Adolescents growing up amidst intractable conflict attenuate brain response to pain of outgroup

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Adolescents' participation in intergroup conflicts comprises an imminent global risk, and understanding its neural underpinnings may open new perspectives. We assessed Jewish-Israeli and Arab-Palestinian adolescents for brain response to the pain of ingroup/outgroup protagonists using magnetoencephalography (MEG), one-on-one positive and conflictual interactions with an outgroup member, attitudes toward the regional conflict, and oxytocin levels. A neural marker of ingroup bias emerged, expressed via alpha modulations in the somatosensory cortex (S1) that characterized an automatic response to the pain of all protagonists followed by rebound/enhancement to ingroup pain only. Adolescents' hostile social interactions with outgroup members and uncompromising attitudes toward the conflict influenced this neural marker. Furthermore, higher oxytocin levels in the Jewish-Israeli majority and tighter brain-to-brain synchrony among group members in the Arab-Palestinian minority enhanced the neural ingroup bias. Findings suggest that in cases of intractable intergroup conflict, top-down control mechanisms may block the brain's evolutionary-ancient resonance to outgroup pain, pinpointing adolescents' interpersonal and sociocognitive processes as potential targets for intervention.

intergroup conflict | empathy | alpha oscillations | oxytocin | brain-to-brain synchrony

Intergroup conflicts—among races, religions, cultures, and nations—are one of the world's most imminent problems, particularly with the shift of battlefields into the heart of civilian locations and the participation of increasingly younger adolescents in intergroup conflict. According to the 2015 World Economic Forum, intergroup conflicts comprise the greatest global risk in the foreseeable future (1). However, how can humans, who evolved as a highly social species and whose brain automatically responds to the pain of others, inflict such pain on their fellow human beings? Here, we attempt to address this ancient question from a unique angle, asking whether neuroscience can offer new insights into the mechanisms that enable humans to tolerate the pain imposed on others. Because the success and thriving of our species depends on the capacity to quickly form social groups and instantly distinguish friend from foe (2), we ask whether our brain already processes the pain of our ingroup and that of the outgroup differently at the automatic level or whether higher-order evaluative processes are superimposed upon a uniform brain response to differentiate "us" from "them." That is, we ask whether the "ingroup bias" stems from bottom-up or top-down mechanisms and whether this bias can be predicted by endogenous oxytocin (OT) levels, which are known to play a causal role in regulating intergroup relations (3).

The most evolutionary-ancient precursor of empathy involves emotional arousal/resonance to the distress of conspecifics, expressed as simple physiological mirroring in rodents (4) and more broadly in primates (5). Such rudimentary empathy is observed primarily in the nociceptive mechanism (i.e., pain perception), which promotes responsiveness to one's offspring and social group, thus conferring survival advantage. It appears that evolution has tailored pain perception into the mammalian brain as a basic mechanism for social affiliation, ranging from primitive reward and homeostatic processes of pain sensitivity to the most advanced forms of human compassion and extended caregiving (6). Substantial human neuroimaging research has demonstrated the key role of the somatosensory cortex (S1) in pain empathy via modulations of alpha oscillations, termed "mu" rhythm when originating in S1 and possibly implicating mirror-like mechanisms (7–9). Alpha oscillations are suppressed at the immediate poststimulus time window and then rebound and enhance power compared with baseline in response to both the experience of pain in self and observation of pain in others (10). Such early suppression occurs automatically and is unaffected by attentional demands, whereas the later rebound is modulated by cognitive-regulatory mechanisms (11). Hence, alpha oscillations may integrate quick automatic responses with slower top-down mechanisms for processing vicarious pain empathy. When individuals observe pain to ingroup and outgroup members, empathic resonance in S1 shows group-specific activations (12–14); yet, the time course of such differential responses is unknown, nor is information available as to whether these responses express shared initial activations that diverge at evaluative stages (top-down) or a shutdown of even the most basic automatic response to vicarious pain (bottom-up). This important issue taps an age-old question about human beings' innate nature: How deep is our animosity for those unlike us compared with our compassion for human suffering?

The Israeli–Palestinian conflict is among the most intractable intergroup conflicts worldwide, generating aggression and suffering for over a century, thus providing ecologically valid context for investigation (15). Recently, adolescents' involvement in this conflict has increased at alarming rates, paralleling the global epidemic of adolescents' participation and recruitment into conflict via social media; hence, the present focus on Jewish-Israeli

Significance

Intergroup conflicts are among the world's most imminent problems, particularly with the shift of battlefields into the heart of civilian locations and the participation of increasingly younger adolescents in intergroup conflict. We found that Israeli and Palestinian adolescents reared in a climate of long-standing strife shut down the brain's automatic response to outgroup pain. This neural modulation characterized a top-down process superimposed upon an automatic response to the pain of all and was sensitive to hostile behavior toward outgroup, uncompromising worldviews, and brain-to-brain synchrony among group members. Findings pinpoint adolescents' sociocognitive top-down processes as targets for intervention.

