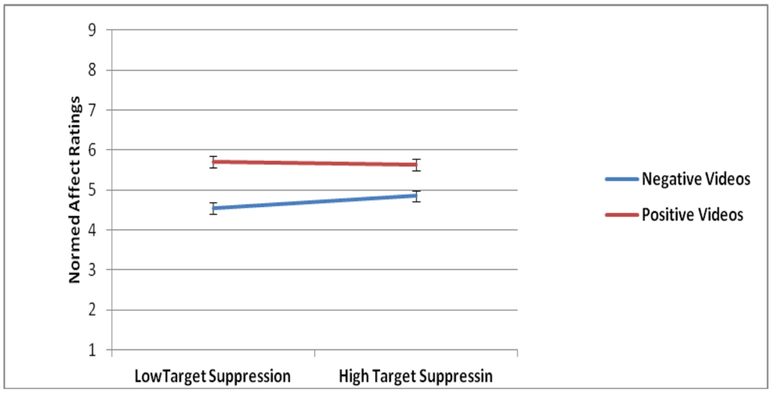

Figure 1.
The relationship between the social target's expressive suppression use and the normed affect ratings of his negative and positive silent videos obtained in the validation study that preceded the fMRI session.

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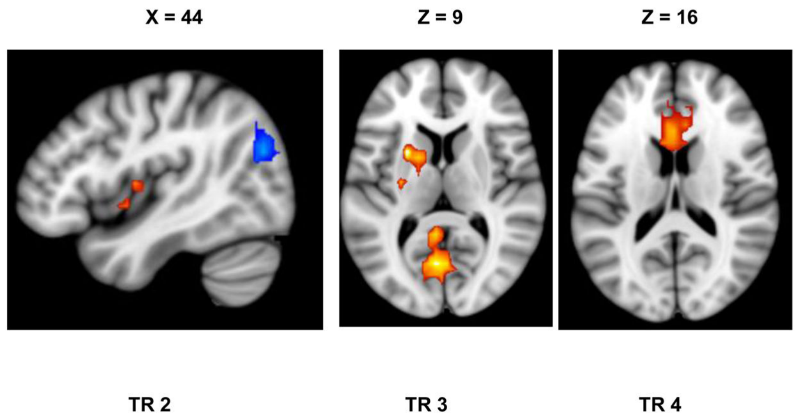
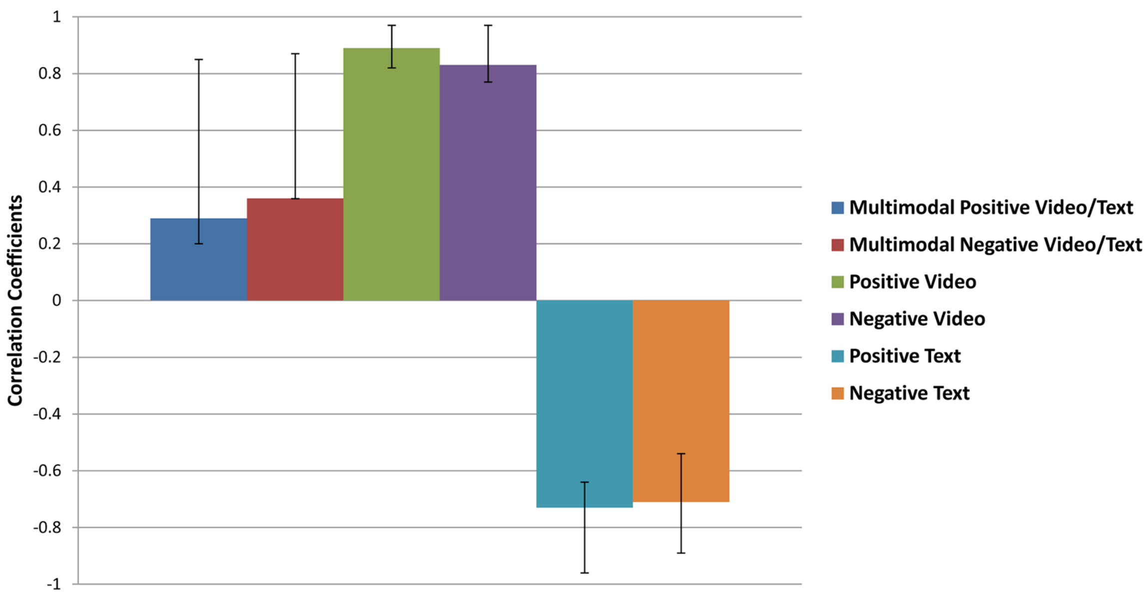


(a)



(b)

Figure 2.

Results of the behavioral-PLS analysis are shown on slices from the MNI152 average structural brain. In the brain images, presented in Panel (a), greater activity in regions shown in warm-colored areas is seen in the two multimodal conditions and the two video only conditions, whereas greater activity in cool-colored areas is seen in the two text only conditions. Table 1 lists the regions pictured in panel (a) and their respective coordinates. The graph in panel (b) shows the correlations between brain scores and perceiver expressive suppression use score for each condition. Error bars are the 95% CIs from the bootstrap procedure.

