1	Neural mechanisms of modulations of empathy and altruism by beliefs of others' pain
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Abstract

24	Perceived cues signaling others' pain induce empathy which in turn motivates
25	altruistic behavior toward those who appear suffering. This
26	perception-emotion-behavior reactivity is the core of human altruism but does not
27	always occur in real life situations. Here, by integrating behavioral and multimodal
28	neuroimaging measures, we investigate neural mechanisms underlying modulations of
29	empathy and altruistic behavior by beliefs of others' pain. We show evidence that lack
30	of beliefs of others' pain reduces subjective estimation of others' painful feelings and
31	decreases monetary donations to those who show pain expressions. Moreover, lack of
32	beliefs of others' pain attenuates neural responses to their pain expressions within 200
33	ms after face onset and modulates neural responses to others' pain in the insular,
34	post-central, and frontal cortices. Our findings suggest that beliefs of others' pain
35	provide a cognitive basis of human empathy and altruism and unravel the intermediate
36	neural mechanisms.
37	

38 Introduction

39 Aesop's fable 'The boy who cried wolf' tells a story that villagers run or do not run 40 to help a shepherd boy who cries wolf depending on whether or not they believe that the 41 boy's crying indicates his actual emotion and need. This story illustrates an important 42 character of human altruistic behavior, that is, perceived cues signaling others' suffering 43 drives us to do them a favor only when we believe that their suffering is true. Although 44 this character of human altruism was documented over 2000 years ago in Aesop's fable 45 and is widely observed in current human societies, its psychological and neural 46 underpinnings have not been fully understood. The present study investigated how 47 beliefs of others' pain (BOP) modulate human altruistic behavior independently of 48 perceived cues signaling others' suffering and whether the modulation effect, if any, is 49 mediated by changes in empathy for others' pain and relevant brain underpinnings. 50 Empathy refers to understanding and sharing of others' emotional states (Decety 51 and Jackson, 2004) and has been proposed to provide a key motivation for altruistic 52 behavior in both humans and animals (Batson et al., 2015; De Waal, 2008; Decety et al., 53 2016). Empathy can be induced by perceived cues signaling others' pain that activate 54 neural responses in brain regions underlying sensorimotor resonance (e.g., the 55 sensorimotor cortex), affective sharing (e.g., the anterior insula (AI) and anterior 56 cingulate cortex (ACC)), and mental state inference/perspective taking (e.g., the medial 57 prefrontal cortex (mPFC) and temporoparietal junction (TPJ)) (Singer et al., 2004; 58 Jackson et al., 2005; Avenanti et al., 2005; Saarela et al., 2007; Fan and Han, 2008;

59	Shamay-Tsoory et al., 2009; Han et al., 2009; Sheng and Han, 2012; Fan et al., 2011;
60	Lamm et al., 2011; Zhou and Han, 2021). Neural responses to others' pain in the
61	empathy network and functional connectivity between its key hubs can predict motives
62	for subsequent altruistic actions (e.g., Hein et al., 2010; 2016; Mathur et al., 2010; Luo
63	et al., 2015). These brain imaging findings revealed neural mechanisms underlying the
64	perception-emotion-behavior reactivity (e.g., perceived pain-empathy-help) that occurs
65	often in everyday lives (Eisenberg et al., 2010; Hoffman, 2008; Penner et al., 2005).
66	However, empathic neural responses are influenced by multiple factors such as
67	perceptual features depicting others' pain (Gu and Han, 2007; Li and Han, 2019),
68	observers' perspectives and attention (Gu and Han, 2007; Li and Han, 2010; Jaunizux et
69	al., 2019), and perceived social relationships between observers and empathy targets
70	(Xu et al., 2009; Avenanti et al., 2010; Hein et al., 2010; Mathur et al., 2010; Sheng and
71	Han, 2012; Azevedo et al., 2013; Sheng et al., 2014; 2016; Han, 2018; Zhou and Han,
72	2021). What remains unclear is whether and how BOP modulates empathic brain
73	activity through which to further influence altruistic behavior. To address these issues is
74	crucial for understanding variations of empathy and altruism during complicated social
75	interactions as that illustrated in the Aesop's fable.
76	Beliefs refer to mental representations of something that is not immediately present
77	to the scenes but allows people to think beyond what is here and now (Fuentes, 2019).
78	Beliefs reflect organism's endorsement of a particular state of affairs as actual (McKay
79	and Dennett, 2009). Beliefs that best approximate reality enable the believers to act

