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Neural activity patterns evoked by a spouse's incongruent emotional reactions when recalling marriage-relevant experiences

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Abstract

Resonance with the inner states of another social actor is regarded as a hallmark of emotional closeness. Nevertheless, sensitivity to potential incongruities between one's own and an intimate partner's subjective experience is reportedly also important for close relationship quality. Here, we tested whether perceivers show greater neurobehavioural responsiveness to a spouse's positive (rather than negative) context-incongruent emotions, and whether this effect is influenced by the perceiver's satisfaction with the relationship. Thus, we used fMRI to scan older long-term married female perceivers while they judged either their spouse's or a stranger's affect, based on incongruent nonverbal and verbal cues. The verbal cues were selected to evoke strongly polarized affective responses. Higher perceiver marital satisfaction predicted greater neural processing of the spouse's (rather than the strangers) nonverbal cues. Nevertheless, across all perceivers, greater neural processing of a spouse's (rather than a stranger's) nonverbal behavior was reliably observed only when the behavior was positive and the context was negative. The spouse's positive (rather than negative) nonverbal behaviour evoked greater activity in putative mirror neuron areas, such as the bilateral IPL. This effect was related to a stronger inhibitory influence of cognitive control areas on mirror system activity in response to a spouse's negative nonverbal cues, an effect that strengthened with increasing perceiver marital satisfaction. Our valence-asymmetric findings imply that neurobehavioral responsiveness to a close other's emotions may depend, at least partly, on cognitive control resources, which are used to support the perceiver's interpersonal goals (here, goals that are relevant to relationship stability).

Keywords

social-cognitive conflict; emotion; married couples

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The affective states of others have the power to permeate our own, particularly if we share a personal connection with the experiencer, whether s/he is a romantic partner (Anders et al., 2011; Cheng et al., 2010; Singer et al., 2004), a friend (Beckes, Coan, & Hasselmo, 2012; Beeney, Franklin, Levy, & Adams, 2011) or merely a member of our social or ethnic group (Azevedo et al., 2013; Gutsell & Inzlicht, 2012; Xu, Zuo, Wang, & Han, 2009). Importantly, it is this ability to "feel what they are feeling", or affective resonance, that allows us to better understand them (Levenson & Ruef, 1992), motivates us to act prosocially (Hein et al., 2013), and, thus, paves the way to smoother interpersonal coordination (Engen & Singer, 2012).

The neural underpinnings of affective resonance processes, triggered by the mere exposure to a social actor's nonverbal behavior, have been investigated extensively. These processes are thought to be supported by the putative mirror neuron system (Zaki & Ochsner 2012), which comprises premotor, inferior frontal gyrus [IFG] (Carr et al., 2003; Pfeiffer et al., 2008) and inferior parietal regions (Adolphs et al., 2000; Zaki et al., 2010), together with areas involved in visceral state resonance (anterior insula [AI], dorsal anterior cingulate cortex [dACC]; for a review, see Zaki & Ochsner, 2012).

Our understanding of how perceivers may experience another social actor's emotions has been based on paradigms in which affectively laden nonverbal behaviors were presented either in isolation or in a congruent context (e.g., a target receives painful stimulation and his/her nonverbal behavior is indicative of pain) (see Beckes et al., 2012; Beeney et al., 2011; Singer et al., 2004). Consequently, it is still poorly understood how perceivers may respond to the nonverbal behavior of a social target when the behaviour is incongruent with the context in which it occurs. Recent social perception studies have documented the critical function of cognitive control areas in solving the conflict among incompatible social cues (Hehman, Ingbretsen, & Freeman, 2014; Mende-Siedlecki, Baron, & Todorov, 2013) by biasing activity toward downstream, more domain-specific systems, involved in responding to the social cue deemed to be most task-relevant (Zaki, Weber, Bolger, & Ochsner, 2009).

Although existing work has focused on responses to a stranger's context-incongruent behaviors, evidence is accruing that perceivers' processing of discrepant social cues is critically determined by their relationship with the scrutinized social target. For example, in a study with minimally acquainted perceiver-social target dyads, the degree to which perceivers attended to a social target's context-unexpected behaviors was dependent on the social target's potential to influence their chances of obtaining a monetary reward (Ames & Fiske, 2013).

Interestingly, evidence that a social target's personal relevance can influence perceivers' processing of dissonant social cues is consistent with findings from the close relationship research, which underscore the beneficial interpersonal consequences of being sensitive to potential incongruities between one's own and an intimate partner's subjective experience. For example, in a study involving memory for shared positive events among long-term elderly married spouses, those who reported greater overlap between their own and their partner's subjective states were perceived to be more controlling in the marriage, which in turn predicted lower relationship satisfaction in the perceiving partner (Petrican, Burris, Bielak, Schimmack, & Moscovitch, 2011). The authors proposed that the observed maladaptive relational consequences are due to the fact that perceptions of greater overlap, and, thus, reduced sensitivity to subtle incongruities between one's own and a partner's internal states, may be indicative of a reduced ability to differentiate one's own subjective experience from that of their partner. The clinical literature suggests that this reduced ability to differentiate self from a close other tends to be associated with a host of overly solicitous, controlling, smothering behaviors (Green & Werner, 1996) that may be regarded by the receiving partner as a threat to his/her autonomy and, thus, lead to lower satisfaction with the relationship.

This earlier study focused on the adverse relational implications of reduced sensitivity to subtle incongruities between one's own and a spouse's predominantly positive emotions during shared positive personal events. Therefore, the respective research could not illuminate the potential relational implications linked to receptivity towards an intimate partner's negative internal states, when they are distinct from one's own. The latter question is of particular significance in light of a sizeable literature on social support provision, which documents the divergent interpersonal consequences of responsiveness to an intimate partner's disclosure of positive versus negative personal events. Indeed, responsiveness to an intimate partner's disclosure of a positive personal event promotes relational health and is foundational to the partner's perceptions of being supported in the relationship (Gable, Gonzaga, & Strachman, 2006; Gable, Gosnell, Maisel, & Strachman, 2012). In contrast, responsiveness to an intimate partner's disclosure of a negative personal event appears to contribute only weakly to the partner's perceptions of emotional support in the relationship (e.g., Haber et al., 2007) and is only sparsely associated with favorable outcomes, being occasionally even linked to adverse consequences (e.g., Collins et al., 1993; Bolger et al., 2000; Kaul and Lakey, 2003). The paradoxically mixed relational consequences of responding supportively to a partner's disclosure of a negative event are presumably rooted in their potential to augment the partner's emotional turmoil by indirectly underscoring his/her inability to cope with the stressor and thus highlighting feelings of indebtedness to the support provider (Bolger et al., 2000; Gleason et al., 2003; Shrout et al., 2006).

The findings of the social support literature reviewed above thus point to the key role of responsiveness to a partner's positive emotions in fostering stable and fulfilling close relationships. In light of the results reported by Petrican et al. (2011), they further raise the possibility that receptivity to incongruities between one's own and a partner's subjective experience may have particularly beneficial relational implications when acknowledging a partner's unique experience of positive, rather than negative, emotions. If this line of reasoning were true, then it would imply that intimates in happy, stable relationships would be likely to show increased responsiveness to their partner's positive, rather than negative, emotions, even when they are distinct from one's own feelings.

To probe this issue, we focused on a sample of long-term married elderly perceivers, who reported moderately high to very high relationship satisfaction (see Method below). We opted to do so in light of existing evidence that older adults tend to focus on maximizing their emotional well-being (for a review, see Mather & Carstensen, 2005) and that close relationships constitute a very important source of affective fulfillment in later adulthood

(Charles & Carstensen, 2003). Consequently, we reasoned that an elderly, overall happily married sample would be particularly likely to be focused on maintaining the quality of their relationship and, thus, if our reasoning were correct, would be most likely to evidence the hypothesized pattern of relationship-promoting responding to their spouse's affective behaviors. 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 predicted effects.

Our aim was to investigate behavioral and brain responses to the context-incongruent positive versus negative emotional behavior of the perceivers' spouse. As a baseline, we examined neurobehavioral responses evoked by a stranger, age-matched to the perceiver's spouse. Prior research suggests that individual differences in the use of specific emotion regulation strategies impact the ability of others to interpret a person's nonverbal behavior (Gross & John, 2003). Specifically, individuals who tend to control their emotions by suppressing them demonstrate more muted nonverbal affective behaviors. Consequently, to control for any differences in emotional behavior clarity, perceivers were presented with a stranger, matched not only on age, but also on expressive suppression use with their spouse.

We thus used fMRI to scan older long-term married, female perceivers as they completed a modified version of Zaki et al.'s (2010) task, which juxtaposes a silent video and a verbal description, which evokes affect either similar or opposite in valence to that expressed by the target in the video. In our adaptation of the task, perceivers viewed either their spouse, or a matched stranger, describing marriage-relevant emotional events.

As in Zaki et al.'s study, our verbal descriptions were selected to elicit polarized affective reactions. Moreover, in the case of the spouse being the target, most of the events were expected to be highly familiar and associated with strong emotional responses among perceivers (see Petrican et al., 2011, who, using a demographically similar sample, obtained memory reports from both spouses on a similar range of events; for event examples, see Supplemental Note 1). Consequently, because the verbal labels were clearer than the nonverbal cues in suggesting the social target's affect, we expected that perceivers' affect evaluations would show greater overall reliance on the verbal label, rather than the silent videos (for similar results with younger adults viewing strangers, see Zaki et al., 2010). Nevertheless, we were interested in whether the identity of the social target and the valence of his nonverbal behavior would impact perceivers' behavioral reliance on the verbal event descriptions. Specifically, in light of extant evidence on the greater relational benefits associated with responsiveness to a partner's positive, rather than negative, emotions during disclosure of personal events (Gable et al., 2006, 2012), we tested whether on incongruent trials featuring the spouse, perceivers would show weaker reliance on the verbal event descriptions when their spouse's behavior was positive rather than negative. Such an effect would be consistent with our hypothesis that perceivers may be more sensitive to incongruities between their own and a partner's emotions, when the latter are positive. Because this effect was assumed to be a manifestation of the perceivers' chronic relationship-promoting efforts (i.e., triggered even when the partner was not physically present to see the perceivers' reactions), we did not expect to observe it in response to a videotaped stranger.

