

Compassion Training Alters Altruism and Neural Responses to Suffering

Psychological Science
24(7) 1171–1180
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DOI: 10.1177/0956797612469537
pss.sagepub.com


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Abstract

Compassion is a key motivator of altruistic behavior, but little is known about individuals' capacity to cultivate compassion through training. We examined whether compassion may be systematically trained by testing whether (a) short-term compassion training increases altruistic behavior and (b) individual differences in altruism are associated with training-induced changes in neural responses to suffering. In healthy adults, we found that compassion training increased altruistic redistribution of funds to a victim encountered outside of the training context. Furthermore, increased altruistic behavior after compassion training was associated with altered activation in brain regions implicated in social cognition and emotion regulation, including the inferior parietal cortex and dorsolateral prefrontal cortex (DLPFC), and in DLPFC connectivity with the nucleus accumbens. These results suggest that compassion can be cultivated with training and that greater altruistic behavior may emerge from increased engagement of neural systems implicated in understanding the suffering of other people, executive and emotional control, and reward processing.

Keywords

compassion, meditation, altruism, emotion regulation, fMRI, social behavior, neuroimaging, decision making, emotional control, individual differences

Received 3/21/12; Revision accepted 11/1/12

Compassion and altruism are of great interest to philosophical and scientific inquiry because of their central role in successful societies (Darwin, 1871/2004; Fehr & Fischbacher, 2003; Smith, 1759/2010; Sober, Wilson, & Wilson, 1999). Compassion is the emotional response of caring for and wanting to help those who are suffering (Batson, 1991; Eisenberg, Fabes, & Spinrad, 2006; Goetz, Keltner, & Simon-Thomas, 2010) and may have evolved in humans to foster altruistic acts that increase survival of kin as well as nonkin (Darwin, 1871/2004; Goetz et al., 2010; Sober et al., 1999). Such acts include enhancing the welfare of vulnerable offspring, promoting intimate bonds between partners, and facilitating cooperation among genetically unrelated strangers (Batson, 1991; Darwin, 1871/2004; Goetz et al., 2010; Sober et al., 1999). Despite the clear societal benefits of cultivating compassion, little

is known about whether compassion and altruism can be trained and about the neural mechanisms that might underlie such effects.

Contemplative traditions claim that compassion can be enhanced with meditation training and that this results in greater real-world altruistic behavior (Lutz, Brefczynski-Lewis, Johnstone, & Davidson, 2008). In compassion training, compassion is cultivated toward different people, including loved ones, strangers, and difficult persons, as well as toward the self (Salzberg, 1997). Studies indicate

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that compassion training can improve personal well-being, including stress-related immune responses (Pace et al., 2009), positive affect (Fredrickson, Cohn, Coffey, Pek, & Finkel, 2008; Hutcherson, Seppala, & Gross, 2008), and psychological and physical health (Fredrickson et al., 2008). Compassion training also enhances responses toward other people. Expert meditation practitioners show greater empathic neural responses when listening to sounds of other people's suffering during compassion meditation practice than control subjects do (Lutz, Brefczynski-Lewis, et al., 2008). Recent work suggests that compassion training can increase prosocial behavior (Leiberg, Klimecki, & Singer, 2011; Condon, Desbordes, Miller, & DeSteno, in press), positive emotions toward people who are suffering (Klimecki, Leiberg, Lamm, & Singer, 2012), and empathic accuracy (Mascaro, Rilling, Tenzin Negi, & Raison, 2013).

The neural mechanisms by which compassion training alters altruistic responses to suffering remain unknown. In the study reported here, we investigated whether short-term compassion training would enhance altruistic behavior toward a victim encountered outside of the training context. Altruistic behavior was assessed using the redistribution game, a novel economic decision-making task that models both unfair treatment of a victim and costly redistribution of funds to the victim. Furthermore, we measured brain activation before and after 2 weeks of training using functional MRI (fMRI) and investigated whether increased altruism could be explained by training-induced changes in the neural response to human suffering.

To rigorously test these hypotheses, we compared altruistic responses of participants given compassion training with responses of participants given an active control intervention of reappraisal training. Compassion trainees cultivated compassion for different targets, and reappraisal trainees practiced reinterpreting personally stressful events to decrease negative affect. Both interventions trained emotion-regulation strategies that promote well-being, but they differed in that the goal of compassion training was to increase empathic concern and the desire to relieve suffering (Lutz, Brefczynski-Lewis, et al., 2008), whereas the goal of reappraisal training was to decrease one's personal distress (Ochsner & Gross, 2005). Reappraisal training provided an ideal control for compassion training because although the combination of decreased distress and increased empathic concern predicts helping behavior (Batson, 1991; Eisenberg et al., 2006), reappraisal training only decreases distress without enhancing concern.

We hypothesized that compassion training would increase altruistic behavior by enhancing neural systems involved in (a) the recognition and understanding of another person's suffering and (b) emotion regulation of

responses to suffering that support affiliation and helping behavior. The neuroscience of empathy highlights two systems for understanding the states of other people: experience sharing, which involves vicariously sharing the states of others, and mentalizing, which involves explicitly considering and understanding others' mental states through social inferences as well as through self-referential processes (Lamm, Decety, & Singer, 2011; Zaki & Ochsner, 2012). If the neural representation of suffering is increased by compassion training, then regulatory systems are needed to respond to this suffering with an approach rather than an avoidance response.