80	effectively and maximize their survival (Fodor, 1985; Millikan, 1995). Previous
81	research has shown that beliefs affect multiple mental processes such as visual
82	awareness (Sterzer et al., 2008) and processing of emotions (Petrovic et al., 2005)
83	including experiences of pain (Wager et al., 2004; Colloca and Benedetti, 2005). The
84	function of beliefs is also manifested in increasing efficiency of neural processes
85	involved in decision making and goal setting (Garces and Finkel 2019; Régner et al.,
86	2019). Potential effects of beliefs on empathic neural responses were tested by
87	presenting participants with photographs showing pain inflicted by needle injections
88	into a hand that was believed to be or not to be anesthetized (Lamm et al., 2007).
89	Functional magnetic resonance imaging (fMRI) of brain activity suggested modulations
90	of insular responses to perceived pain by beliefs of anesthetization. However, the results
91	cannot be interpreted exclusively by BOP because the stimuli (i.e., needles) used to
92	induce beliefs of numbed and non-numbed hands were different. An ideal paradigm for
93	testing modulations of empathy by BOP independently of perceived cues signaling
94	others' pain should compare brain activities in response to identical stimuli under
95	different beliefs and enable researchers to test how BOP influences altruistic behavior.
96	In six behavioral, electroencephalography (EEG), and fMRI experiments, the
97	current study tested the hypothesis that BOP affects empathy and altruistic behavior by
98	modulating brain activity in response to others' pain. Specifically, we predicted that lack
99	of BOP may result in inhibition of altruistic behavior by decreasing empathy and its
100	underlying brain activity. Our behavioral, EEG, and fMRI experiments were designed

101	based on the common beliefs that patients show pain expressions to manifest their
102	actual feelings of pain whereas pain expressions performed by actors/actresses do not
103	indicate their actual emotional states. To examine BOP effects on empathy, we
104	experimentally manipulated BOP by asking participants to learn and remember different
105	identities (i.e., patient or actor/actress) of a set of neutral faces during a learning
106	procedure. Thereafter, we measured self-reports of others' pain and own unpleasantness
107	from the participants when they viewed learned faces with pain or neutral expressions.
108	During EEG/fMRI recording the participants were asked to discriminate patient or
109	actor/actress identities of faces with pain or neutral expressions. We compared
110	self-reports of others' feelings and brain activities related to pain (vs. neutral)
111	expressions of patients' faces with those related to actors/actresses' faces. If perception
112	of patients' pain expressions implicitly activates BOP whereas perception of
113	actors/actresses' pain expressions does not activate BOP, we expected that lack of BOP
114	(i.e., to compare actors/actresses vs. patients) would reduce self-report of empathy,
115	empathic brain activity, and altruistic behavior. We further predicted that BOP effects
116	on altruistic behavior might be mediated by decreased empathy and empathic brain
117	activity due to lack of BOP.
118	Similar to previous research (Jackson et al., 2005; Fan and Han, 2008; Hein et al.,
119	2010; Mathur et al., 2010; Sheng and Han, 2012), we adopted both subjective and
120	objective estimations of empathy for others' pain. Subjective estimation of empathy for
121	pain depends on collection of self-reports of others' painful feelings and ones' own