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and Arab-Palestinian adolescents is timely and relevant. Despite pioneering behavioral (16) and fMRI (17, 18) work on empathic attitudes in the context of the Israeli-Palestinian conflict, comprehensive understanding of the mechanisms via which conflict impedes empathy for others' suffering is lacking. Moreover, it remains unknown how the neural markers of empathy relate to adolescents' dialog styles in interpersonal situations and their attitudes toward the intergroup conflict. We also addressed the implications of the ancient OT system on modulations in neural responses to ingroup or outgroup's pain. Animal studies and human OT administration research have shown that OT increases ingroup affiliation (19), and yet, under conditions of threat it also prepares for defensive aggression toward outgroup targets (3). OT administration was found to increase ingroup bias of the brain's empathic response and this bias was linked with positive implicit attitudes toward ingroup members (20). Whereas studies mainly tested the effect of OT administration on ingroup bias, the role of endogenous OT has been largely ignored. Here, we tested whether endogenous OT could predict the brain's empathic response within the intergroup context.

To investigate the neural marker for ingroup bias in pain resonance and its interactional, attitudinal, and neuroendocrine correlates, we recruited Jewish-Israeli and Arab-Palestinian adolescents ($N = 80$), representing the majority and main minority groups, respectively, in Israel (*SI Methods*). We first sought to pinpoint a neural marker of pain empathy, reflecting the time course of the brain's empathic resonance with others' pain, by using magnetoencephalography (MEG). MEG integrates excellent temporal resolution with good spatial localization and is thus uniquely suited for probing oscillatory dynamics in targeted cortical areas. We used MEG to probe alpha oscillations and their neural source while empathizing with vicarious pain. We then hypothesized that priming of group membership of the target protagonist may bias either early or later neural signature, reflecting bottom-up cascade or top-down regulatory input. Finally, to examine correlates of these neural patterns, we assessed behavioral hostility and empathy during interactions with an outgroup member, attitude of compromise toward the intergroup conflict, and peripheral levels of OT measured at baseline and before and after social interactions.

Results

Adolescents watched a set of well-validated visual stimuli depicting limbs in painful or nonpainful conditions (14), preceded by a prime-linking stimuli to either an Arab-Palestinian or Jewish-Israeli protagonist (in total four within-subject conditions), while we measured ongoing oscillatory neural activity using MEG (Fig. 1). The detection rate in the attentional filler task (Fig. 1) was high (mean ± SD, 93.05 ± 8.58%). As expected, the MEG sensor-array detected that the neural response to Pain (P) and to no-Pain (no-P) stimuli was expressed above central sensors (Fig. S1) as alpha (7- to 11-Hz) suppression (descent to suppression peak at ∼50–500 ms), presumably mirroring bottom-up processing (purple rectangle) (Fig. 2*A*, *Upper*); it was then followed by alpha (9- to 15-Hz) rebound (ascent to rebound peak at ∼700–950 ms), presumably mirroring top-down processing (yellow rectangle) (Fig. 2*A*, *Middle*). We then proceeded to localizing the neural substrates characterizing pain empathy (P vs. no-P). Alpha enhancement was localized ($P_{\text{cluster-cor}} < 0.05$) primarily in the right sensorimotor cortex (S1) (in BA3); yet, no significant source emerged for the early alpha suppression ($P_{\text{cluster-cor}} > 0.70$), suggesting that the sample of 80 adolescents consistently revealed the main effect of pain empathy (i.e., P compared with no-P) through the alpha rebound in the right S1 (Fig. 2*B*, *Lower*), with ascent to rebound peak at ∼500–920 ms (Fig. 2*A*, *Lower*).