Dovetailing our behavioral predictions, we hypothesized that the identity of the social target and the valence of his nonverbal behavior would also impact perceivers' neural responses while watching the incongruent video-text pairs. Specifically, there is evidence that perceivers show greater neural processing of the context-incongruent behavior produced by personally relevant social targets (Ames & Fiske, 2013). Consequently, we hypothesized that our long-term married perceivers would evidence greater neural processing of their spouse's (compared to the stranger's) context-incongruent non-verbal behaviour. In light of prior findings on the greater relational benefits associated with responsiveness to a significant other's positive, rather than negative, event disclosures (Gable et al., 2006, 2012), we reasoned that our hypothesized effect would be stronger on incongruent trials during which the nonverbal behavior was positive rather than negative. We predicted that greater neural responsiveness to a spouse's positive, rather than negative, emotions would be detected in areas of the putative mirror neuron system, involved in the processing of nonverbal affective cues (cf. Zaki & Ochsner, 2012). We further assumed that such valence-specific neural processing patterns serve a relationship-promoting function (cf. Gable et al., 2006, 2012) and would thus implemented in a top-down manner via cognitive control centers that guide behaviour under emotionally conflicting circumstances (cf. Zaki et al., 2010). Finally, because the differential behavioral and neural effects hypothesized to emerge in response to the spouse versus the stranger were predicated on the perceiver's motivation to maintain their marriage, we also predicted that these effects would become stronger with increasing perceiver marital satisfaction.

To test the hypothesized effects of target identity and nonverbal cue valence on whole-brain activity patterns, 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 (task PLS), or patterns that vary as a function of individual differences variables (behavioral PLS). We thus used task PLS to investigate whether on incongruent trials, perceivers would evidence whole-brain activity patterns suggestive of greater processing of their spouse's (rather than the stranger's) nonverbal behavior and whether this effect would be stronger on positive video-negative text trials. We further used behavioral-PLS to test whether the perceiver's marital satisfaction would impact the brain activity patterns, identified with the task PLS. Based on extant evidence that, in affectively congruent contexts, the emotions of personally significant social targets are more likely to evoke spontaneous activity in the putative mirror neuron system (Beckes et al., 2012; Beeney et al., 2011; Singer et al., 2004), we also reasoned that the behavioral PLS would identify the mirror neuron regions, recruited in response to the spouse as a function of his increasing positive emotional significance as reflected in the perceiver's greater satisfaction with the marriage.

To test whether activity in cognitive control areas would predict perceivers' greater neural responsiveness to their spouse's positive rather than negative emotions, specifically, we focused on the mirror neuron areas identified through the behavioral PLS. We thus first probed whether those mirror neuron system components with the greatest susceptibility to the perceiver's pro-relationship motivation, would show greater recruitment in response to a spouse's positive nonverbal behavior. Subsequently, we tested whether, in response to a spouse's positive nonverbal cues, mean activity levels in cognitive control areas in the PFC would be more strongly correlated with mean activity levels in the mirror neuron regions, sensitive to the perceivers' pro-relationship motivation (i.e., the mirror neuron regions identified in the behavioral PLS), and whether this effect would strengthen with increasing perceiver marital satisfaction. We focused on the correlation between mean activity levels, rather than between the raw time course, of the cognitive control and mirror neuron areas, because we hypothesized a hierarchical relationship between the two, with cognitive control areas being instrumental in implementing relationship-promoting behaviors in a top-down manner. We reasoned that activity in cognitive control areas at one time point would lead, at a subsequent time point, to an enhancement in mirror area activity in response to a spouse's positive nonverbal cues and/or a dampening in mirror area activity in response to a spouse's negative nonverbal cues. Given the relatively poor temporal resolution of fMRI, we regarded a focus on the correlation between mean activity levels as an acceptable approach to capture the presumed hierarchical relationship between cognitive control and mirror neuron areas in the present study.

Method

Participants

Fifteen female participants (mean age 72.14 ± 7.09 years) were recruited from an initial sample of 52 elderly married couples (average marriage length 42.14 ± 9.48 years), who participated in a behavioral study two years prior to the scanning session. All 15 participants were screened for neurological/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. These 15 participants were the only female participants from the initial behavioral session who were both willing and eligible to participate in the fMRI study. Only four participants reported taking medication for heart and/or blood pressure problems. None of these participants was an outlier on any of the study measures. 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; average marriage length 40.17 ± 11.84 years at the time of scanning).

Relationship Measures

In the initial behavioral session, participants completed Norton's (1983) 6-item Quality of Marriage Index, one of the most widely used measures of marital satisfaction. In this scale, four items assess respondents' global evaluations of their marriage as happy ("We have a good relationship."; "The degree of happiness, everything considered, in my relationship is 100%.") and stable ("My relationship with my partner is stable"; "My partner and I have often discussed ending our relationship." [reverse-coded]). The remaining two items gauge the respondents' sense that the relationship brings them a sense of fulfillment ("My relationship with my partner makes me happy") and that the self and the partner constitute a unit (“I really feel like part of a team with my partner.”). Cronbach’s alpha was .89 (*M* = 4.26, *SD* = .75 for the 14 fMRI participants).

fMRI Stimuli Construction

Social target selection and control measure: Two years prior to the scanning session, as part of the aforementioned larger behavioral study, potential male social targets completed the Emotion Regulation Questionnaire (ERQ; Gross & John, 2003). The four-item expressive suppression subscale from the ERQ was used to assess individual differences in the tendency to control one’s emotions by not expressing them (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.”). Previous research suggests that it is habitual engagement in expressive suppression, specifically, rather than habitual engagement in any emotion control strategy, that interferes with the legibility of one’s nonverbal behavior (cf. Gross & John, 2003). In our sample of potential male social targets, engagement in the two emotion regulation strategies was significantly positively correlated, $r(51) = .35$, $p < .05$. Consequently, to ensure that the social targets were matched with respect 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 involving the social targets featured on the fMRI task.

Stimuli acquisition: One year prior to the scanning session, the fMRI participants’ male spouses and two other male participants from the initial sample (17 targets in total; mean age 72.41 ± 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 first five years of their marriage, as well as of 15 positive and 15 negative personal events from the 5 years preceding their laboratory visit (for examples of personal events identified, see Supplemental Note 1). When creating the verbal event descriptions, the social targets were advised to eliminate any identifying information (e.g., names of people or places) and use the simplest sentence structure (i.e., whenever possible, use only subject and verb or, if that failed, use a maximum of one direct and/or indirect object). Subsequently, they were videotaped (from shoulders up), while they described each event to R.P. for about 1-2 minutes. The social targets were instructed to talk about the events in a casual manner, as if they were conversing with an acquaintance and allow any emotions that may surface to do so naturally. This was done in order to avoid having the social targets demonstrate their emotions for the camera. One 10 s video segment, capturing the emotional climax of the event described and representing the moment when the social target peaked with respect to his nonverbal expressivity, was selected from each recording (by R.P.). The sound was eliminated from all the selected segments, and during the debriefing for both the norming study (detailed below) and the fMRI study, we confirmed with the participants that they were unable to derive any information from lip-reading.

Stimuli norming: 70 female raters, who were matched on age with the social targets and the participants in the fMRI study and who were unacquainted with both groups, evaluated first the valence (from 1 *very negative* to 9 *very positive*) of each 10 s silent clip, and, subsequently, of each event description. Each video and each verbal event description was evaluated in isolation (i.e., videos and their associated event descriptions were not presented together) by 14 independent raters. There was good inter-rater agreement in valence ratings of both nonverbal and contextual cues (Cronbach's alphas of .83 and .98, respectively), and the female judges' evaluations were congruent with those provided by the male targets. Importantly, the female judges' valence ratings in response to target-rated negative videos were lower than the ones provided in response to target-rated positive videos (i.e., mean rating of 4.70 ± .91 versus 5.67 ± 1.10 for target-rated negative versus positive videos). Similarly, the female judges' valence ratings in response to target-rated negative verbal event descriptions were lower than the ones provided in response to target-rated positive event descriptions (mean rating of 2.71 ± 1.10 versus 7.70 ± .78 for target-rated negative versus positive verbal descriptions). The norming sample's affect ratings were used in analyzing the responses of our fMRI participants.

Social target control measure: To verify that the social target's use of expressive suppression impacts the legibility of his nonverbal behavior (cf. Gross & John, 2003), we conducted a multilevel regression analysis (HLM 7.01, Raudenbush, Bryk, & Congdon, 2013), predicting the female judges' 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 expected, target-rated positive (relative to target-rated negative) videos received higher valence ratings from perceivers, $b = .97$, $SE = .06$, $t(1001) = 16.64$, $p < .001$, but this effect was weaker in response to targets who reported greater suppression use, $b = -.21$, $SE = .08$, $t(1001) = -2.78$, $p = .003$ (see Supplemental Figure 1). Moreover, speaking to the specificity of the effect of expressive suppression on nonverbal affective behavior, there was no evidence that the target's use of expressive suppression affected the female judges' valence ratings of his positive versus negative verbal event descriptions ($p > .96$).

fMRI Task Structure

Trial types: The fMRI task comprised two main multimodal trial types (i.e., congruent and incongruent) and two unimodal trial types (i.e., nonverbal video only and contextual text only). Each trial type is described next.

Congruent trials: On congruent 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).

Incongruent trials: On incongruent trials, perceivers were presented with a social target's silent video, accompanied by a one-sentence description, opposite in valence to the video, but selected from the set of contextual cues provided by the same social target. Apart from one pair, which differed by 1.24 points, the 339 remaining video-sentence pairs in incongruent trials differed by a minimum of 1.83 points on the 9-point Likert scale (mean difference of 3.45 ± .80 points).

Unimodal trials: The unimodal nonverbal video trials comprised the silent videos from a male target, not featured on the multimodal trials. The unimodal contextual text trials included the one-sentence event descriptions provided by the social target featured on the unimodal nonverbal video trials.

Stimuli types: The fMRI task featured three distinct social targets. Specifically, the multimodal trials featured the perceiver's spouse and a stranger, matched on expressive style with the perceiver's spouse (paired-samples t [13] = 1.48, p = .16 for the expressive suppression scores of the entire sample of social targets[1]). We reasoned this would be an important control because, as mentioned above, in the norming study, perceivers gave less differentiated affect ratings in response to the positive versus negative videos of social targets reporting greater expressive suppression use. Thus, it seemed plausible that individual differences in the target's use of expressive suppression may influence the relative salience of nonverbal, relative to contextual, cues on the incongruent trials, although the direction of such an effect was difficult to predict (for a detailed rationale, see Supplemental Note 3).

The third social target, featured only in the unimodal trials, was pseudo-randomly selected from the available social targets who were mid-range scorers on expressive suppression. The unimodal video trials featured a different social target across participants: only the spouses of the two social targets used in the multimodal trials saw exactly the same social targets on the unimodal trials (i.e., these two participants saw exactly the same targets across all trials).