122	unpleasantness when viewing others' suffering (e.g., Bieri et al., 1990; Jackson et al.,
123	2005; Lamm et al., 2007; Fan and Han, 2008; Sheng and Han, 2012). Objective
124	estimation of empathy for pain relies on recording of brain activities, using fMRI or
125	EEG, that differentially respond to painful versus non-painful stimuli applied to others
126	(e.g., Singer et al., 2004; Jackson et al., 2005; Gu and Han, 2007; Fan and Han, 2008;
127	Hein et al., 2010) or to others' faces with pain versus neutral expressions (Botvinick et
128	al., 2005; Saarela et al., 2007; Han et al., 2009; Sheng and Han, 2012). Brain responses
129	to perceived non-painful stimuli applied to others or neutral expressions were also
130	collected to control empathy-unrelated perceptual or motor processes. fMRI studies
131	revealed greater activations in the ACC, AI, and sensorimotor cortices in response to
132	painful compared to non-painful stimuli applied to others (e.g., Singer et al., 2004;
133	Jackson et al., 2005; Gu and Han, 2007; Hein et al., 2010, see Lamm et al., 2011; Fan et
134	al., 2011, for review). EEG studies showed that event-related potentials (ERPs) in
135	response to perceived painful stimulations applied to others' body parts elicited neural
136	responses that differentiated between painful and neutral stimuli over the frontal region
137	as early as 140 ms after stimulus onset (Fan and Han, 2008; see Coll, 2018 for review).
138	Moreover, the mean ERP amplitudes at 140-180 ms predicted self report of others' pain
139	and ones' own unpleasantness (Fan and Han, 2008).
140	Particularly related to the current work are neuroimaging findings that compared
141	brain responses to pain versus neutral expressions. fMRI studies found that viewing
142	video clips (Botvinick et al., 2005) or pictures (Sheng et al., 2014) showing faces with

143	pain versus neutral expressions or viewing photos of faces of patients who were
144	suffering from provoked pain versus chronic pain (Saarela et al., 2007) induced
145	activations in the ACC, AI, and inferior parietal cortex. Moreover, the cortical areas
146	activated by facial expressions of pain were also engaged by the first-hand experience
147	of pain evoked by thermal stimulation (Botvinick et al., 2005). Moreover, the strengths
148	of AI activations during observation of others' pain were correlated with subjective
149	feelings of others' pain (Saarela et al., 2007). ERP studies found that neural responses to
150	pain expressions occurred as early as 130 ms after face onset over the frontal/central
151	regions as indexed by the increased amplitude of a positive component at 128–188 ms
152	(P2) in response to pain compared neutral expressions (Sheng and Han, 2012; Sheng et
153	al., 2013; 2016; Han et al., 2016; Li and Han, 2019). In addition, the P2 amplitudes in
154	response to others' pain expressions positively predicted subjective feelings of own
155	unpleasantness induced by others' pain and self-reports of one's own empathy traits
156	(Sheng and Han, 2012). In addition, source estimation of the P2 component in response
157	to others' pain expressions suggested a possible origin in the ACC. Taken together,
158	these brain imaging findings suggest effective subjective and objective measures of
159	empathy (i.e., understanding and sharing of others' pain) that are suitable for
160	investigation of neural mechanisms underlying modulations of empathy and altruism by
161	BOP.
162	In Experiment 1 we randomly assigned patient or actor/actress identities to faces to

163 test how experimentally manipulated BOP associated with face identities caused

164	changes in empathy (i.e., subjective evaluation of others' pain) and altruistic behavior
165	(i.e., monetary donations). We predicted that lack of BOP related to actors/actresses (vs.
166	patients) would result in reduced empathy and altruistic behavior. In Experiment 2,
167	based on the common belief that an effective medical treatment reduces a patient's pain,
168	we tested whether decreasing BOP due to knowledge of effective medical treatments of
169	patients also reduced empathy and altruistic behavior.
170	In Experiments 3 and 4 we investigated whether BOP modulates empathic brain
171	activity by recording EEG signals in response to pain or neutral expressions of faces
172	with patient or actor/actress identities. Brain activities related empathy were quantified
173	by comparing neural responses to pain versus neutral expressions to exclude neural
174	processes of facial structures, social attributes (e.g., gender), and other
175	empathy-unrelated information. Given previous findings that the P2 amplitude
176	increased to pain compared to neutral expressions and was associated with self-report of
177	sharing of others' pain (Sheng and Han, 2012; Sheng et al., 2013; 2016; Han et al., 2016;
178	Li and Han, 2019), we focused on how the P2 amplitude in response to pain (vs. neutral)
179	expressions was modulated by facial identities (i.e., patient or actor/actress) that link to
180	different beliefs (i.e., patients' pain expressions manifest their actual feelings whereas
181	actors/actresses' pain expressions do not). Our ERP results showed evidence that
182	actor/actress compared to patient identities of faces decreased the empathic neural
183	responses (i.e., P2 amplitudes in response to pain (vs. neutral) expressions) within 200
184	ms post-stimulus. In Experiment 5 we further revealed behavioral and EEG evidence