A Top-Down Neural Ingroup Bias. To examine whether priming of protagonists' group membership bias (i.e., pain of ingroup vs. outgroup) taps top-down processing, a repeated-measures ANOVA examined group bias (Arab-Palestinian/Jewish-Israeli) and stimulus bias (ingroup/outgroup) effects in S1 (ratio of P/no-P). A significant main effect emerged for ingroup/outgroup stimulus bias ($P_{\text{cluster-cor}} < 0.005$), but no significant group or interaction effects emerged between the Jewish-Israeli and the Arab-Palestinian adolescents; that is, adolescents of both nationality responded differently to pain

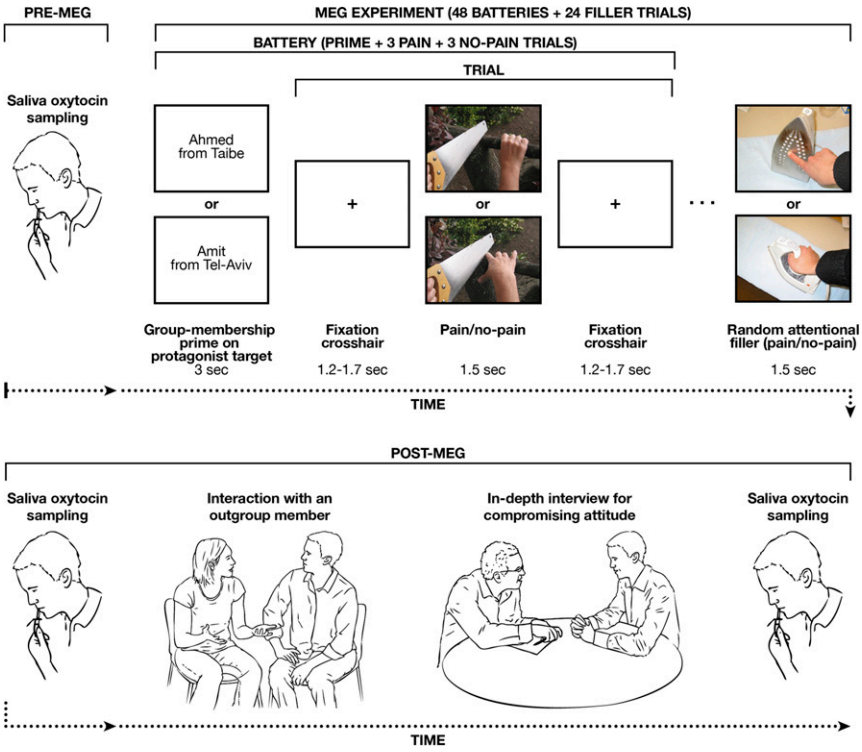

Fig. 1. Experimental procedures are depicted with the upper panel showing the pre-MEG experiment sampling of saliva OT and then the course of the MEG experimental session ($N = 80$). *Lower* shows the post-MEG procedures (saliva OT sampling, outgroup interaction and in-depth interview for compromising attitude).