Prior theoretical and empirical work suggests that altruistic responses toward another person's suffering can be strengthened through either of two regulatory pathways (Decety & Jackson, 2006): (a) decreasing personal distress, which reduces negative arousal and avoidance behavior, or (b) increasing empathic concern, which strengthens the motivation to approach and relieve another person's suffering (Batson, 1991). In response to suffering, we predicted that greater altruism in compassion trainees would be associated with increased activation in prefrontal cortex (PFC), given its role in controlled processing (Miller & Cohen, 2001), emotion regulation (Ochsner & Gross, 2005; Urry et al., 2006; Wager, Davidson, Hughes, Lindquist, & Ochsner, 2008), and fronto-parietal control networks (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). We also predicted that compassion training would be associated with decreased amygdala activation, given the amygdala's role in responding to negative stimuli and distress (Zald, 2003). Further, we hypothesized that greater prosocial behavior after compassion training would be associated with higher levels of activation in anterior insula, which has been implicated in studies of empathy and compassion (Immordino-Yang, McColl, Damasio, & Damasio, 2009; Lamm et al., 2011; Lutz, Brefczynski-Lewis, et al., 2008; Singer et al., 2006) and predicts helping behavior (Hein, Silani, Preuschoff, Batson, & Singer, 2010; Masten, Morelli, & Eisenberger, 2011). This greater prosocial behavior would also be correlated with increased activation in nucleus accumbens (NAcc), which has been linked to charitable giving (Harbaugh, Mayr, & Burghart, 2007; Moll et al., 2006) and positive appraisals of aversive stimuli (Wager et al., 2008).

We specifically tested these hypotheses against the reappraisal group, in which the psychological goal was self-focused (to decrease one's own suffering) rather than other-focused (to decrease other people's suffering through compassion). Although many of the same regions are implicated in reappraisal as in compassion (Wager et al., 2008), we expected that the hypothesized changes (e.g., increases in PFC activity) would not be associated

with altruistic behavior because the behavior is not congruent with reappraisal's goals.

Method

Participants

Fifty-six participants completed the entire protocol, and the final sample consisted of 41 participants who believed that they were interacting with real players in the redistribution game (the other 15 participants expressed suspicion about the manipulation and were therefore excluded from the analysis; see Tables S1 and S2 and Supplementary Method and Analyses in the Supplemental Material available online for further information about the sample). Each participant was randomly assigned to receive either compassion training ($n = 20$; 12 female, 8 male; mean age = 21.9 years) or reappraisal training ($n = 21$; 13 female, 8 male; mean age = 22.5 years), completed 2 weeks of training (11 out of 14 practice days were required), and attended an fMRI session both before the start of training and after training finished. The groups did not differ in age, gender, baseline trait compassion, or the amount of practice time they received. Participants were healthy adults (18–45 years of age), right-handed, and had no previous experience in meditation or cognitive-behavioral therapy. No participant had issues that would pose a risk for his or her safety in the scanner. The experiment was approved by the University of Wisconsin–Madison Health Sciences Institutional Review Board. All subjects gave informed consent and were paid for participation.

Procedure

Overview. Participants came to the laboratory on three occasions. At Visit 1, each participant was randomly assigned to compassion training or reappraisal training and briefly instructed in the assigned strategy, following which he or she practiced the fMRI task in a mock MRI scanner. Visit 2 occurred approximately 1 week later; during this visit, participants completed the pretraining fMRI scan and began training later that day. Visit 3 occurred immediately after the 2 weeks of training were completed; this visit included the posttraining fMRI scan and the altruistic behavior task (performed outside of the scanner). For more details about the procedure, see Supplementary Method and Analyses in the Supplemental Material.

Trainings. Training consisted of practicing either compassion or reappraisal using guided audio instructions (via the Internet or compact disc) for 30 min per day for 2 weeks. Compassion trainees practiced cultivating

feelings of compassion for different targets (a loved one, the self, a stranger, and a difficult person), and reappraisal trainees practiced reinterpreting personally stressful events to decrease negative affect (see Trainings and Fig. S1 in the Supplemental Material).¹

Altruistic behavior task: redistribution game. We tested whether compassion training could affect altruistic behavior outside of the training context using the redistribution game. This economic decision-making task models both unfair treatment of a victim and costly redistribution of funds to the victim. Using anonymous online interactions, participants first observed a dictator (endowed with \$10) transfer an unfair amount of money (\$1) to a victim who had no money (Fig. 1a). After witnessing this violation of the fairness norm (Fehr & Fischbacher, 2003), participants could choose to spend any amount of their own endowment (\$5) to compel the dictator to give twice that amount to the victim (Fig. 1b). Participants were paid the amount that was left in their endowment after making the decision. (See Supplementary Method and Analyses in the Supplemental Material for full details of the redistribution game.)

Participants were told that they were playing the game with live players over the Internet. Effects of demand characteristics on behavior were minimized by presenting the game as a unique study, describing it in purely economic terms, never instructing participants to use the training they received, removing the physical presence of players and experimenters during game play, and enforcing real monetary consequences for participants' behavior. Because compassionate behavior is specifically evoked by unfairness, all participants observed the same preprogrammed unfair dictator offer. At the end of the entire protocol, participants were debriefed and asked whether they believed they were playing against real people in the game. Data were analyzed only for participants who believed the paradigm (see Table S2 in the Supplemental Material).

fMRI task and stimuli. To determine whether altruistic behavior was predicted by changes in neural responses to human suffering, we scanned participants using fMRI before and after training while they employed their assigned emotion-regulation strategy. Participants in the two groups were presented with images of human suffering and nonsuffering (neutral condition). Compassion trainees were instructed to evoke feelings of compassion while silently repeating compassion-generating phrases. In contrast, reappraisal trainees were instructed to decrease negative emotions by silently reinterpreting the emotional meaning of the images. (See Supplementary Method and Analyses in the Supplemental Material for fMRI data-acquisition parameters).