Task instructions: For all 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. We anticipated that perceivers would find it more difficult to integrate the nonverbal and verbal affective cues on incongruent trials. To help them to do so, we told participants that on some trials, the featured social target may behave in ways that could appear to be at odds with the event that he was describing. We emphasized to the perceivers that on these trials they should do their best to integrate both nonverbal and verbal information by keeping in mind that recollection of positive events may be tainted by negative emotions and vice versa (e.g., recalling the disorderly behavior of a drunken guest on one's wedding day or recalling the support one received from close friends when a loved one passed away). 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).

[1]The perceiver's spouse and the stranger, featured on the multimodal trials, were even more stringently matched with respect to their expressive suppression use, if their raw suppression scores (rather than their suppression scores from which their reappraisal scores had been partialed out) were taken into account. Indeed, by this account, the stranger matched on expressive style to the spouse had either exactly the same (for 11 of the 14 perceivers) or a highly similar (a difference of .25 points on a 7-point Likert-type scale) expressive suppression score (ERQ; Gross & John, 2003) to the perceiver's spouse (paired-samples t [13] = .56, p = .58 for the entire sample).

The participants' task was to evaluate how the social target felt when he recalled the respective event.

Task structure: Before entering the scanner, participants were given instructions and completed 10 practice trials, involving unimodal and multimodal cues, obtained from a male target who was not featured in the subsequent scanner task. In the scanner, participants completed 24 unimodal text trials (half of each valence), 24 unimodal video trials (half of each valence), 40 congruent trials (20/target, half of each valence for each target) and 40 incongruent trials (20/target; within each target, 10 positive sentence-negative video pairs and 10 negative sentence-positive video pairs). These trial types were presented across 12 task runs of 14 trials each. Supplemental Table 1 contains the description of the task trials included in the present report.

Run structure: Each run contained two unimodal text trials (one positive, one negative), two unimodal video trials (one positive, one negative), as well as 10 multimodal trials (five congruent and five incongruent)[2]. The valence of the multimodal trials was counterbalanced across the 12 runs, such that each run contained both positive and negative congruent trials, as well as both types of incongruent trials (i.e., positive video-negative sentence and negative video-positive sentence). The multimodal trials in each run featured the perceiver's spouse and the expressive suppression-matched stranger, with each social target appearing in at least one congruent and incongruent trial, respectively. Within-run trial order was randomized across participants.

Trial procedure: A trial began with a 5-s fixation cross, followed by the 12 s presentation of a unimodal or multimodal cue, depending on trial type. 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. 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. We introduced this control because participants used a bilateral response box to rate the stimuli (buttons 1-4 assigned to the right hand and 6-9 assigned to the left hand), which may have resulted in incidental laterality effects. 5 *neutral* was not an available response option and participants were made aware of this in the practice session outside the scanner. We omitted a *neutral* response because we feared that perceivers would choose this response alternative as a proxy for "I don't know" when the verbal and nonverbal cues conflicted and use it on the majority of incongruent trials as a way of avoiding to process a more complex set of stimuli. Such disengagement would have had repercussions on behavioral, as well as brain responses.

[2]The fMRI task contained a total of 120 multimodal trials because it also featured a second stranger on the multimodal trials, who was either the highest (for perceivers whose spouse scored under the midpoint on the expressive suppression scale) or lowest (for perceivers whose spouse scored over the midpoint on the expressive suppression scale) expressive suppression scorer among all the social targets. For the reasons outlined in the Method section, in the present report, we focused on the perceivers' neural and behavioral responses to their spouse and the stranger matched on expressive style to their spouse. For the sake of concision, we described the task only with respect to these two targets. Mention of the third target is included here only in order to clarify the total number of multimodal trials.

fMRI Data Acquisition—Images were obtained used a Siemens Trio 3T scanner. 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 slices of 3.12 × 3.12 mm in-plane resolution, 5 mm thick, no gap). 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.

Behavioral Analysis

Coding of incongruent trial responses: Our behavioral analyses focused on the incongruent trials from the two targets matched on expressive suppression levels (i.e., stranger and spouse). Thus, for each incongruent trial, we (1) computed an average of the normative affect ratings received by the sentence and video alone; (2) subtracted this average from a perceiver's rating to the respective video-sentence pair to obtain an information usage index (IUI, Zaki et al., 2010). Thus, greater reliance on the nonverbal, rather than the contextual, information would be reflected in a positive IUI value for negative sentence-positive video pairs and a negative IUI value for positive sentence-negative video pairs. To harmonize the direction of the IUI across all incongruent trial types, such that greater IUI values would indicate greater reliance on the nonverbal, rather than the contextual, information, we multiplied by (−1) the IUI for positive sentence-negative video pairs. Because perceivers saw different stimuli on the incongruent trials, we created a "standardized" IUI by dividing each perceiver's IUI on a given trial by the absolute value of the difference in normed affect ratings received by the individual video and sentence. Thus, for each of the two incongruent trial types, the standardized IUI was computed using the formula

$$\text{Standardized IUI}=[\text{fMRI Perceiver Rating}-\text{MEAN (Normed VIDEO Valence Rating, Normed TEXT Valence Rating)}]/\text{ABSOLUTE VALUE (Normed VIDEO Valence Rating}-\text{Normed TEXT Valence Rating)}].$$

For example, let's say that the normed affect rating of a given video seen in isolation is 3 and the normed affect rating of a sentence seen in isolation is 8. If a perceiver sees the respective negative video and positive sentence together on an incongruent trial and gives an affect rating of 6, then her IUI would be computed as 6 − (3 + 8)/2 = .50, the positive value of the IUI reflecting relatively greater reliance on the (positive) text, rather than the (negative) video. To harmonize the direction of the IUI across all incongruent trial types, such that greater IUI values would indicate greater reliance on the nonverbal, rather than the contextual, information, we would multiply .50 by (−1). Subsequently, to obtain a "standardized" value, we would divide the IUI value of −.50 by the absolute value of the difference between the normed affect rating of the video and sentence alone (in this case, 5), which would result in a standardized IUI value of −.10. This standardized IUI was used in the behavioral analyses reported below. Figure 1 contains the distribution of the mean standardized IUI values across all fMRI perceivers.

fMRI Data Analysis—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). In the context of our sample, the last preprocessing step also served the function of minimizing the influence of inter-individual differences in age-related neurovascular decline.

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 patterns of activity (i.e., latent variables or LVs) related to different experimental conditions, either globally (task-PLS) or as a function of individual differences variables (behavioral PLS). An advantage of PLS is that it contrasts all experimental conditions simultaneously, thereby circumventing the need for post-hoc correction of p-values due to multiple comparisons (McIntosh et al., 2004). It has been argued that PLS can be regarded as a hybrid between completely hypothesis-driven (e.g., univariate general linear models [GLM], ROI-based approaches) and completely data-driven (e.g., independent components analysis [ICA]) approaches (Lin et al., 2003). Indeed, unlike ICA, the data decomposition is not performed across all possible dimensions, but it is restricted to the identified experimental conditions. Nevertheless, PLS is also distinct from completely hypothesis-driven approaches, which test a single hypothesized contrast across conditions (i.e., univariate GLM) and/or test for changes in activity within an a priori defined set of brain regions (i.e., ROI-based approaches). Instead, PLS identifies the most robust contrasts in the data, provides an estimate of how much of the covariance in the data each component accounts for and indicates the brain activity pattern that tracks with the identified contrasts. Consequently, within the framework of PLS, if a hypothesized contrast emerges as significant, it means that it represents a robust way of distinguishing among the activity patterns evoked by the different experimental conditions.

In all the reported analyses, the significance of each LV was determined using a permutation test with 5000 permutations. 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, since these parameters are 10 times greater than the standard ones (i.e., 500 permutations/100 bootstrap samples), recommended by McIntosh and Lobaugh (2004) for use in PLS analyses of neuroimaging data. Peak voxels with a weight/SE ratio ≥ 4.00 (the bootstrap ratio, or BSR, $p < 0.0001$) were considered to make a robust contribution to the LV. For both task and behavioral PLS analyses, we report activity clusters containing at least 20 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 and using the same voxel-wise *p*-value (i.e., < .0001) in order to produce a Type I error probability lower than .0001.

The PLS analyses focused on neural activity during the first 5 TRs (10 s) of each trial. Their purpose was to elucidate whether perceivers would exhibit greater processing of their spouse's (rather than the stranger's) non-verbal behaviors and whether this effect would be impacted by the valence of the respective nonverbal cues. To this end, we conducted a task PLS analysis, comparing the brain activity patterns observed on the unimodal positive and negative video and text trials, respectively, with those observed on incongruent (positive video-negative text and negative video-positive text) trials, featuring the spouse and the stranger, respectively. Subsequently, we conducted the same comparison in a behavioral PLS analysis, probing the potential role of the perceiver's marital satisfaction in moderating any of the observed brain activity patterns. Although for the sake of parsimony and consistent with prior investigations using a similar paradigm (Zaki et al., 2010), the analyses reported here focus on unimodal and incongruent trials, we have nonetheless verified that the reported results are unchanged if the congruent trials are included in the PLS analysis. Specifically, none of the four congruent trial types (i.e., positive/negative, featuring the stranger/perceiver's spouse) loaded preferentially in either the direction of the unimodal video or unimodal text trials[3].

Multivariate HLM Analyses—Complementing our whole-brain PLS analyses, we also used two- and one-level multivariate HLM analyses (HLM 7.01, Raudenbush et al., 2013) to test our predictions regarding the relationship between cognitive control and the mirror neuron areas as a function of target identity and nonverbal behavior valence. An advantage of multivariate HLM is that it allowed us to test the effect of our predictor of interest (i.e., cognitive control area activity) simultaneously on multiple outcome variables (i.e., all the mirror neuron areas, identified through behavioral PLS as described above), while controlling for their interrelatedness. Consequently, we had more power to test for our effect of interest (i.e., the link between cognitive control and mirror neuron area activity) and we did not need to control for multiple comparisons. For all multivariate HLM analyses, we report the estimates obtained from the homogenous level-1 variance output.