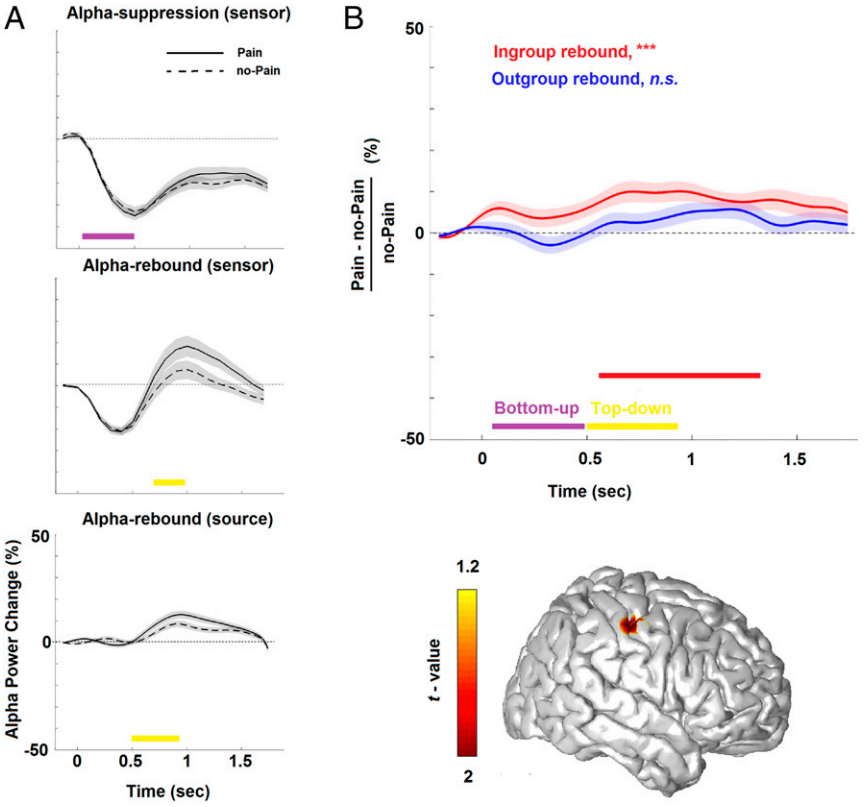

Fig. 2. Alpha power change in response to vicarious pain ($N = 80$). (*A*) Plots of the temporal evolution of alpha-band–induced power change (normalized to baseline activity) in response to P and no-P stimuli. (*B*) Alpha rebound in the somatosensory cortex (see peak activity in the bottom panel illustrating the overlaid cortical surface) for pain empathy (P/no-P ratio) of ingroup (red) and outgroup (blue) protagonists. Shades represent ±1 SEM. Rectangles describe descent to peak suppression (purple) and ascent to peak rebound (yellow), thereby, respectively, mirroring bottom-up and top-down processes. Red rectangle describes statistically (cluster-based statistics) significant effect (***$P_{\text{cluster-cor}} < 0.001$) on the time axis. The color bar illustrates masked statistical significance ($P_{\text{cluster-cor}} < 0.05$).

of ingroup and outgroup protagonists. Fig. 2*B*, *Upper* illustrates the pain empathy effect (P/no-P ratio in S1), which was biased by the protagonists' group membership. As seen in the figure, the expected significant enhancement of rebound from baseline in response to protagonists' pain (P vs. no-P) occurred only toward the ingroup target (540–1,360 ms, $P_{\text{cluster-cor}} < 0.001$) and clearly occurred within the range of top-down processing (see red rectangle in Fig. 2*B*, *Upper*); there was no P vs. no-P effect when priming was toward the outgroup target stimuli (no clusters). These findings suggest that group membership of the protagonist who is experiencing the pain strongly biases alpha oscillations' late rebound, such that they occur only toward ingroup protagonists and not at all toward outgroup protagonists. Notably, no significant difference emerged in the early component of the alpha oscillations, the sensor-level alpha suppression, toward ingroup versus outgroup protagonists ($P > 0.8$).

Brain-to-Brain Synchrony. Once we identified a neural marker in S1 for ingroup bias in pain resonance in both Jewish-Israeli and Arab-Palestinian adolescents, we explored how this ingroup bias may relate to group cohesion at a neural level. Brain-to-brain synchrony was measured using the intersubject correlation (ISC) index (*SI Methods*). Repeated-measures ANOVA yielded a significant demographic background by ingroup-bias interaction effect [$F(1,78) = 5.10$, $P = 0.02$] but no significant effects for ingroup bias [$F(1,78) = 1.72$, $P = 0.19$ or demographic-background $F(1,78) = 2.16$, $P = 0.14$]. Post hoc t tests revealed that Arab-Palestinian adolescents showed significantly higher ISC when protagonists were members of their ingroup (mean = 9.6, SD = 24.71) than when the protagonists were outgroup members [mean = 0.25, SD = 11.55; $t(39) = 2.25$, $P = 0.03$]. The Jewish-Israelis showed no such ISC difference [$t(39) = -0.77$, $P = 0.44$ (Fig. S2)]. In line with this finding, an ethnocentricity questionnaire revealed that Arab-Palestinian adolescents reported greater ethnocentricity compared with Jewish-Israeli adolescents [$t(73) = -4.15$, $P < 0.0001$].

The Neural Ingroup Bias Is Related to Social Behavior, Attitudes Toward Conflict, and Oxytocin. Having identified this neural marker of ingroup-bias in S1, along with the synchronized ISC ingroup bias for the Arab-Palestinians, we next examined its behavioral, cognitive, and neuroendocrine correlates. We first observed adolescents' social behavior toward an outgroup member in two one-on-one interactions: a "conflict dialog" where the dyad negotiated a conflict of their choice and a "positive dialog" where the dyad planned a fun day (*SI Methods*). Next, using an in-depth interview to tap attitudes toward the intergroup conflict, we measured the degree to which adolescents perceived Compromise as the path for resolving conflicts in general, and the Israeli-Palestinian conflict in particular (*SI Methods*). The two groups revealed a medium-low level (on a scale of 1 to 5: mean = 1.98, SD = 0.37) of intergroup hostility (Fig. 3*A*, *Left*) during actual interactions and expressed a rather low level (on a scale of 1 to 3: mean = 1.30, SD = 0.21) of willingness for intergroup compromise, with no significant difference between the two nationalities on these two measures ($P > 0.15$). By contrast, the Arab-Palestinians showed less [$t(58) = -2.45$, $P = 0.01$] empathy (on a scale of 1 to 5: mean = 2.41, SD = 0.53) toward the outgroup member than did Jewish-Israelis (on a scale of 1 to 5: mean = 2.78, SD = 0.62) (Fig. 3*B*, *Left*).