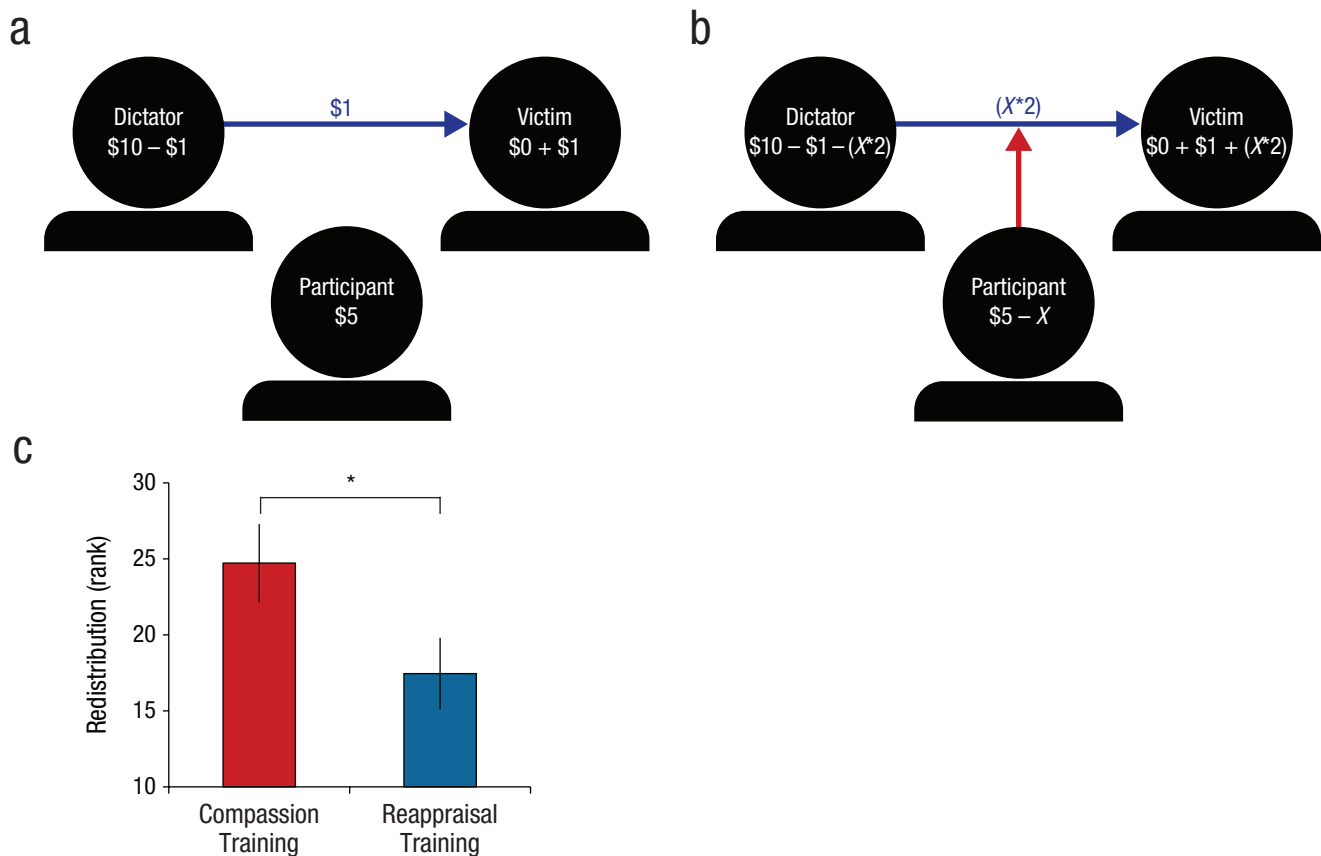


Fig. 1. Paradigm of and results for the redistribution game. In the first stage of the redistribution game (a), the dictator (endowed with \$10) transfers an unfair amount of money (\$1) to the victim while the participant (endowed with \$5) observes. In the second stage (b), the participant can spend any amount (X) up to \$5 to compel the dictator to give twice that amount to the victim. The graph (c) shows the average rank-transformed redistribution amount as a function of the type of training participants received. Redistribution of \$4 (i.e., $X = \$2$; rank = 35.5 of 41) results in an equal distribution between the dictator and the victim (\$5 each). The asterisk indicates that there was a significant difference between groups ($p < .05$). Error bars denote standard errors of the mean.

Images of suffering depicted emotional distress, physical pain, or acts of violence (e.g., a burn victim, a crying child). Neutral images depicted people in nonemotional situations, such as working or walking down a street. Two parallel sets of images (20 suffering and 16 neutral) were created to ensure that participants viewed different images before and after training. Set order was counter-balanced and randomized. Images were pseudorandomized so that three or more images from either condition were not presented in a row. Image randomization was performed once for each set and then fixed. Images were balanced across sets for published normative ratings of valence and arousal, as well as for properties of hue, luminance, and saturation (all $ps > .1$).

Participants were instructed to regulate their emotional responses to the images over three blocks. Each block began with a 20-s fixation baseline period. Participants then received both an auditory and visual instruction (3 s) stating that they should invoke either “compassion”

or “reappraisal” (depending on group assignment), which was followed by a fixation cross (5–7 s). They then applied the assigned regulation strategy to a series of 12 images. Each image was presented for 12 s and separated by a fixation interval (5–11 s, randomized). Blocks ended with a final fixation baseline (17–38 s). After each block, participants saw each image again for 2 s and rated the arousal of each image (1 = *least arousing*, 7 = *most arousing*).

Behavioral analysis

Across all participants, the redistribution response was positively skewed (skewness = 1.5, $SE = 0.37$), and 2 participants qualified as outliers ($> 3 SD$ from the population mean). Because of these violations of normality, we rank-ordered the behavioral response across both groups so that strong assumptions were not made about the scaling or normality of the residuals. Parametric tests were then

performed on the ranked data. To test the mean difference between groups, we performed an independent-samples t test on the ranks. For in-depth analyses and discussion of redistribution values and ranks, see Supplementary Method and Analyses in the Supplemental Material.

fMRI analyses

Overview. A series of tests were conducted to identify regions in which changes due to training predicted greater redistribution in compassion training than in reappraisal training. A whole-brain interaction contrast (Group \times Redistribution Rank) was tested on neural-change scores. Follow-up tests were conducted using both across- and within-subjects analyses to identify regions that were functionally connected to clusters identified in the interaction analysis and networks involved in emotion regulation. Finally, we investigated whether reported arousal was associated with either redistribution or neural changes. See Supplementary Method and Analyses in the Supplemental Material for full details.