[3]We are nonetheless reluctant to interpret this null effect, since it may be largely due to the fact that congruent and incongruent trials, featuring the perceiver's spouse, by definition, could not be matched with respect to autobiographical memory involvement, a variable that could have, in turn, affected the salience of the nonverbal videos on the congruent trials featuring the spouse (i.e., perceivers' autobiographical representation of the event could have overshadowed their spouse's nonverbal behavior in the silent video, cf. Rabin & Rosenbaum, 2012). Specifically, in order to maximize cognitive conflict on the incongruent trials, we selected events with which, in the case of the target being their spouse, the perceivers were very familiar because they were directly involved in the respective event (see Supplemental Note 1). Consequently, on some of the congruent trials, featuring their spouse, the event descriptions were bound to trigger autobiographical memory processes. Thus, rather than integrating their spouse's nonverbal behavior in the nonverbal video with the associated verbal event description, it seems more likely that perceivers used the verbal event description as a retrieval cue for their autobiographical representation of the respective event, which, in turn, served as a basis for their judgments of their spouse's emotions. Indeed, consistent with this line of reasoning, a study by Rabin and Rosenbaum (2012) documented heavy reliance on autobiographical memory processes when perceivers judge the affect of a familiar other during an event in which they were also involved. Reliance on autobiographical memory was unlikely on incongruent trials featuring the spouse and was, of course, irrelevant for congruent or incongruent trials, featuring the stranger. Consequently, because congruent versus incongruent trials, featuring the perceiver's spouse, could not be well-matched with respect to reliance on autobiographical memory processes, in our analyses, we opted to focus on the incongruent and unimodal trials.

Results

Behavioral Results

Preliminary analyses—The vast majority (91% and 89%, respectively) of stimuli presented on congruent and unimodal text trials, respectively, received valence evaluations congruent with the ones provided by the targets themselves (i.e., target-rated negative events received < 5 ratings, whereas target-rated positive events received > 5 ratings). Likewise, silent videos of target-rated negative events received lower ratings relative to those of target-rated positive events ($M = 4.52 \pm 2.09$ versus $M = 5.75 \pm 2.44$, $t(319) = -4.86$, $p < .001$). On incongruent trials, perceivers' ratings were closer to the normed affect ratings of the individual context sentences, rather than the individual nonverbal videos, (mean standardized IUI −.31 ± .51, $t(550) = 14.36$, $p < .0001$), although there was considerable inter-perceiver variance in the tendency to do so (IUI ranged from −1.86 to 2.42). Nevertheless, if perceivers had indeed paid attention to both contextual and nonverbal cues on the incongruent trials, then we expected them to experience greater cognitive load on incongruent (relative to congruent) trials, and, thus, in line with well-documented findings from studies on domain-general cognitive control, we expected them to be slower in making a response. This was indeed the case, since response times were longer on incongruent, relative to congruent, trials ($M = 2.01 \pm 1.26$ s versus $M = 1.79 \pm 1.21$ s, $t(1101) = 2.94$, $p = .003$). This finding thus gave us some confidence that on incongruent trials, participants attempted to integrate contextual and nonverbal cue information.

Incongruent trial data—A regression analysis, using a two-level hierarchical linear model (HLM 7.01, Raudenbush et al., 2013; see also Nezlek, 2008), with responses on each trial (level-1) nested within individuals (level-2), revealed a two-way interaction between target identity and nonverbal cue valence of the incongruent trials on IUI, $b = .27$, $SE = .08$, $t(531) = 3.43$, $p < .001$, which was further qualified by a three-way interaction among target identity, nonverbal cue valence and the perceiver's marital satisfaction, $b = .30$, $SE = .11$, $t(531) = 2.74$, $p = .006$[4]. To shed light on these interactions, we conducted a series of follow-up analyses. Analysis of the data from the incongruent trials, featuring the perceiver's spouse, revealed a significant main effect of nonverbal cue valence, which was further qualified by a two-way interaction between nonverbal cue valence and perceiver marital satisfaction. Specifically, in line with our hypothesis, on incongruent trials, featuring their spouse, perceivers gave relatively greater weight to nonverbal cues, $b = .19$, $SE = .06$, $t(260) = 3.32$, $\boldsymbol{p = .001}$, when their spouse expressed positive, rather than negative, emotions (see Figure 2-a). This effect became stronger with greater marital satisfaction, $b = .27$, $SE = .08$, $t(260) = 3.40$, $p < .001$ (see Figure 2-b). In contrast, contextual/nonverbal cue valence did not exert any significant effects on incongruent trials featuring the stranger (all ps > .13; see Figure 2-c).

[4]We initially ran two sets of HLM analyses. In the first analysis, we used only target identity, nonverbal cue valence on the incongruent trials and their interaction as predictors of the IUI. In the second analysis, we introduced as additional predictors the perceiver's marital satisfaction and its interaction with the independent variables from the first regression. Because the two-way interaction of target identity and nonverbal cue valence from the first regression emerged virtually identical in the second analysis, for the sake of concision, we opted to present the results from the second regression analysis.

Neuroimaging Results

Task PLS—The task PLS identified only two significant patterns (LVs) of whole-brain activity, differentiating among the four incongruent and four unimodal trial types. The first LV ($p < .001$, accounting for 42.52% of the covariance) discriminated multimodal from unimodal trial activity (see Figure 3-a), particularly spouse multimodal from video unimodal trial activity. Thus, given their increased cognitive demands, the multimodal incongruent trials evoked greater recruitment of brain regions involved in social cognition, both mirror neuron areas (precentral gyrus bilaterally, right inferior frontal gyrus, posterior cingulate cortex bilaterally), as well as areas involved in reading others' inner states based on contextual cues (right parahippocampal gyrus, medial frontal gyrus; for a complete list of regions see Table 1).

The second LV ($p < .001$, accounting for 21.86% of the covariance) was the one most relevant to our hypotheses, since it distinguished activity patterns on the two unimodal video trial types and the two incongruent trial types, featuring the spouse, from activity patterns on the two unimodal text trial types (see Figure 3-b). On the latter trial types, perceivers demonstrated greater engagement of areas involved in contextual cue (i.e., cuneus bilaterally, left angular gyrus, cf. Zaki et al., 2010) or semantic processing (i.e., left middle frontal gyrus, e.g., Hamilton, Martin, & Burton, 2009). In contrast, when watching their spouse's context-incongruent behaviour, perceivers evidenced whole brain activity patterns suggestive of greater processing of his nonverbal cues, rather than of the accompanying contextual information, thereby showing greater activity in mirror neuron areas (right inferior frontal gyrus, right anterior insula), as well as in areas involved in the perceptual processing of nonverbal cues (extrastriate cortex, posterior cingulate cortex, Zaki et al., 2010), including faces (fusiform gyrus, middle temporal gyrus, see Dinkelacker et al., 2011; Garrido et al., 2009; Lobmaier et al., 2008; Paller et al., 2003) and facial emotional expressions (superior temporal gyrus, Bigler et al., 2007; Radua et al., 2010) (see Table 1). In contrast, neither of the two incongruent trial types featuring the stranger loaded preferentially in either the direction of the unimodal video or unimodal text trials, or showed activity that differed from the mean across all trial types, thereby implying that on those trials, perceivers attended equally to both contextual information and to the stranger's nonverbal behavior. Importantly, though, there was also supportive evidence for our hypothesis that not only target identity, but also the valence of his nonverbal cues impact perceivers' processing of context-incongruent behaviors. Specifically, as presented in Figure 3-b, perceivers evidenced whole-brain activity patterns indicative of reliably greater processing of their spouse's, rather than the stranger's, non-verbal behaviour, but only on incongruent trials in which the behavior is positive. In contrast, the difference between activity evoked by their spouse's versus a stranger's negative nonverbal cues was not reliable (see Figure 3-b)[5].

Behavioral PLS—The behavioral PLS identified only one significant pattern ($p < .002$), accounting for 19.96% of the covariance. The respective LV was directly relevant to our

[5]The results are virtually unchanged from the pattern seen in LV2 in task PLS (i.e., mirror neuron and face processing areas vs. areas involved in contextual cue processing, cf. Zaki et al., 2010) if we specify a contrast that distinguishes video trials and incongruent trials featuring the spouse from text trials and incongruent trials featuring the stranger. This can be done using a version of PLS that allows for testing of pre-specified contrasts.

hypotheses regarding the role of the perceiver's pro-relationship motivation, as it distinguished activity on the unimodal video trials and incongruent trials, featuring the perceiver's spouse, from activity on the unimodal text trials and incongruent trials, featuring a stranger, as a function of the perceiver's marital satisfaction (Figure 4). With increasing marital satisfaction, perceivers faced with conflicting socioemotional cues evidenced brain activity patterns suggestive of greater processing of their spouse's nonverbal cues. Processing of the spouse's nonverbal cues by those with higher marital satisfaction was associated with greater activity in areas of the mirror neuron system, i.e., activation in right IPL, left IPL/SMG (see Table 1). No regions showing more activity for text and incongruent trials, featuring the stranger, as a function of marital satisfaction passed the statistical threshold of our analyses. Thus, dovetailing extant neural evidence that perceivers are more likely to attend to the context-incongruent behavior of personally relevant social targets (Ames & Fiske, 2013), the results of our behavioral PLS analysis suggest that those perceivers with higher marital satisfaction have more activity in parietal mirror neuron regions when viewing their spouse's context-incongruent non-verbal behavior (both positive and negative) than when viewing a stranger's incongruent behavior. Our present neural findings complement prior behavioral evidence on the beneficial relational consequences of attending to potential incongruities between one's own and a close partner's subjective experience.

Further analyses of the mirror neuron regions revealed by behavioral PLS— We next carried out a series of analyses to test whether the two mirror neuron regions found in the behavioral PLS analysis to show increasing recruitment with increasing perceiver marital satisfaction (right IPL, left IPL/SMG; see Table 1 for coordinates) would also show greater activity in response to a spouse's positive rather than negative nonverbal behaviors. Secondly, we investigated whether mean activity levels in these two mirror neuron areas would be more strongly correlated with mean activity levels in cognitive control areas on trials in which the spouse exhibited positive, rather than negative, nonverbal behaviors. To test the latter hypothesis, we averaged the time courses of the three conflict resolution ROIs identified by Zaki et al. (2010) (mean intra-class correlation coefficient of the three time courses of .35): ventrolateral prefrontal cortex (VLPFC) (MNI coordinates: 48, 24, −8), dorsal anterior cingulate cortex (ACC) (MNI coordinates: −4 40 34) and posterior dorsomedial prefrontal cortex (pDMPFC) (MNI coordinates: −12 24 58). We used the average value of the three cognitive control area time courses because we sought to correlate mean activity levels in all three regions with the mean activity levels of the two mirror neuron areas, found in behavioral PLS to be most responsive to a social target's positive emotional significance. Consistent with their posited role in conflict resolution, mean activity level in the three cognitive control areas was greater on the incongruent (mean % signal change .05 ± .02), relative to the congruent trials (mean % signal change −.02 ± .03), $b = .07$, $SE = .03$, $t(97) = 2.36$, $p = .02$.