We next examined whether the neural marker of ingroup bias can be predicted by hostile social behavior toward outgroup or by low scores on compromise. Given that hostility levels were similar across groups, we examined whether it would predict individual differences in the neural ingroup bias for the entire sample. As expected (Fig. 3*A*, *Right*), the neural ingroup bias was explained by increased hostility during interaction with outgroup members ($r_p = 0.36$, $P = 0.01$) and by lack of compromise in the context of the conflict ($r = -0.37$, $P = 0.002$), whereas no significant correlation emerged for behavioral empathy ($r_p = -0.11$, $P = 0.50$).

Arab-Palestinians expressed less empathic behavior toward their Jewish peers than vice versa; thus, we measured whether this finding can explain their greater brain-to-brain cohesion

(ISC scores) toward ingroup targets. Brain-to-brain synchrony (ISC scores) to the pain of ingroup protagonists target stimuli did not significantly correlate with behavioral empathy ($r_p = -0.21$, $P = 0.17$) or with hostility ($r_p = 0.20$, $P = 0.16$). Because group scores in both brain-to-brain synchrony and behavioral empathy significantly differed, we looked at the association between behavioral empathy and brain-to-brain synchrony within each group. We found that the two variables were significantly correlated in the Arab-Palestinian group ($r = -0.63$, $P = 0.0001$) (Fig. 3*B*, *Right*) but not in the Jewish-Israeli group ($r = 0.03$, $P = 0.86$).

Finally, the OT system develops in the context of mammalian parenting and is highly sensitive to variability in maternal touch, contact, and behavioral synchrony (2, 21). Parent–infant interactions in Jewish-Israeli and Arab-Palestinian societies show markedly different patterns, particularly in the amount of touch (higher in Arab-Palestinians) and behavioral synchrony (higher in Jewish-Israelis) (22). We thus examined OT levels and its covariation with neural ingroup bias for each group separately. For Jewish-Israeli participants, OT levels linearly increased with the extent of the neural ingroup bias ($r = 0.32$, $P < 0.05$), corroborating a previous report on the tight link between ingroup bias and OT (19); nevertheless, there was no link between ingroup-bias and OT levels for the Arab-Palestinian participants ($r = -0.03$, $P = 0.84$).

Discussion

At least one-fifth of humanity lives in regions of the world experiencing significant violence, political conflict, and chronic insecurity. Following the recent call in social neuroscience to ground investigations in real-life social issues and focus on brain-to-brain mechanisms (23–25), our study examines the neural basis of intergroup conflict by using magnetoencephalography integrated with behavioral, attitudinal, and neuroendocrine measures. Among youth growing up within one of the world's most intractable conflicts, we identified a neural marker for ingroup bias and pinpointed its oscillatory frequency, temporal course, and cortical generator. Specifically, we found that adolescents shut down their brain response to the pain of outgroup targets while showing the expected alpha rebound to ingroup protagonists in a specific area of the somatosensory cortex (S1), which has been repeatedly shown in both electrophysiology and fMRI studies to activate in response to others' pain (7–9). Such consistency of S1 recruitment across studies and methods suggests that the S1 source localization described here can be assumed as accurate, despite relying on inverse estimate solution. Importantly, our study targeted the adolescent brain, which is considered a brain in transition whose development marks a shift from visceral-emotional to more evaluative processing (26). It would be relevant for future studies to test how responses to ingroup versus outgroup develop from childhood to adulthood. One possibility is that the more developed evaluative function in adults would attenuate the ingroup bias; alternatively, the higher brain plasticity in children and adolescents may lead to more pronounced bias in adulthood.

Consistent with prior research, vicarious pain empathy was expressed via modulations of alpha oscillations (7, 9), suggesting that up- and down-regulation of mirror-like mechanisms may be implicated in the human capacity to empathize with, as well as walk away from the pain inflicted on others. Importantly, this differential alpha response in S1 characterized a top-down process, observed at 540–1,360 ms poststimulus that followed a uniform automatic response to the pain of all, indicating that sociocognitive processes are superimposed upon an evolutionary-ancient response to human suffering to differentiate friend from foe. Interestingly, previous work showed that ipsilateral alpha power increases to suppress distracting input (27). In the context of the current experiment, it may suggest that participants' (right-hemispheric) brain response to right-sided limbs reflected S1 disengagement. Finally, individual differences in hostile behavior toward outgroup during one-on-one encounters and uncompromising attitudes toward the conflict enhanced the neural marker. Thus, our findings have clear translational relevance and indicate that opportunities for personal contact with outgroup members and respect for multiple worldviews may chart one avenue for youth interventions based on neuroscience insights.