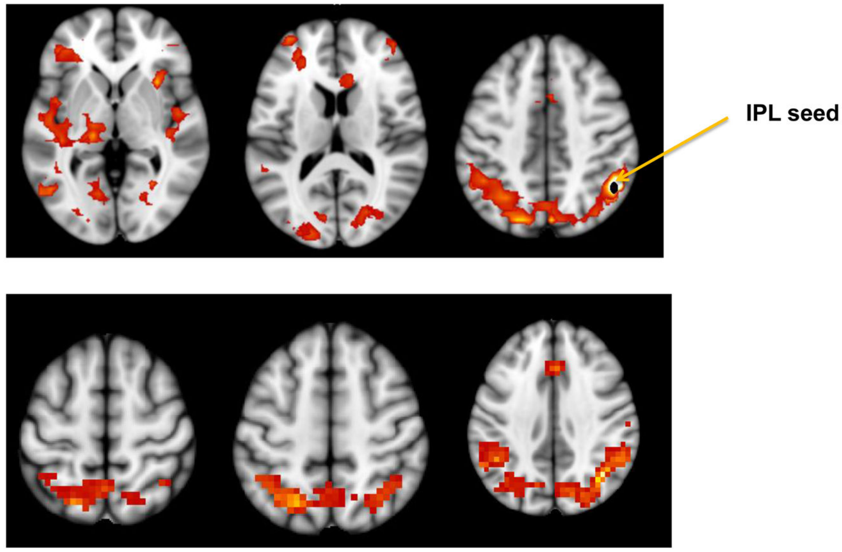


Figure 3.

Regions showing significant positive activations (BSR [Bootstrap ratio] > 3, *p* < .003) with the IPL seed across all 4 TRs are shown on slices from the MNI152 average structural brain. The list of canonical FPC regions and their coordinates appear in Table 2.

Table 1

Brain activity associated with unimodal video trials, unimodal text trials, as well as multimodal trials as a function of perceiver expressive suppression use.

Region	MNI coordinates			BSR	TR	Cluster size (voxels)
	x	y	z			
LV1 (behavioral-PLS): *Multimodal & Video only > Text only*						
R insula	44	−4	8	5.91	2	73
L putamen/insula	−24	8	8	7.27	3	153
L Posterior cingulate cortex	−4	−72	12	5.90	3	234
Anterior cingulate cortex (M)	0	24	16	6.61	4	96
LV1 (behavioral-PLS): *Text only > Multimodal & Video only*						
R angular gyrus	48	−72	28	6.95	2	78

Note. L = left. R = right. M =middle. BSR = bootstrap ratio. TR = time point in the trial where activity was maximal.

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Table 2

Clusters of Activity Observed in the Canonical FPC regions in the IPL-based Seed PLS Analysis

Region	MNI coordinates			BSR	TR	Cluster size (voxels)
	x	y	z			
L Precuneus	−12	−76	20	7.62	2	74
R Precuneus	24	−76	16	7.30	2	124
R Insula	32	16	0	9.23	3	74
R Anterior cingulate cortex	8	28	20	7.68	3	85
L Supramarginal gyrus/Inferior parietal lobe	−44	−48	40	10.62	4	151
R Insula	40	−24	4	9.74	4	62
L Middle frontal gyrus	−36	56	16	7.54	4	73
R Middle frontal gyrus	40	32	−12	8.47	5	90
R Precuneus	4	−76	44	10.15	5	287
L Anterior cingulate cortex	−24	28	20	7.43	5	66

Note. L = left. R = right. M =middle. BSR = bootstrap ratio. TR = time point in the trial where activity was maximal. Listed are the largest spatial extent clusters of activity in the canonical FPC regions. All the FPC regions that contained activity clusters ≥ 60 voxels at a BSR ≥ 3 are pictured in Figure 3.

Table 3

Multivariate HLM Regression Analyses Describing the Interrelationships among the Nonverbal Processing Brain Areas, FPC and VS

Fixed Effect	Coefficient	Standard Error	*t*-value (dfs)
1. Outcome: Nonverbal Processing Behavioral PLS LV Brain Scores			
For overall INTERCEPT, β_0			
INTERCEPT, β_{00}	−3.83	1.39	−2.76 (13) *
For FPC Brain Scores SLOPE, β_1			
INTERCEPT, β_{10}	.23	.07	3.09 (25) **
Expressive Suppression SLOPE, β_{11}	.14	.07	1.89 (25)
2. Outcome: VS seed mean activity			
For overall INTERCEPT, β_0			
INTERCEPT, β_{00}	-.04	.02	−2.59 (13) *
For Nonverbal Processing Behavioral PLS LV Brain Scores SLOPE, β_1			
INTERCEPT, β_{10}	.003	.003	1.09 (25)
Expressive Suppression SLOPE, β_{11}	.007	.003	2.80 (25) **

Note.

* $p < .05$.,

** $p < .01$.