Interaction analysis. Individual functional and structural MRI brain data were preprocessed and normalized to Montreal Neurological Institute (MNI) space. Each participant's neural response to suffering during regulation was estimated with the contrast between activation to images of suffering and activation to neutral images at each fMRI scan time point (before training, after training) using standard first-level analyses (see Supplementary Method and Analyses in the Supplemental Material), and beta coefficients were converted to percentage signal change (PSC). Training-induced changes were calculated by subtracting PSC values before each scan from PSC values after each scan. To identify regions where training-related changes specifically predicted greater redistribution in compassion trainees than in reappraisal trainees, a second-level Group \times Redistribution Rank voxel-wise analysis was performed, controlling for main effects of group and redistribution.

First, whole-brain analyses were conducted and corrected for multiple comparisons ($p < .01$ after an initial voxel-wise threshold of $p < .01$) using Monte Carlo simulation. This analysis identified the right inferior parietal cortex (IPC). To decompose the interactions, we extracted mean PSC-change scores from the clusters for each participant and analyzed them to yield parameter estimates and determine the directionality of the relationship for each group. These values were used for descriptive and diagnostic purposes only (Vul, Harris, Winkielman, & Pashler, 2009). In region-of-interest (ROI) analyses, data from the Group \times Redistribution Rank interaction were

corrected for multiple comparisons ($p < .01$ after an initial voxel-wise threshold of $p < .01$) using Monte Carlo simulation within bilateral a priori ROIs of the amygdala, insula, and NAcc.

IPC conjunction analysis. To identify regions that may be functionally connected to the IPC in order to increase the amount participants redistributed in each training group, we performed a conjunction analysis requiring voxels to be (a) correlated with changes in IPC activation across participants in both groups (voxel-wise $p < .01$) and (b) identified in the original Group \times Redistribution Rank interaction (voxel-wise $p < .01$). This analysis identified a cluster in the dorsolateral PFC (DLPFC; whole-brain corrected at $p < .01$ after a conjunction voxel-wise threshold of $p < .001$).

Psychophysiological interaction (PPI) analysis. To determine regions in which altered PFC connectivity predicted higher amounts of redistribution in compassion trainees than in reappraisal trainees, we performed a PPI analysis using the DLPFC seed region identified by the IPC conjunction analysis. The PPI regressor consisted of comparing DLPFC connectivity in response to images of suffering with DLPFC connectivity in response to neutral images. Training-induced PPI changes were calculated by subtracting PPI betas before each scan from PPI betas after each scan. To identify regions where training-related PPI changes specifically predicted greater redistribution in compassion trainees than in reappraisal trainees, we performed a second-level Group \times Redistribution Rank voxel-wise analysis, controlling for main effects of group and redistribution. Voxel-wise regression maps were corrected for multiple comparisons ($p < .01$ after an initial voxel-wise threshold of $p < .01$) using Monte Carlo simulation within each bilateral ROI (amygdala, insula, and NAcc). For descriptive purposes, mean PPI-change betas were extracted from the clusters for each participant and analyzed to yield parameter estimates and determine the directionality of the relationship for each group.

Correlational analyses. Compassion training may increase altruistic behavior by decreasing personal distress evoked by suffering (Batson, 1991; Eisenberg et al., 2006). To test this, we computed arousal-change scores (analogous to the neural-change scores) and correlated them with altruistic redistribution in each group. To examine whether changes in arousal were associated with changes in neural responses to suffering, we computed correlations between arousal-change scores and neural-change scores identified in the previous fMRI analyses in each group.

Results

Altruistic redistribution

Findings in an independent validation sample² ($N = 72$) confirmed that altruistic redistribution is a behavioral signature of compassion: Individuals who endorsed greater levels of trait empathic concern (Davis, 1980) redistributed more money, $r(70) = .43$, $p < .001$ (Fig. S2 in the Supplemental Material). In the main study, after 2 weeks of training, compassion trainees spent more money to redistribute funds to the victim compared with reappraisal trainees (Fig. 1c), independent-samples $t(39) = 2.09$, $p < .05$, $d = 0.65$. Compassion trainees also spent more than individuals with no training in the validation sample (Fig. S3 in the Supplemental Material). Compassion trainees spent 1.84 times more money than reappraisal trainees (\$1.14 vs. \$0.62, respectively) and increased the distribution between the dictator and the victim by 57%. In contrast, reappraisal trainees increased the distribution by only 31%. This demonstrates that purely mental training in compassion can result in observable altruistic changes toward a victim, even when individuals are not explicitly cued to generate compassion.

Neuroimaging

Group differences in neural change and altruistic redistribution. We hypothesized that greater altruism resulting from compassion training would be predicted by training-related changes in the neural responses to images of suffering. The whole-brain Group \times Redistribution Rank interaction test revealed that training-induced changes in right IPC activation were differentially associated with altruistic redistribution in the two training groups (Fig. 2a; $p < .01$, corrected; see Tables S3 and S4 in the Supplemental Material). In compassion trainees, greater IPC activation due to training was associated with greater redistribution, but this was not found in reappraisal training (Fig. 2b; also see Table S5 in the Supplemental Material). Within the a priori ROIs, no region survived correction at $p < .01$. See Fig. S4 and Supplementary Method and Analyses in the Supplemental Material for exploratory analyses within the ROIs.

The IPC is implicated in experience sharing as part of the mirror-neuron network (Gallese, Keysers, & Rizzolatti, 2004; Lamm et al., 2011), and we investigated whether the IPC was functionally connected to other regions that also differentially predicted redistribution between groups. The IPC conjunction test identified only the DLPFC (Fig. 2c; also see Tables S3 and S4 in the Supplemental Material; $p < .01$ whole-brain corrected), where greater increases in DLPFC activation predicted greater altruistic redistribution in compassion trainees, and the opposite relationship was found in reappraisal trainees (Fig. 2d; also see Table S5 in the Supplemental Material). The changes in IPC and

DLPFC were highly coupled—compassion training: $r(18) = .92$, $p < .001$; reappraisal training: $r(19) = .79$, $p < .001$, and both regions differentially predicted redistribution between groups. These findings suggest that frontoparietal executive control networks (Dosenbach et al., 2008; Vincent et al., 2008) may be recruited by compassion training in order to regulate emotions and increase altruistic behavior.