Mechanisms that enable humans to understand the emotions and actions of others function through online crosstalk between bottom-up and top-down processes, fast sensory–motor integration and slower sociocognitive predictions (23, 28), with specific dynamics defining distinct end products. Top-down processes are shaped by prior learning, attentional demands, regulatory abilities, and social goals, and authors have suggested that brain oscillations provide a useful vantage-point to tap the balance of bottom-up automaticity and top-down-regulation in understanding social phenomena (21). Human vicarious pain empathy integrates evolutionary-ancient automaticity with higher-order regulation; thus, understanding its neural underpinnings requires attention to both and such integration has rarely been examined in human research. Our study—which tests vicarious pain empathy using MEG while integrating social behaviors, interviews, and hormones—provides a unique example for how the balance of fast and slow processing may address critical questions in social neuroscience that cannot be answered by other tools (e.g., fMRI). The findings that both Jewish-Israeli and Arab-Palestinian youth exhibited the same bottom-up activation to ingroup member and the same top-down attenuation to outgroup member may suggest that we have detected a universal mechanism whose correlates may differ across cultures, but its core components remain constant.

Brain-to-brain synchrony and OT showed culture-specific associations with the neural ingroup bias; brain-to-brain synchrony was

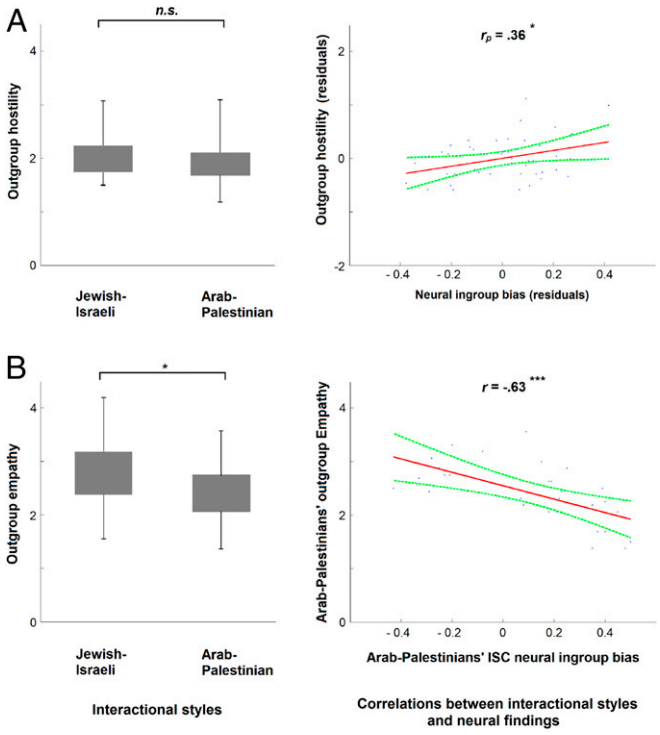

Fig. 3. Relations between neural ingroup-bias and interactional behavior during dyadic interactions. (*A*) Groups' hostility ($N = 67$) scores (*Left*) and partial pairwise correlation (r_p) with both groups' dyadic ($N = 50$) neural ingroup-bias (*Right*). (*B*) Groups' empathy ($N = 60$) scores (*Left*) and the correlation (Pearson's *r*) of the Arab-Palestinian scores ($N = 32$) with their ISC neural scores (*Right*). Error bars represent ±1 SEM. Asterisks describe statistically significant (independent *t* tests) effect (*$P < 0.05$; **$P < 0.005$; ***$P < 0.0005$).

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associated with increased ingroup bias among Arab-Palestinians and higher OT correlated with greater bias in the Jewish-Israeli group. Even low ISC values in electromagnetic recordings strongly predict heightened attention (29) and preference (30). This finding is suggestive of brain-to-brain synchrony among Arab-Palestinians to reflect preference to attend to the suffering of their group members. Brain-to-brain synchrony is also suggested to underlie shared psychological experiences and to bind members of a group into a collective unit (31). This interpretation fits well with the minority status of Arab-Palestinians and accords with the survival function of such group-binding mechanism to enhance group cohesion in the face of external threats (32). Possibly, in more collectivistic societies and in minority groups that feel a threat to group identity, this mechanism is more active, as seen in our findings, and may reflect an often-observed strategy of minority groups to gain power by acting collectively (33). Because social cooperation differs by social status (33), the difference between groups in brain-to-brain synchrony may relate to the social status differences between Arab-Palestinians and Jewish-Israelis. At the same time, our results demonstrate the downside of such group-binding mechanism; the greater the ISC index of Arab-Palestinian adolescents, indicating greater neural binding to the group, the lower was their behavioral empathy to outgroup member, suggesting that in such contexts brain-to-brain synchrony may be a mechanism to cope with disempowerment perhaps by excluding the outgroup majority (34). Indeed, Arab-Palestinian adolescents reported greater ethnocentricity compared with Jewish-Israeli adolescents, and the collectivistic schema may have shaped the ingroup-bias at the neural level, consistent with recent findings in a priming experiment (35).