that neural responses to pain expressions of faces mediate BOP effects on empathy andmonetary donations.

187	In Experiment 6 we employed fMRI to examine brain regions in which blood
188	oxygen level dependent (BOLD) signals are modulated by BOP. We examined BOLD
189	responses to faces that had either patient or actor/actress identities, received
190	painful/non-painful stimulations, and showed pain or neutral expressions. fMRI results
191	allowed us to test whether empathic neural responses in the cognitive (i.e., the dorsal
192	mPFC and TPJ, Völlm et al., 2006; Schnell et al., 2011; also see Lamm et al., 2011; Fan
193	et al., 2011; Shamay-Tsoory, 2011), sensorimotor/affective (i.e., the ACC, insula, and
194	sensorimotor cortex, Jackson et al., 2006; Singer et al., 2004; Avenanti et al., 2005), or
195	both nodes of the empathic neural network would be modulated by BOP that was
196	manipulated by assigning different identities (i.e., patient or actor/actress) to empathy
197	targets. In addition, we examined whether neural responses in the empathic network
198	would be able to predict variations of subjective feelings of others' pain due to lack of
199	BOP.
200	. Together, our behavioral and brain imaging results showed consistent evidence that
201	lack of BOP or decreasing BOP resulted in reduced empathy and altruistic behavior.
202	Our findings suggest that BOP may provide a cognitive basis for human empathy and
203	altruism and uncover intermediate brain mechanisms by which BOP influences empathy
204	and altruistic behavior.

Results

Experiment 1: Lack of BOP reduces subjective estimation of empathy and altruistic behavior

208	In Experiment 1 we tested the predictions that lack of BOP decreases empathy and
209	altruistic behavior by experimentally manipulating individuals' BOP. We presented
210	participants (N = 60) with photos of faces of 16 models (half males) with pain
211	expressions (see Methods for details). The participants were informed that these photos
212	were taken from patients who suffered from a disease. In the 1 st _round test the
213	participants were shown with each photo and asked to report perceived pain intensity of
214	each patient by rating on a Likert-type scale ($0 = not$ painful at all; $10 = extremely$
215	painful). This rating task was adopted from previous research (Bieri et al., 1990;
216	Jackson et al., 2005; Lamm et al., 2007; Fan and Han, 2008; Sheng and Han, 2012) to
217	assess the participants' understanding of others' pain feeling $-$ a key component of
218	empathy. Thereafter, the participants were invited to donate money to the patient in the
219	photo by selecting an amount from an extra bonus payment for their participation (0 to
220	10 points, 1 point = ± 0.2) as a measure of altruistic behavior. The participants were
221	informed that the amount of one of their donation decisions would be selected randomly
222	and endowed to a charity organization to help those who suffered from the same disease.
223	After the 1 st _round test the participants were asked to perform a 5-minute
224	calculation task to clean their memory of performances during the 1 st _round test. The
225	participants were then informed that this experiment actually tested their ability to
226	recognize facial expressions and the photos were actually taken from 8 patients and 8