DLPFC PPI connectivity changes and altruistic redistribution.

Emotion regulation is thought to involve the influence of the PFC over other regions such as the amygdala, insula, and NAcc (Ochsner & Gross, 2005; Urry et al., 2006; Wager et al., 2008). Using PPI, we tested whether changes in task-related functional connectivity between DLPFC and amygdala, DLPFC and NAcc, or DLPFC and insula predicted greater altruistic redistribution in compassion training than in reappraisal training. Using the DLPFC cluster defined by the IPC conjunction test as a seed (Fig. 3a), we found a significant interaction in the NAcc, demonstrating that DLPFC-NAcc connectivity was differentially associated with redistribution in compassion training compared with reappraisal training (Fig. 3b; $p < .01$, corrected within the ROI; see Tables S3 and S4 in the Supplemental Material). Compassion trainees who showed greater DLPFC-NAcc connectivity redistributed more funds after training, whereas reappraisal trainees who showed greater DLPFC-NAcc connectivity redistributed less money after training (Fig. 3c; see also Table S5 in the Supplemental Material; see Supplementary Method and Analyses in the Supplemental Material for discussion of the directionality of the connectivity). No relationship was found in the insula or the amygdala.

Arousal correlations with altruistic redistribution and neural change.

Compassion training may increase altruistic behavior by decreasing personal distress evoked by suffering (Batson, 1991; Eisenberg et al., 2006). We found that decreases in reported arousal to images of suffering were correlated with increased redistribution in compassion trainees, $r(18) = -.45$, $p < .05$, but not in reappraisal trainees, $r(19) = .09$, $p = .70$. We further investigated whether decreases in arousal were associated with neural changes and found that greater DLPFC-NAcc connectivity was correlated with decreases in arousal in compassion trainees, $r(18) = -.64$, $p < .01$, but not in reappraisal trainees, $r(19) = -.13$, $p = .59$. Decreases in arousal were not associated with IPC or DLPFC changes in either group (all $ps \geq .21$).

Discussion

Individuals who trained in compassion for 2 weeks were more altruistic toward a victim after witnessing an unfair social interaction compared with individuals who trained