OT functioned in the same way in the Jewish-Israeli group. Whereas higher peripheral OT has been linked with social collaboration, trust, and generosity, research has also implicated OT in ingroup love and outgroup derogation, particularly when the ingroup experiences threat from the outgroup (3). Throughout animal evolution, the ancient OT molecule, which presumably evolved ∼600 million years ago via gene duplication in jawed fish, enabled organisms to adapt to harsh ecologies by forming social collaboration but also by refining differentiation of ingroup from outgroup members (36). The present findings may be interpreted in the context of the Israeli-Palestinian conflict. Because violence is often experienced between Israeli officials (i.e., police, military) and Arab-Palestinian adolescents, Jewish-Israeli adolescents may see Arab-Palestinian adolescents as a direct threat, rather than vice versa. Hence, outgroup threat experienced by Jewish-Israeli adolescents may trigger the OT system. Future studies should further probe these interesting speculations on the various biological mechanisms (i.e., brain-to-brain synchrony and OT) that bind groups together while at the same time sustain the ingroup bias.

In sum, our findings offer a perspective on the global epidemic of adolescents' exposure to intractable conflict by testing the neural underpinning of the ingroup bias and its temporal dynamics. We detected a neural marker for the adolescent brain's differential response to the pain of a person in their own ingroup versus someone who is in the outgroup with whom they are in intractable conflict. We demonstrated that youngsters who grow up in a climate of long-standing intergroup strife shut down the brain's automatic response to the pain of outgroup members through a late and sustained rhythmic top-down mechanism for processing vicarious pain empathy. We further showed that behavioral hostility and unwillingness for intergroup compromise explain this ingroup-bias. Dehumanization of outgroup members was underpinned by unique neural processes in each group: increased brain-to-brain synchrony in the more collectivistic Arab-Palestinian minority society and increased functioning of the oxytocinergic system in the more individualistic Jewish-Israeli majority. Because the brain's top-down control mechanisms develop on the basis of prior experience and are highly sensitive to social construals, education, and propaganda, our findings pinpoint targets for youth interventions that may promote compassion at the neural level: provision of opportunities for one-on-one encounters with outgroup members, helping adolescents understand the sociopolitical value of compromise and adult modeling on how to conduct dialog with respect and empathy.

Methods

Subjects. Eighty-five healthy human adolescents were recruited for this study via social media, advertisement in schools, and in adolescents' organizations. Inclusion criteria were defined so that participants were right-handed, without history of neurological or psychiatric disorders, wore no metallic items (which could not be removed before the experiment) and whose head did not deviate from the initial position in the MEG helmet. Five of the participants were excluded: two participants did not complete the experiment (reported unbearable pain staying in the MEG without movement), one constantly coughed and moved, one moved excessively (deviation of more than 2 cm), and one moved more moderately (deviation of ∼1 cm) but was still excluded to match the two groups' sample size. Hence, a final cohort of 80 adolescent high school students (50% Arabs-Palestinians; 52.5% males; age: 15.5–18.5 y, mean ± SD, 16.63 ± 0.89 y). The study received approval from the Bar-Ilan University ethics committee, and participants gave written informed consent before the experiment in line with Bar-Ilan University's Institutional Review Board. Subjects received monetary compensation for their participation. See *SI Methods* for further demographic information on the subjects.

Experimental Procedure. Participants lay in supine position inside the MEG system while facing a screen projecting the stimuli. Subjects received instructions to remain relaxed and not move their limbs; the experimenter observed their compliance using an infrared camera. We programmed and operated the experiment using E-Prime software (Psychology Software Tools). We presented all words and experimental instructions in the participant's mother tongue (either Hebrew or Arabic).

We used four conditions: ingroup P, ingroup no-P, outgroup P, and outgroup no-P. The purpose of pain (P) stimuli was to elicit empathy, whereas that of no-pain (no-P) stimuli was to not elicit empathy but to control for the other parameters induced by the visual stimuli; filler stimuli were used to maintain attention throughout the experiment (Fig. 1). See *SI Methods* for more information on the stimuli used.