To test our hypotheses of greater mean activity levels and patterns of correlated activity evoked by a spouse's positive nonverbal behavior during incongruent trials, we used two-level multivariate HLM models (HLM 7.01, Raudenbush et al., 2013), with experimental conditions (level-1) embedded in individuals (level-2). This method allowed us to run our tests simultaneously on both mirror neuron regions (correlation coefficient of the two averaged time courses of .38).

Activity in mirror neuron areas—A multivariate HLM regression analysis, controlling for perceiver marital satisfaction, revealed an interactive effect of target identity and nonverbal cue valence on the mean activity level in the two mirror neuron regions, $b = .10$, $SE = .05$, $t(52) = 2.00$, $p = .05$ (see regression 1 in Supplemental Table 2 and Figure 5-a). A follow-up analysis focused on the incongruent trials featuring the perceiver's spouse revealed greater activity in the two mirror neuron regions in response to the spouse's positive, rather than negative, nonverbal cues, $b = .08$, $SE = .04$, $t(26) = 2.03$, $p = .05$ (see regression 2 in Supplemental Table 2). No significant effects on activity in mirror neuron areas were observed on incongruent trials featuring the stranger ($p > .56$).

Correlation between mean activity levels in the conflict resolution areas and mean activity levels in the mirror neuron areas—We tested the hypothesis that the observed differential recruitment of the two mirror neuron areas, in response to positive versus negative nonverbal cues, is coordinated in a top-down manner via the three aforementioned conflict resolution areas, and is influenced by marital satisfaction. We thus investigated whether mean activity levels in the two mirror neuron regions would show distinct patterns of correlation with mean activity levels in the three conflict resolution areas in response to the spouse's positive, rather than negative, nonverbal cues as a function of the perceiver's marital satisfaction. To examine this hypothesis, we tested a series of multivariate HLM models to determine whether activity in the conflict resolution areas predicted activity in the two mirror neuron areas, as a function of target identity, nonverbal cue valence and perceiver marital satisfaction. In these models, the outcome variable had two indicators, specifically, the mean activity of the (1) right IPL and (2) left IPL/SMG. For the predictor variable, the two indicators were identical and equal to the mean activity level of the three conflict resolution ROIs. Figure 6 indicates the models that were significant. For the first global model (model 1 in Figure 6), the three-way interaction of target identity, nonverbal cue valence, and marital perceiver satisfaction was significant, $b = 1.42$, $SE = .59$, $t(102) = 2.41$, $p = .02$ (see regression 3 in Supplemental Table 2). To break down the interaction, we ran a second set of models, probing the effects of nonverbal cue valence and perceiver marital satisfaction on the correlation between mean activity levels in the cognitive control areas and mean activity levels in the mirror neuron regions, separately for the perceiver's spouse and for the stranger. The interactive effect of nonverbal cue valence and perceiver marital satisfaction was significant only for the spouse, $b = .97$, $SE = .47$, $t(50) = 2.06$, $p = .05$ (model 2 in Figure 6; see also Figure 5-b and c and regression 4 in Supplemental Table 2). Specifically, on these trials, when the nonverbal behavior was negative (i.e., dummy value of 0), increasing perceiver marital satisfaction predicted a more negative correlation between mirror and cognitive control area activity (i.e., β_{101} in regression 4, Supplemental Table 2), an effect that was attenuated on incongruent trials on which the spouse's behavior was positive (i.e., β_{111} in regression 4, Supplemental Table 2). Thus, on incongruent trials on which the spouse's behavior was negative (relative to those on which the behavior was positive), increasing perceiver marital satisfaction predicted an increasingly stronger inhibitory effect of cognitive control areas on activity in the right IPL and left IPL/SMG areas (see Figure 5-b). No significant interactive effects of perceiver marital satisfaction and nonverbal cue valence were observed on incongruent trials featuring the stranger (all *p*s > .27). Nevertheless, across all incongruent trials featuring the stranger, greater perceiver marital satisfaction predicted an increasingly stronger negative correlation between mean activity levels in the cognitive control areas and mean activity levels in the two mirror neuron regions (see Figure 5-c) (see Supplemental Notes 4 and 5 for further analyses of the relationship between behavioral reliance on the text versus the video on the incongruent trials and cognitive control-mirror area activity correlations).

Discussion

Although resonance with the emotions of a significant other constitute a hallmark of intimacy (Beckes et al., 2012; Beeney et al., 2011; Singer et al., 2004), recent evidence suggests that sensitivity to potential incongruities between one's own and a partner's inner states may also be important for close relationship quality (Petrican et al., 2011). Dovetailing a sizeable behavioral literature on the greater relational benefits of being responsive to a partner's disclosure of positive, rather than negative, events (Gable et al., 2006, 2012), our study is the first, to our knowledge, to provide both neural and behavioral evidence of such an asymmetry in circumstances in which one's emotions related to the memory of an emotional event appear to be distinct from the ones experienced by the partner. Specifically, in contexts presumed to elicit polarized affective responses, perceivers demonstrated whole-brain activity patterns suggestive of greater processing of their spouse's (rather than a stranger's) incongruent nonverbal behavior, only when this behavior was positive. Importantly, with increasing perceiver marital satisfaction, and, thus, arguably, higher perceiver-social target interdependence (i.e., sense of being a "team"), there was evidence of comparatively greater neural processing of the spouse's nonverbal cues, whether positive or negative in valence (cf. Ames & Fiske, 2013).

Of note, in a more direct support of our hypothesis of greater neural responsiveness to a spouse's positive, rather than negative emotions, we also found evidence of a valence-related bias in two areas of the mirror neuron system (right IPL, left IPL/SMG), which are presumably recruited during the processing of nonverbal affective cues (cf. Zaki & Ochsner, 2012). Although these regions exhibited increasingly greater activity to the spouse (rather than the stranger) as a function of greater perceiver marital satisfaction, they evidenced weaker recruitment in response to the spouse's negative, rather than positive, nonverbal cues. The latter effect appeared to be driven by the stronger inverse relationship between mirror neuron and cognitive control areas on incongruent trials containing negative (rather than positive) nonverbal behavior of the spouse, a relationship that strengthened with greater perceiver marital satisfaction. Thus, under emotionally conflicting circumstances, it seems plausible that the nonverbal affective cues of social targets who are personally relevant to the perceiver may spontaneously evoke mirror neuron system activity (as it happens in situations with congruent contextual and nonverbal cues; Beckes et al., 2013; Cheng et al., 2010). The role of cognitive control areas in the PFC here appears to be that of dampening neural responsiveness to a spouse's negative affective states, an effect that is accentuated among higher marital satisfaction perceivers. Dovetailing these neural activity findings, there was also behavioral evidence of greater reliance on positive, rather than negative, nonverbal cues when judging a spouse's affect, a finding that strengthened with higher perceiver marital satisfaction. In light of prior findings on the beneficial consequences of being responsive to an intimate partner's disclosure of positive events, but the more problematic implications of being responsive to his/her disclosure of negative events (Gable et al., 2006, 2012), it seems plausible that the current results reflect perceivers' relationship-protective strategies, activated in the face of conflicting emotional information. Thus, processing of the context-inappropriate behaviour exhibited by familiar, emotionally significant targets is likely impacted by the perceiver's interpersonal goals with respect to these social targets.

In the case of our happily long-married sample, we assumed that perceivers harboured stability-relevant relationship goals. Nevertheless, a promising research venture may be to investigate perceivers' neural responses to the context-inappropriate behaviour exhibited by social targets for whom perceivers harbour negative feelings (e.g., stigmatized social groups, disliked others). Prior research that focuses on a social target's context-appropriate behavior suggests that perceivers are less likely to resonate with the emotions of outgroup members (who are less valued/liked than ingroup members; e.g., Azevedo et al., 2013; Gutsell & Inzlicht, 2012; Xu et al., 2009). Perceivers may even evidence brain activity patterns suggestive of counter-empathic responses in reaction to outgroup members who are more disliked (i.e., perceivers exhibit greater activation in the "pain matrix" when viewing positive, rather than negative, events experienced by envied outgroup members, cf. Cikara & Fiske, 2011). Nevertheless, it is unknown how perceivers may respond to a disliked social target's context-inappropriate behaviour, particularly if the latter can be used to further devalue the target. For example, although perceivers may exhibit reduced neural resonance or even "counter-neural resonance" (cf. Cikara & Fiske, 2011) in response to a stigmatized target's nonverbal behaviors of either valence, they may evidence increased recruitment of areas involved in the lower level perceptual processing of nonverbal cues (e.g., visual cortex) and greater functional coupling between the latter and cognitive control areas in response to the target's "compromising" nonverbal behaviors (e.g., laughing when talking about a close other's misfortune, sadness when describing a friend's achievements). Thus, increased functional connectivity between cognitive control areas and regions involved in the perceptual processing of nonverbal cues may constitute the neural mechanism underlying the perpetuation of social attitudes towards groups or individuals.

Our present findings on the valence-asymmetric neurobehavioral responses to an intimate partner's emotions complement the existing literature on perceivers' ability to "feel" the pain of other, particularly emotionally significant, social actors (e.g., Anders et al., 2011; Meyer et al., 2012; Singer et al., 2004). Specifically, to the best of our knowledge, our study is the first to compare both behavioral and neural responses to a close other's not only negative but also positive emotions. While our findings of greater neural and behavioral responsiveness to a spouse's positive nonverbal affective behaviors fit well with findings from the social support literature on the greater relational benefits associated with responsiveness to a close other's disclosure of positive, rather than negative, events (Gable et al., 2006, 2012), in the context of our experimental design, they also invite an additional explanatory framework. Specifically, given the instructions we gave to our social targets (see Supplemental Note 1), (almost) all of the recalled episodes were directly relevant to the perceiver's marriage. Studies have shown that memory for such relationship significant events makes a key contribution to maintaining relationship intimacy (Alea & Bluck, 2007). Importantly, though, there is also evidence that once the memory for an event is reactivated (e.g., by being present with a brief description of the respective event), the representation of the initial episode may be updated with new information that surfaces during retrieval, a process that, although weakened, is still observable among older adults (St. Jacques, Montgomery, & Schacter, *in press*). Consequently, in our study, responsiveness to a spouse's positive emotions during the recall of a negative relationship-relevant event may have had the potential to cast the respective autobiographical representation in a new and more positive light by incorporating the spouse's present positive emotions and, thus, indirectly strengthen the marital bond (cf. Alea & Bluck, 2007). In contrast, responsiveness to a spouse's negative emotions during the recall of a positive relationship event may have had the potential to corrupt an autobiographical episode that previously enhanced intimacy. Future research testing whether perceivers' responsiveness to their spouse's positive versus negative context-incongruent behavior during autobiographical recall would subsequently bias perceivers' recall of the respective episode may make an important contribution to elucidating the dyadic significance of autobiographical memory.