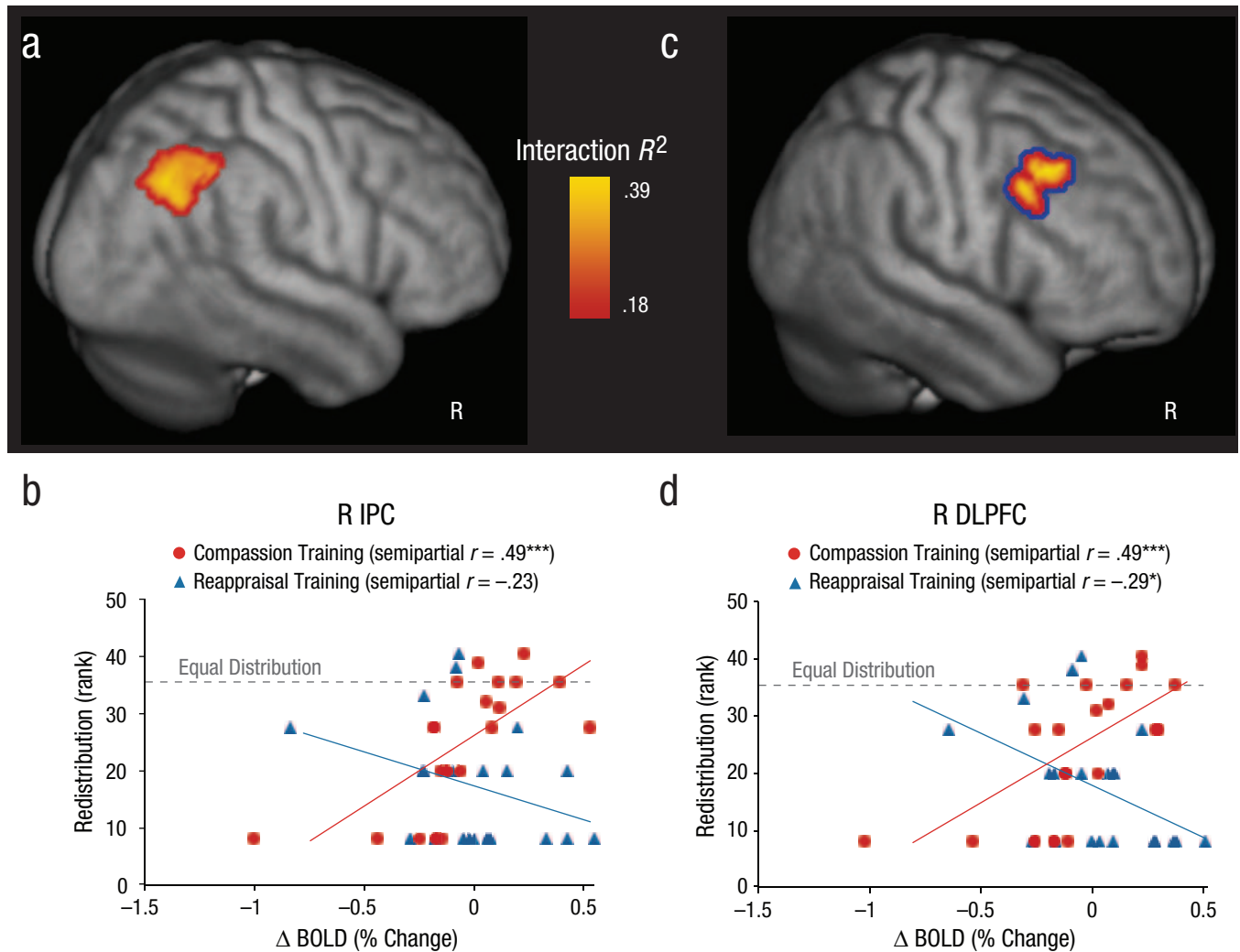


Fig. 2. Activation in right inferior parietal cortex (IPC) and right dorsolateral prefrontal cortex (DLPFC). The brain images in (a) and (c) show blood-oxygen-level-dependent (BOLD) changes in right IPC and right DLPFC, respectively, from before to after training in compassion trainees; in both sessions, participants regulated their emotional responses while viewing images of human suffering. Images are in Montreal Neurological Institute space. The color coding indicates the amount of variance accounted for by the Group \times Redistribution Rank interaction. The blue outline in (c) indicates that the cluster was identified by a conjunction test. The scatter plots (with best-fitting regression lines) in (b) and (d) show rank-transformed redistribution amounts for the two training groups as a function of the percentage signal change in BOLD responses from before training to after training. The dashed line indicates the rank of a redistribution of \$4 (rank = 35.5 of 41), which results in an equal \$5 distribution between the dictator and the victim. Asterisks indicate significant results ($*p < .05$, $***p < .001$). R = right.

in reappraisal and individuals in a validation control group. This demonstrates that a purely mental training can generalize to behavioral domains by affecting social behavior outside of the training context. Furthermore, increases in altruistic responses were correlated with training-related changes in the neural response to suffering, which provides evidence for functional neuroplasticity in the circuitry underlying compassion and altruism.

The pattern of neural changes in compassion training suggests that increased altruistic behavior is achieved by

enhancing neural mechanisms that support the understanding of others' states, greater fronto-parietal executive control, and up-regulation of positive emotion systems. Greater IPC activation specifically predicted greater redistribution in compassion trainees and not in reappraisal trainees, which suggests that IPC recruitment is a unique neural marker for altruism induced by compassion training. This region has been implicated in the human mirror-neuron system (Gallese et al., 2004) and may reflect increased simulation of the suffering of other people. If

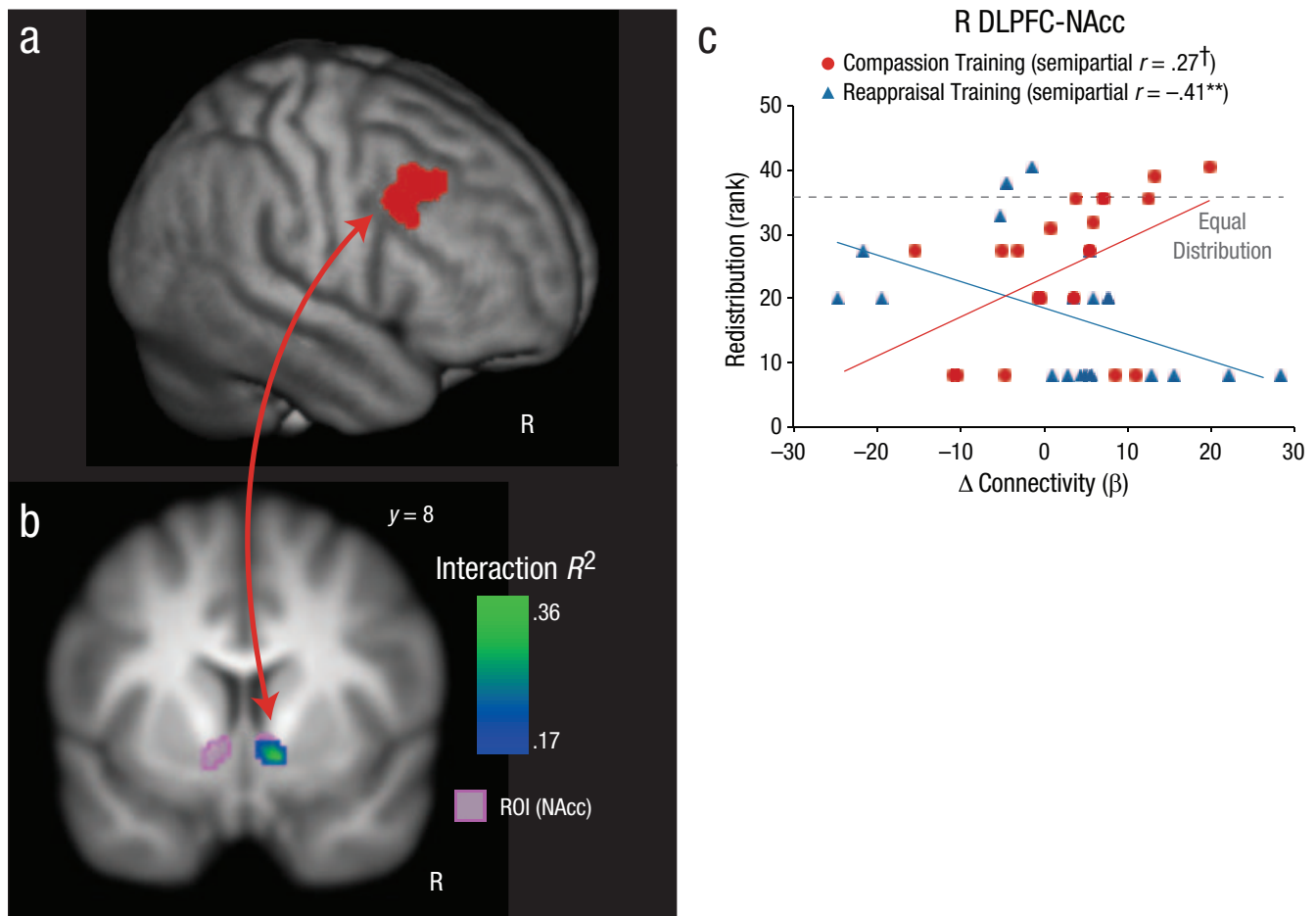


Fig. 3. Results for connectivity between right dorsolateral prefrontal cortex (DLPFC) and nucleus accumbens (NAcc). The image in (a) shows the DLPFC cluster identified by the conjunction test, which was used as the seed region in the psychophysiological interaction analysis. The image in (b) shows the regions of NAcc in which there was differential activation in response to images of human suffering before and after training in compassion trainees. Images and coordinates are in Montreal Neurological Institute space. The color coding indicates the amount of variance accounted for by the Group \times Redistribution Rank interaction. The scatter plot (with best-fitting regression lines) in (c) shows rank-transformed redistribution amounts for the two training groups as a function of changes in right DLPFC-NAcc connectivity. The dashed line indicates the rank of a redistribution of \$4 (rank = 35.5 of 41), which results in an equal \$5 distribution between the dictator and the victim. Asterisks indicate significant results (** $p < .01$, † $p = .07$). R = right; ROI = region of interest.