The stimuli presented while measuring participants' brain activity comprised a total of 288 trials, grouped into 48 batteries of 6 trials each (3 P and 3 no-P trials). We counterbalanced the order of the six-trial series and the pictures assigned to the protagonist targets across participants, to avoid unspecific stimulus or structure effects. Every six-trial series began with explicit priming for 3 s on the group membership of the Arab-Palestinian or Jewish-Israeli protagonist whose limbs would be presented over the next six screens. Hence, all six of the stimuli in each series (the three P stimuli and the three no-P stimuli) were primed as belonging to the same Jewish-Israeli or Arab-Palestinian individual. P and no-P stimuli were presented for 1.5 s each, interleaved with crosshair fixation screens randomly varying in duration between 1,169 and 1,670 ms (Fig. 1). In addition, filler trials comprised ca. 8% of all trials. The experimenter asked participants to recall and report the occurrences of the filler trials at each pause (every ca. 1.5 min; there were 12 pauses throughout the experiment). We did not include the filler trials in the experimental stimuli database or analyze them.

MEG Recordings and Data Preprocessing. We recorded ongoing brain activity (sampling rate, 1,017 Hz, online 1- to 400-Hz band-pass filter) using a whole-head 248-channel magnetometer array (Magnes 3600 WH; 4-D Neuroimaging) inside a magnetically shielded room. Reference coils located ∼30 cm above the head, oriented by the *x*, *y*, and *z* axes, enabled removal of environmental noise. See *SI Methods* for more information on data cleaning. We segmented the data into 1,950-ms epochs, including a baseline period of 470 ms and then filtered it in the 1- to 200-Hz range with 10 s padding and then resampled them to 400 Hz.

Source and Spectral Analyses. We attached five coils to the participant's scalp to record head position relative to the sensor. We performed analyses using MATLAB 7 (MathWorks) and the FieldTrip software toolbox (37). We built a single shell brain model based on an MNI postpuberty template brain (38), which we modified to fit each subject's digitized head shape using SPM8 (Wellcome Department of Imaging Neuroscience, University College London; www.fil.ion.ucl.ac.uk). Head shape underwent manual digitization (Polhemus FASTRAK digitizer). We applied adaptive spatial filtering (39) relying on partial canonical correlations. See *SI Methods* for more information on head shape model (grid) and source reconstruction.

Finally, we extracted time series from regions of interest by applying a linear constrained minimum variance beam former. We applied tapers to each time

window to compute time–frequency representations (TFRs) of power for each trial and to calculate the fast Fourier transform (FFT) for short sliding time windows. We analyzed data in alignment to stimulus onset and then averaged the power estimates across tapers. A Hanning taper, applied to each epoch of the 248-sensor data, yielded the FFT for short sliding time windows of 0.5 s in the broad alpha 7- to 15-Hz frequency range, resulting in a spectral resolution of 2 Hz. We obtained induced activity by subtracting evoked-components' power from oscillatory power. These time series were also used to calculate ISCs (ISC–Pearson). See *SI Methods* for more information on the ISC analysis.

Statistical Analysis. In all statistical comparisons between groups on the behavioral and endocrinal measures, we applied an independent two-sided *t* test. Correlations between neural and behavioral data for each group applied Pearson's *r*, whereas correlations for both groups completed at the dyadic level by applying partial pairwise correlations r_p (40). Furthermore, statistical procedures on the MEG data assessed significance of the power values using a randomization procedure (41). See *SI Methods* for more information on this statistical procedure.

Behavioral and Hormonal Measurements. To test adolescents' social behavior toward an outgroup member during one-on-one interactions, after MEG sessions (Fig. 1), we applied two well-validated paradigms, a positive dialog and a conflict dialog (42), between same-sex mixed-group partners, one Jewish-Israeli and one Arab-Palestinian, randomly assigned. To tap views and attitudes regarding the Israeli-Palestinian conflict, we conducted an in-depth structured individual interview with each participant. See *SI Methods* for information on the dialogs, interview, and coding procedures. Finally, we collected saliva samples using Salivette (Sarstedt) at three time points: upon arrival, after the MEG experiment, and before departure. We kept saliva samples ice-chilled for up to 1 h before centrifuge at 4 °C at 1,500 × *g* for 15 min and then stored liquid samples at −80 °C. To concentrate the samples by three to four times, we lyophilized liquid samples overnight and kept them at −20 °C until assayed. We reconstructed dry samples in the assay buffer immediately before analysis using the Oxytocin ELISA kit (Assay Design; through ENZO). We performed measurements in duplicate, calculating the concentration of samples using MATLAB 7 (MathWorks) according to relevant standard curves. The intraassay and interassay coefficients were <12.3 and <14.5%, respectively.

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