Notwithstanding the above proposal, it is worth noting that, in response to a spouse's negative nonverbal cues, greater perceiver marital satisfaction predicted an increasingly stronger cognitive control area inhibitory effect on neural resonance based on the two mirror system regions. Thus, it is possible that, despite any potential hedonic costs, perceivers with greater marital satisfaction may have exhibited greater neural responsiveness to a spouse's negative nonverbal cues early in the trial, but that activity was subsequently inhibited via PFC-mediated cognitive control mechanisms (hence, the resultant null effect of perceiver marital satisfaction on mean-level neural resonance in the respective condition). Indeed, such a line of reasoning is compatible with the hierarchical relationship we assumed to exist between the cognitive control and the mirror neuron areas, with earlier cognitive control activity, relevant to the implementation of relationship-relevant goals, biasing subsequent mirror area activity. Future EEG research is warranted to shed light on the time course of a perceiver's responses to her spouse's negative emotional cues.

Finally, we would like to underscore that our aim in the present research was to gather evidence on whether differential sensitivity to an intimate partner's positive, rather than negative, context-incongruent behavior could be regarded as a marker of relationship-protective responding, as implied by the existing social support literature (Gable et al., 2006, 2012). Because emotional well-being is a priority (Mather & Carstensen, 2005) and close relationships are a particularly important determinant of well-being in older adulthood (Charles & Carstensen, 2003), we reasoned that an elderly, overall happily married sample would be most likely to demonstrate our hypothesized patterns of pro-relationship responding (if we were right to reason that such patterns would indeed be relationship-promoting). It may be nonetheless worthwhile for future studies to investigate the neural and behavioral responses of younger adults in (inevitably) shorter relationships. Our prediction would be that their responses would be similar to the ones reported with the present sample only to the extent that the younger individuals would themselves prioritize emotional well-being and regard the respective relationship as a critical determinant of their affective fulfillment. That being said, although we find it difficult to explain our valence asymmetric findings in response to the spouse as the result of age-related deficits in social cognition and processing of nonverbal affective cues (for a review, see Moran, 2013), such age-related deficits may be detected in response to a stranger's context-incongruent nonverbal behavior. Indeed, future studies probing age-related differences in attending to a stranger's positive versus negative context-incongruent behaviors may make a valuable contribution to a growing literature on lifespan changes in subtler neurobehavioral aspects of social cognition (e.g., Moran, Jolly, & Mitchell, 2012).

In sum, the present study provided neural evidence testifying to the perceivers' greater sensitivity to incongruities between one's own and a close other's (rather than a stranger's) subjective experience. Most importantly, though, it also suggested that the time course and associated behavioral outcomes of such processes are under the perceivers' control and, thus, shaped by their momentary and/or longer-term pursuits.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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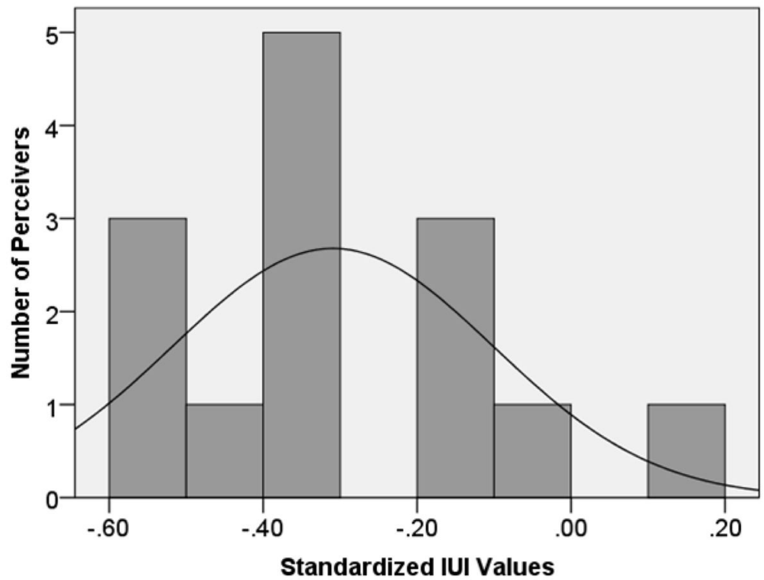
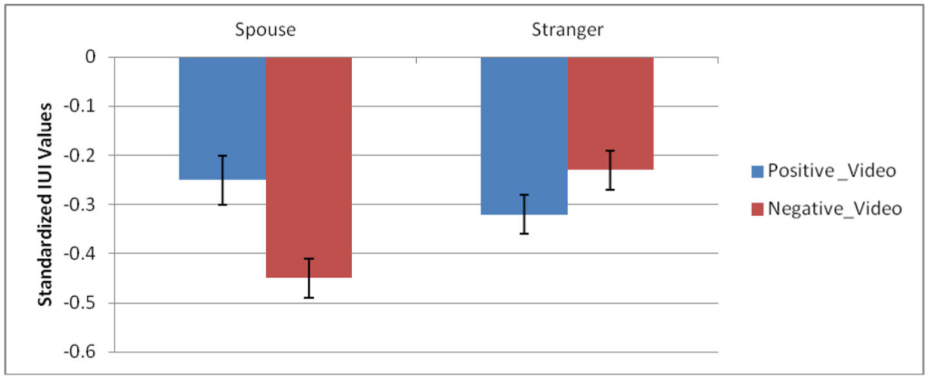
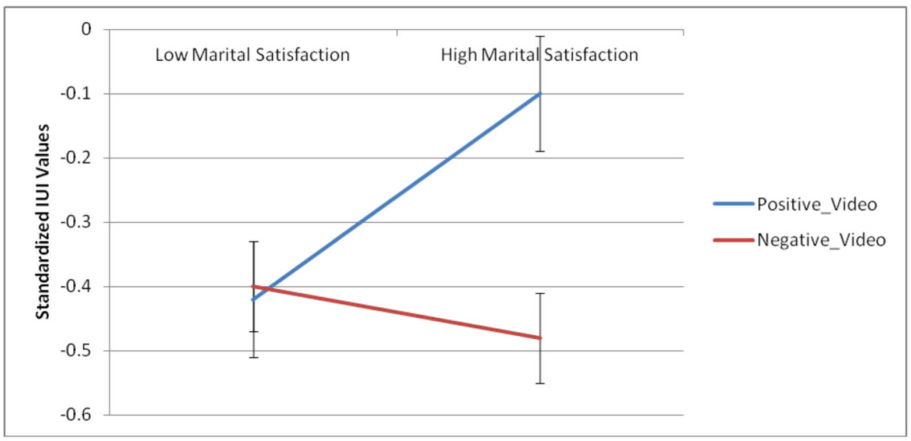


Figure 1.

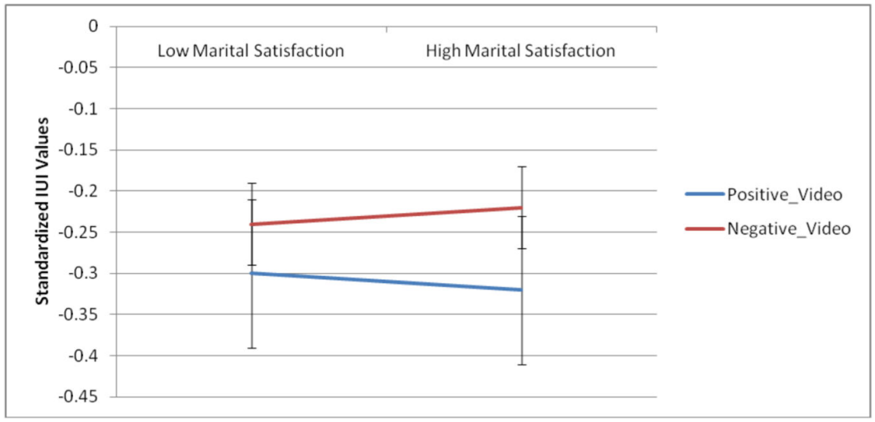
Histogram of the mean standardized IUI values across all 14 fMRI perceivers. Perceivers with negative mean IUI values demonstrate a greater overall tendency to rely on the verbal event descriptions. Perceivers with positive mean IUI values demonstrate a greater overall tendency to rely on the silent videos.


Spouse
Stranger
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
Standardized IUI Values
Positive_Video
Negative_Video

(a)


0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
Low Marital Satisfaction
High Marital Satisfaction
Standardized IUI Values
Positive_Video
Negative_Video

(b)



(c)

Figure 2.

Panel a Standardized IUI values for incongruent trials as a function of target identity and nonverbal cue valence. **Panel b.** Judgments of the spouse's affect on incongruent trials. **Panel c.** Judgments of the stranger's affect on incongruent trials. In all three panels, greater IUI values reflect greater reliance on nonverbal cues. In panel (a), the negative IUI values indicate a greater overall tendency to rely on contextual cues for incongruent trials.