the signal of other people's suffering is indeed increased by compassion training, this leads to an emotion-regulatory challenge that requires trainees to approach rather than avoid suffering in order to engage in prosocial behavior. This transformation of emotional response may have been instantiated by a fronto-parietal executive control network (Dosenbach et al., 2008; Vincent et al., 2008) in order to increase altruistic behavior in compassion trainees. The coordinated activation of the IPC and DLPFC in compassion trainees may reflect greater sustained attention and goal maintenance (Miller & Cohen, 2001) to help other individuals, as well as integration of information from systems that process both external information (of other

people's suffering) and internal information (the goal to help; Vincent et al., 2008).

Regulation of internal information may include increasing positive emotions toward other people's suffering, as reflected by the increased DLPFC-NAcc connectivity that predicted redistribution in compassion trainees. This may represent increasing positive appraisals of aversive stimuli (Wager et al., 2008) by enhancing the reward value of the victim's well-being (e.g., caring) and increasing the anticipated reward (Knutson & Cooper, 2005) of helping the victim. Furthermore, decreased reported arousal after compassion training may be due to enhancement of reward-related neural systems. These findings

also support research suggesting that compassion training enhances positive emotions and neural substrates of affiliation (Klimecki et al., 2012).

The relationship between training-induced neural changes (DLPFC activation and DLPFC-NAcc connectivity) and altruistic behavior was not unique to compassion trainees. In fact, greater changes in these regions predicted less redistribution in reappraisal trainees. This finding may be due to the differing regulatory goals between compassion training and reappraisal training. In compassion training, the goal was to increase caring for people who are suffering and to help, whereas the goal in reappraisal training was to decrease personal negative emotions. In a social context, the goals of compassion training and reappraisal training are opposing (other-focused vs. self-focused), and this may explain the cross-over interaction effects. In reappraisal training, neural changes may have resulted in decreased helping of other individuals in order to serve the primary goal of decreasing personal negative affect.

A clear limitation of this study is that altruistic behavior was not measured at pretraining, although a separate validation sample was used to estimate pretraining levels. Future research may build on this study's findings by measuring altruism at baseline, which may strengthen claims that compassion training increases altruism (Leiberg et al., 2011). Furthermore, emotional valence and arousal may be measured using methodology that is less susceptible to demand characteristics, such as facial electromyography and skin conductance response. In future research, longitudinal designs should be employed to determine the length of compassion training needed to have sustained behavioral effects.

In sum, these results build on existing evidence that the adult human brain may demonstrate functional and structural changes after mental training (Davidson & McEwen, 2012; Klingberg, 2010; Lutz, Slagter, Dunne, & Davidson, 2008) and extend these previous findings to include socioemotional domains such as compassion and altruism. Our findings support the possibility that compassion and altruism can be viewed as trainable skills rather than as stable traits. This lays the groundwork for future research to explore whether compassion-related trainings can benefit fields that depend on altruism and cooperation (e.g., medicine) as well as clinical subgroups (Hofmann, Grossman, & Hinton, 2011) characterized by deficits in compassion, such as psychopaths (Blair, 2007).

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

This work was supported by the National Institutes of Health (P01-AT004952 and T32-MH018931—R. J. Davidson, principal

investigator; P30-HD003352—M. Seltzer, principal investigator); University of Wisconsin—Madison Department of Psychology (Hertz Award to A. S. Fox and H. Y. Weng); the Fetzer Institute, John Templeton Foundation, Impact Foundation, J. W. Kluge Foundation, and Mental Insight Foundation (R. J. Davidson); the Mind and Life Institute (H. Y. Weng); and gifts from Bryant Wangard, Ralph Robinson, Keith and Arlene Bronstein, and Ann Down (R. J. Davidson).

Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

Notes

1. Training audio files and written scripts can be downloaded at www.investigatinghealthyminds.org/compassion.html.
2. See Supplementary Method and Results in the Supplemental Material for detailed method and analyses regarding the independent validation study.

References

- Batson, C. D. (1991). *The altruism question*. Hillsdale, NJ: Erlbaum.
- Blair, R. J. R. (2007). The amygdala and ventromedial prefrontal cortex in morality and psychopathy. *Trends in Cognitive Sciences*, *11*, 387–392.
- Condon, P., Desbordes, G., Miller, W., & DeSteno, D. (in press). Meditation increases compassionate responses to suffering. *Psychological Science*.
- Darwin, C. (2004). *The descent of man and selection in relation to sex*. London, England: Penguin. (Original work published 1871)
- Davidson, R. J., & McEwen, B. S. (2012). Social influences on neuroplasticity: Stress and interventions to promote well-being. *Nature Neuroscience*, *15*, 689–695.
- Davis, M. A. (1980). A multidimensional approach to individual differences in empathy. *JSAS Catalog of Selected Documents in Psychology*, *10*, 85.
- Decety, J., & Jackson, P. L. (2006). A social-neuroscience perspective on empathy. *Current Directions in Psychological Science*, *15*, 54–58.
- Dosenbach, N. U. F., Fair, D. A., Cohen, A. L., Schlaggar, B. L., & Petersen, S. E. (2008). A dual-networks architecture of top-down control. *Trends in Cognitive Sciences*, *12*, 99–105.
- Eisenberg, N., Fabes, R. A., & Spinrad, T. L. (2006). Prosocial development. In N. Eisenberg, W. Damon, & R. M. Lerner (Eds.), *Handbook of child psychology, Vol. 3: Social, emotional, and personality development* (pp. 646–718). New York, NY: Wiley.
- Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, *425*, 785–791.
- Fredrickson, B. L., Cohn, M. A., Coffey, K. A., Pek, J., & Finkel, S. M. (2008). Open hearts build lives: Positive emotions, induced through loving-kindness meditation, build consequential personal resources. *Journal of Personality and Social Psychology*, *95*, 1045–1062.
- Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, *8*, 396–403.