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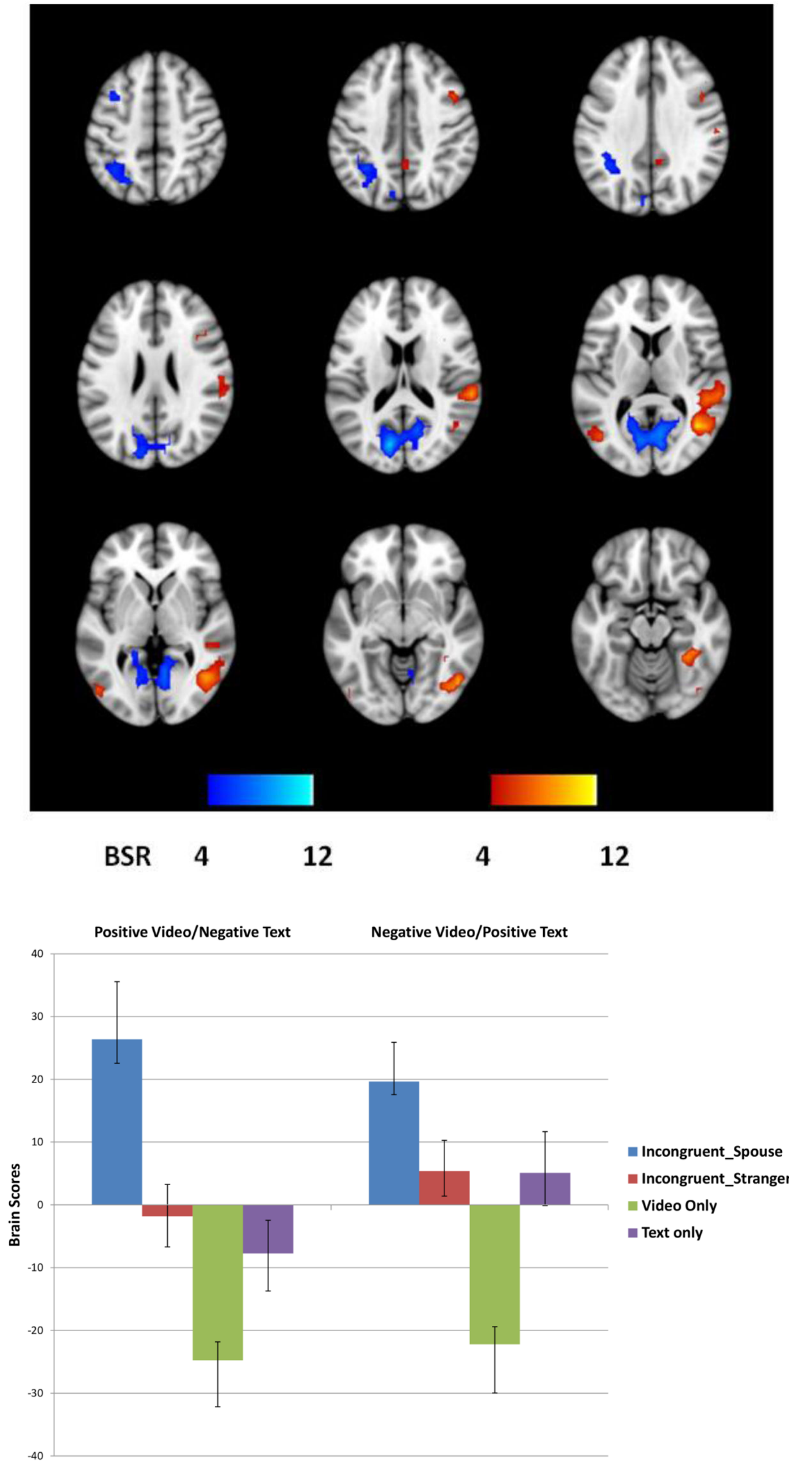
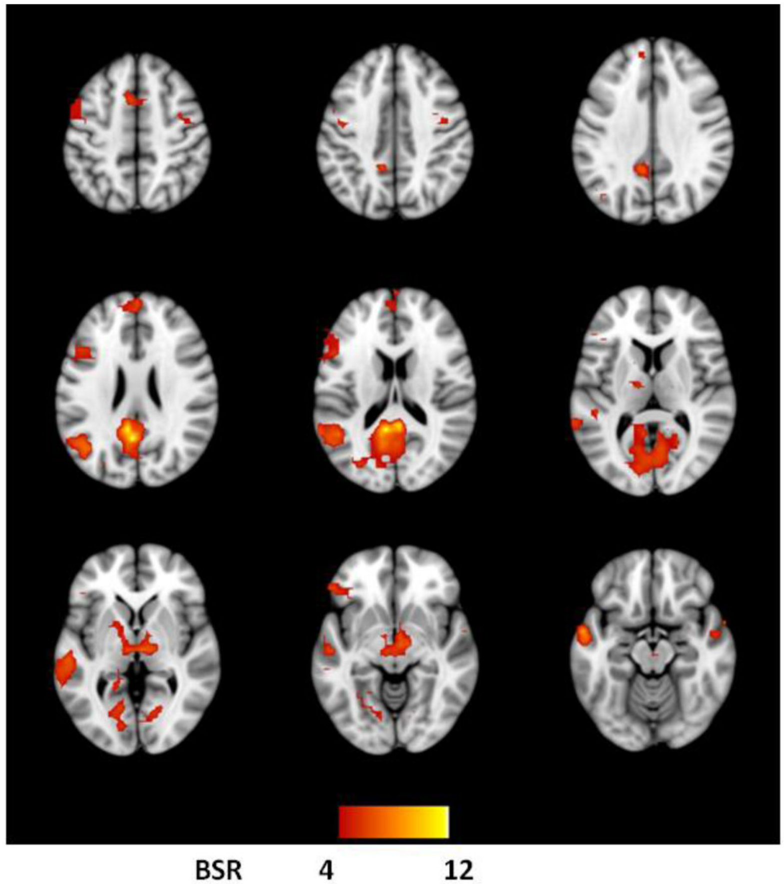
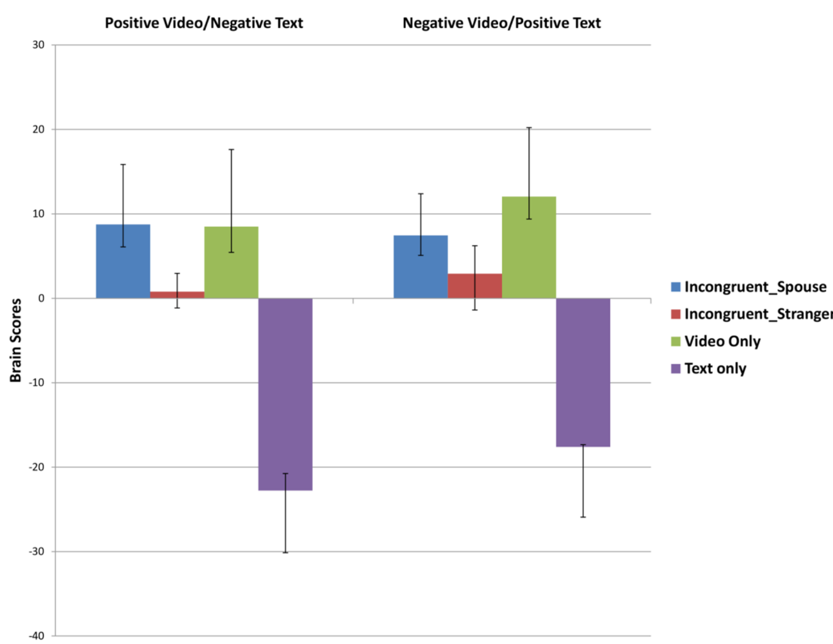


(a)

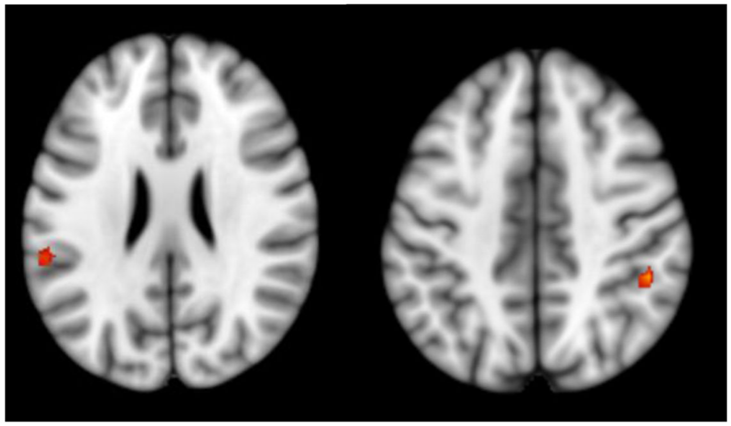

BSR
4
12


Positive Video/Negative Text
Negative Video/Positive Text
Brain Scores
30
20
10
0
-10
-20
-30
-40
Incongruent_Spouse
Incongruent_Stranger
Video Only
Text only

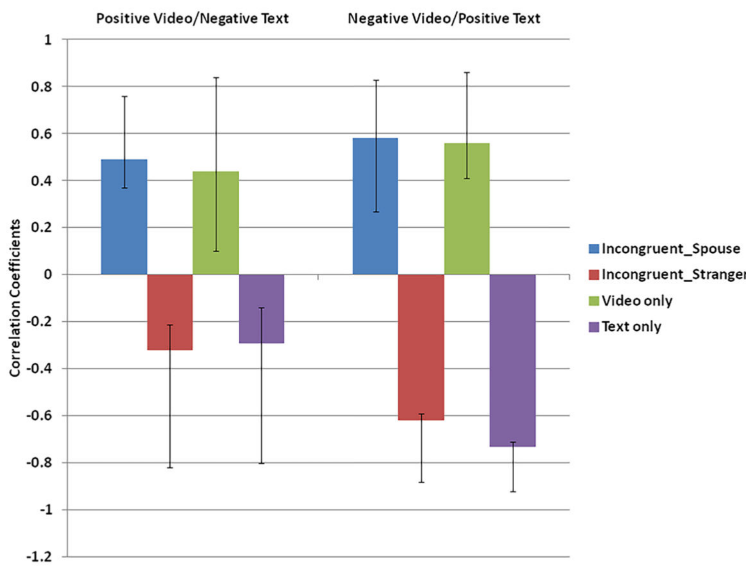
(b)

Figure 3.

Results of the task-PLS analysis are shown on axial slices from the MNI152 average structural brain. Panel (a) shows LV1 and panel (b) shows LV2. In the brain images, greater activity in regions shown in warm-colored areas is seen in those conditions with mean brain scores above zero, whereas greater activity in cool-colored areas is seen in those conditions with mean brain scores below zero (i.e., zero indicates whole-brain mean activity levels). The graphs show the average of the mean-centered brain scores for each condition (error bars are the 95% confidence intervals [CI] from the bootstrap procedure). Non-overlapping CIs indicate differences between conditions.