- Goetz, J. L., Keltner, D., & Simon-Thomas, E. (2010). Compassion: An evolutionary analysis and empirical review. *Psychological Bulletin*, *136*, 351–374.
- Harbaugh, W. T., Mayr, U., & Burghart, D. R. (2007). Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science*, *316*, 1622–1625.
- Hein, G., Silani, G., Preuschhoff, K., Batson, C. D., & Singer, T. (2010). Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. *Neuron*, *68*, 149–160.
- Hofmann, S. G., Grossman, P., & Hinton, D. E. (2011). Loving-kindness and compassion meditation: Potential for psychological interventions. *Clinical Psychology Review*, *31*, 1126–1132.
- Hutcherson, C. A., Seppala, E. M., & Gross, J. J. (2008). Loving-kindness meditation increases social connectedness. *Emotion*, *8*, 720–724.
- Immordino-Yang, M. H., McColl, A., Damasio, H., & Damasio, A. (2009). Neural correlates of admiration and compassion. *Proceedings of the National Academy of Sciences, USA*, *106*, 8021–8026.
- Klimecki, O. M., Leiberg, S., Lamm, C., & Singer, T. (2012). Functional neural plasticity and associated changes in positive affect after compassion training. *Cerebral Cortex*. Advance online publication. doi:10.1093/cercor/bhs142
- Klingberg, T. (2010). Training and plasticity of working memory. *Trends in Cognitive Sciences*, *14*, 317–324.
- Knutson, B., & Cooper, J. C. (2005). Functional magnetic resonance imaging of reward prediction. *Current Opinion in Neurology*, *18*, 411–417.
- Lamm, C., Decety, J., & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *NeuroImage*, *54*, 2492–2502.
- Leiberg, S., Klimecki, O., & Singer, T. (2011). Short-term compassion training increases prosocial behavior in a newly developed prosocial game. *PLoS ONE*, *6*(3), e17798. Retrieved from <http://www.plosone.org/article/info:doi/10.1371/journal.pone.0017798>
- Lutz, A., Brefczynski-Lewis, J., Johnstone, T., & Davidson, R. J. (2008). Regulation of the neural circuitry of emotion by compassion meditation: Effects of meditative expertise. *PLoS ONE*, *3*(3), e1897. Retrieved from <http://www.plosone.org/article/info:doi/10.1371/journal.pone.0001897>
- Lutz, A., Slagter, H. A., Dunne, J. D., & Davidson, R. J. (2008). Attention regulation and monitoring in meditation. *Trends in Cognitive Sciences*, *12*, 163–169.
- Mascaro, J. S., Rilling, J. K., Tenzin Negi, L., & Raison, C. L. (2013). Compassion meditation enhances empathic accuracy and related neural activity. *Social Cognitive and Affective Neuroscience*, *8*, 48–55.
- Masten, C. L., Morelli, S. A., & Eisenberger, N. I. (2011). An fMRI investigation of empathy for "social pain" and subsequent prosocial behavior. *NeuroImage*, *55*, 381–388.
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167–202.
- Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., & Grafman, J. (2006). Human fronto-mesolimbic networks guide decisions about charitable donation. *Proceedings of the National Academy of Sciences, USA*, *103*, 15623–15628.
- Ochsner, K. N., & Gross, J. J. (2005). The cognitive control of emotion. *Trends in Cognitive Sciences*, *9*, 242–249.
- Pace, T. W. W., Negi, L. T., Adame, D. D., Cole, S. P., Sivilli, T. I., Brown, T. D., . . . Raison, C. L. (2009). Effect of compassion meditation on neuroendocrine, innate immune and behavioral responses to psychosocial stress. *Psychoneuroendocrinology*, *34*, 87–98.
- Salzberg, S. (1997). *Lovingkindness: The revolutionary art of happiness*. Boston, MA: Shambhala.
- Singer, T., Seymour, B., O'Doherty, J. P., Stephan, K. E., Dolan, R. J., & Frith, C. D. (2006). Empathic neural responses are modulated by the perceived fairness of others. *Nature*, *439*, 466–469.
- Smith, A. (2010). *The theory of moral sentiments*. London, England: Penguin Classics. (Original work published 1759)
- Sober, P. E., Wilson, P. D. S., & Wilson, D. S. (1999). *Unto others: The evolution and psychology of unselfish behavior*. Cambridge, MA: Harvard University Press.
- Urry, H. L., van Reekum, C. M., Johnstone, T., Kalin, N. H., Thurow, M. E., Schaefer, H. S., . . . Davidson, R. J. (2006). Amygdala and ventromedial prefrontal cortex are inversely coupled during regulation of negative affect and predict the diurnal pattern of cortisol secretion among older adults. *Journal of Neuroscience*, *26*, 4415–4425.
- Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E., & Buckner, R. L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, *100*, 3328–3342.
- Vul, E., Harris, C., Winkielman, P., & Pashler, H. (2009). Puzzlingly high correlations in fMRI studies of emotion, personality, and social cognition. *Perspectives on Psychological Science*, *4*, 274–290.
- Wager, T. D., Davidson, M. L., Hughes, B. L., Lindquist, M. A., & Ochsner, K. N. (2008). Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron*, *59*, 1037–1050.
- Zaki, J., & Ochsner, K. (2012). The neuroscience of empathy: Progress, pitfalls and promise. *Nature Neuroscience*, *15*, 675–680.
- Zald, D. H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Research Reviews*, *41*, 88–123.