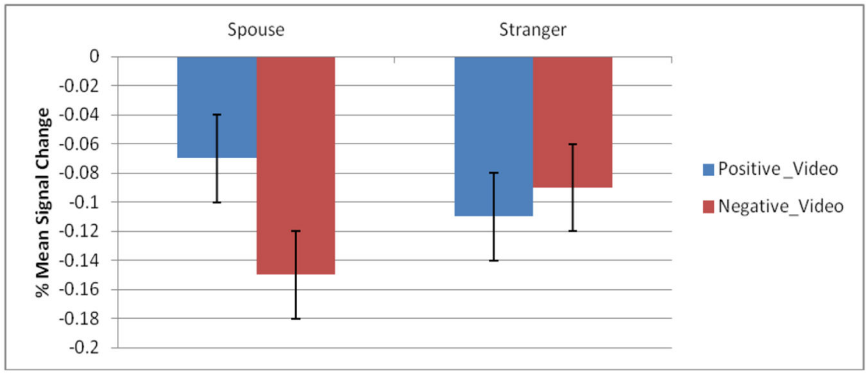
(a) (b)



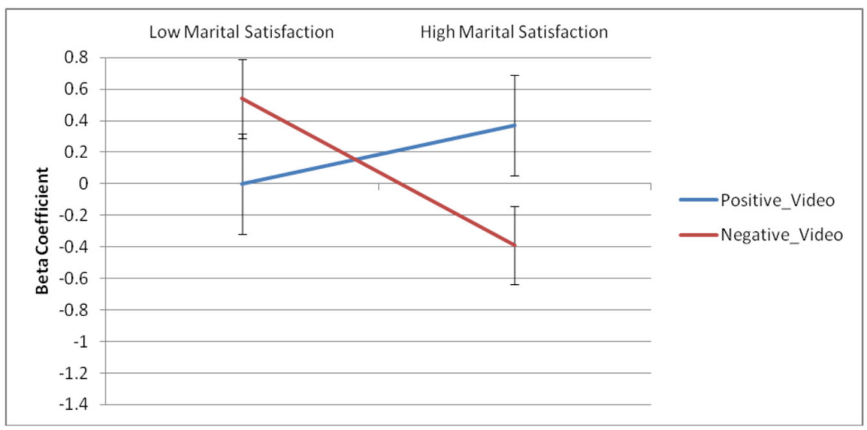
(c)

Figure 4.

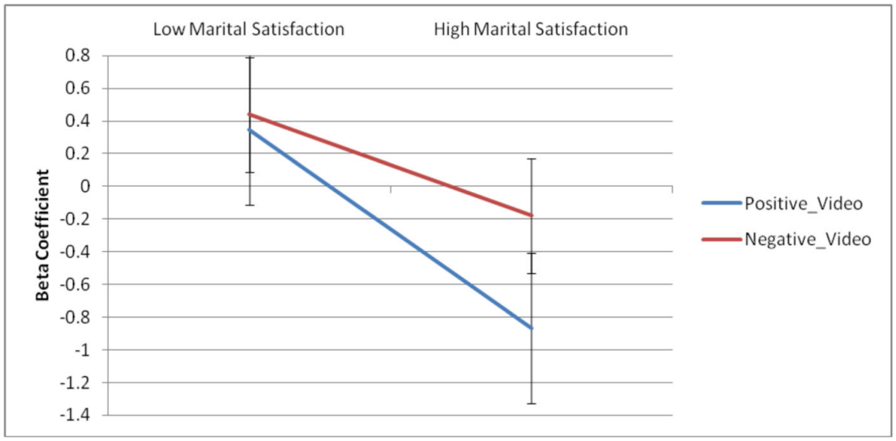
Results of the behavioral-PLS analysis are shown on axial slices from the MNI152 average structural brain. Panels (a) and (b) show the right IPL and left IPL/SMG clusters (4< BSR < 6), respectively. The graph in panel (c) shows the correlations between brain scores and perceiver marital satisfaction for each condition. Error bars are the 95% CIs from the bootstrap procedure.


Spouse
Stranger
% Mean Signal Change
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
-0.14
-0.16
-0.18
-0.2
Positive_Video
Negative_Video

(a)


Low Marital Satisfaction
High Marital Satisfaction
Beta Coefficient
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
-1.4
Positive_Video
Negative_Video

(b)



(c)

Figure 5.

Panel a Mean % signal change in the two mirror seeds, derived from the behavioral PLS, as a function of target identity and nonverbal cue valence on incongruent trials. Note that the effect is significant only after controlling for perceiver marital satisfaction. **Panel b.** Association between mean activity level in the three conflict resolution ROIs and the two mirror seeds, derived from the behavioral PLS, as a function of the perceiver's marital satisfaction, on incongruent trials featuring the perceiver's spouse. **Panel c.** Association between mean activity level in the three conflict resolution ROIs and the two mirror seeds, derived from the behavioral PLS, as a function of the perceiver's marital satisfaction, on incongruent trials featuring the stranger. To compute the beta coefficient for the panel (b) and (c), respectively, we ran the multivariate HLM models, described in the Results, with standardized coefficients, separately, for the data from the incongruent trials, featuring the perceiver's spouse and the stranger, respectively.

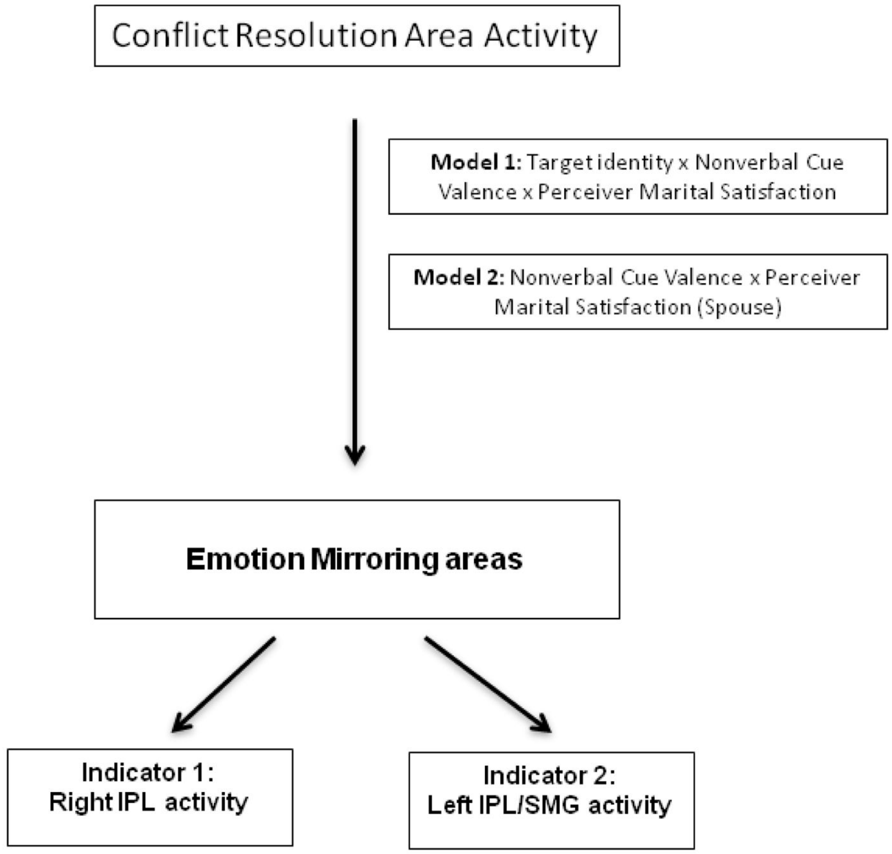


Figure 6.

Outline of the multivariate HLM models tested to determine whether mean activity in the three conflict resolution areas predicted activity in the emotion mirroring regions, as a function of target identity, nonverbal cue valence and perceiver marital satisfaction. See text and Supplemental information for details on these models.

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Table 1

Brain activity associated with unimodal video trials, unimodal text trials, incongruent trials featuring the perceiver's spouse and incongruent trials featuring a stranger.

Region	MNI coordinates			BSR	TR	Cluster size
	x	y	z			
LV1 (task-PLS): *Multimodal spouse, Negative video/Positive text Stranger > Video only, Negative Text*						
M Posterior cingulate cortex/Precuneus	0	−60	20	12.69	3	563
R Parahippocampal gyrus	16	−20	−8	7.66	3	154
M Medial Frontal gyrus	0	8	48	7.26	3	51
L Medial Frontal gyrus	−4	48	24	6.32	3	60
R Middle temporal gyrus	64	4	−20	7.03	3	29
L Middle temporal gyrus	−52	−4	24	9.69	3	302
R Precentral gyrus	40	−8	40	6.71	3	24
L Precentral gyrus	−40	−12	36	5.64	3	53
L Inferior frontal gyrus	−48	32	−12	6.35	3	135
M Supplementary motor area	0	8	48	9.50	4	707
L Posterior cingulate cortex	−4	−52	20	15.57	4	3432
R Middle temporal gyrus	60	0	−20	11.12	4	150
	60	−36	−4	5.50	4	20
R Superior temporal gyrus	60	−52	12	6.83	4	58
R Inferior frontal gyrus	44	32	−12	7.95	4	112
R Precentral gyrus	40	−8	44	7.42	4	22
	44	−12	56	5.98	4	32
R Cerebellum	8	−52	−40	8.11	4	37
R Posterior cingulate cortex	8	−52	24	14.27	5	861
R Middle temporal gyrus	64	0	−20	13.22	5	121
L Middle temporal gyrus	−56	−12	−16	12.85	5	1958
R Inferior frontal gyrus	36	24	−20	8.13	5	70
R Cerebellum	8	−52	−44	7.54	5	38
	16	−84	−36	12.54	5	626
R Superior temporal gyrus	56	−60	16	5.92	5	38

Region	MNI coordinates			BSR	TR	Cluster size
	x	y	z			
L Fusiform gyrus	−20	−36	−16	5.12	5	21
L Lingual gyrus	−20	−72	−12	8.49	5	94
LV2 (task-PLS): *Text only > Multimodal spouse, Video only*						
R Cuneus	20	−72	8	7.45	3	37
R Cuneus	12	−72	8	7.43	4	221
L Angular gyrus	−28	−56	36	6.61	5	131
L Middle frontal gyrus	−32	8	48	6.64	5	33
L Cuneus	−8	−80	12	10.46	5	432
LV2 (task-PLS): *Multimodal spouse, Video only > Text only*						
R Superior temporal gyrus	60	−36	8	8.42	3	51
L Middle occipital gyrus	−40	−76	0	6.34	3	30
R Inferior frontal gyrus	48	8	36	6.61	4	42
L Middle occipital gyrus	−44	−76	0	7.84	4	45
R Middle temporal gyrus	48	−64	0	12.58	4	328
R Fusiform gyrus	36	−48	−20	8.37	4	56
R Posterior cingulate cortex	8	−48	32	5.13	4	21
R Insula	40	12	12	7.01	5	83
L Middle occipital gyrus	−44	−84	0	8.21	5	52
R Middle temporal gyrus	44	−64	0	11.78	5	463
R Fusiform gyrus	40	−48	−20	10.67	5	88
(Behavioral-PLS): *Multimodal spouse, Video only > Multimodal stranger, Text only*						
L Inferior parietal lobule/Supramarginal gyrus	−56	−32	20	6.11	3	34
R Inferior parietal lobule	48	−40	44	6.61	3	20

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