227 actors/actresses. We expected that identity changes from patients to actors/actresses 228 would decrease BOP because patients' pain expressions reflect their actual emotional 229 states whereas pain expressions performed by actors/actresses do not indicate an actual painful state. The participants were then asked to perform the 2^{nd} round test in which 230 231 each photo was presented again with patient or actor/actress identity indicated by a 232 word (i.e., patient, actor, or actress) below the photo. The participants had to perform the same pain intensity rating and donation tasks as those in the 1st_round test. The 233 234 participants were told that an amount of money would be finally selected from their 2nd_round donation decisions and presented to the same charity organization after the 235 236 study. 237 The mean rating scores of pain intensity and amounts of monetary donations were 238 subject to repeated-measures analyses of variance (ANOVAs) of Test Phase (1st_round

239 vs. 2^{nd} _round test) × Identity Change (patient-identity change (patient to actor/actress)

240 vs. patient-identity repetition (patient to patient)) as independent within-subjects

241 variables. As expected, the results revealed that patient-identity change or

242 patient-identity repetition produced opposite effects on both perceived pain intensity

and amounts of monetary donations, as indicated by significant interactions of Test

244 Phase × Identity Change (F(1,59) = 123.476 and 60.638, ps < 0.001, $\eta_p^2 = 0.677$ and

245 0.507, 90% CI = (0.555, 0.747) and (0.351, 0.611), Fig. 1a and 1b). Specifically,

246 patient-identity change (i.e., from patients to actors/actresses) significantly reduced

247 perceived pain intensity and amounts of monetary donations in the 2^{nd} -round (vs.

248	1 st _round) test (F(1,59) = 82.664 and 34.542, ps < 0.001, $\eta_p^2 = 0.584$ and 0.369, 90% CI
249	= $(0.440, 0.673)$ and $(0.207, 0.495)$). By contrast, patient-identity repetition
250	significantly increased both perceived pain intensity and monetary donations in the
251	2^{nd} _round (vs. 1 st _round) test (F(1,59) = 36.060 and 27.457, ps < 0.001, $\eta_p^2 = 0.379$ and
252	0.318, 90% CI = (0.216, 0.503) and (0.159, 0.449)). These results suggest that our
253	manipulations of BOP caused reliable changes in subjective evaluation of others' pain
254	and related monetary donations in opposite directions. Interestingly, to some degree
255	rather than not at all, the participants reported pain and donated to faces with
256	actor/actress identity in the 2 nd _round test, suggesting that lack of BOP did not fully
257	eliminate empathy and altruistic behavior toward those who showed pain expressions.



258

Fig. 1. Behavioral results in Experiment 1. (a) Mean rating scores of pain intensity in 259 the 1^{st} and 2^{nd} round tests. (b) Mean amounts of monetary donations in the 1^{st} and 260 261 2^{nd} round tests. Shown are group means (large dots), standard deviation (bars), 262 measures of each individual participant (small dots), and distribution (violin shape) in (a) 263 and (b). (c) The associations between rating scores of pain intensity and amounts of monetary donations for patients in the 1st round test and for actors/actresses in the 264 2^{nd} round test. (d) The associations between rating scores of pain intensity and amounts 265 of monetary donations for patients in both the 1^{st} and 2^{nd} round tests. (e) Rating scores 266 of pain intensity partially mediate the relationship between patient-identity change and 267 268 reduced monetary donations. (f) Rating scores of pain intensity mediate the relationship 269 between patient-identity repetition and increased monetary donations. The online 270 version of this article includes the following source data for Figure 1: Figure 1-Source 271data 1.



273 experimentally manipulated BOP and monetary donations, we first conducted Pearson

274	correlation analyses of the relationship between empathy and altruism. The results
275	showed that the rating scores of pain intensity of faces whose identities changed from
276	patient in the 1 st _round test to actor/actress in the 2 nd _round test significantly predicted
277	the amount of monetary donations in the 1^{st} _round but not in the 2^{nd} _round test (r =
278	0.608 and 0.187, $p < 0.001$ and $p = 0.152$, 95% CI = (0.422, 0.776) and (-0.069, 0.435),
279	all results were FDR-corrected, Fig. 1c). The rating scores of pain intensity also
280	significantly predicted the amount of monetary donations for faces whose patient
281	identities did not change in the 1^{st} _round and 2^{nd} _round tests (r = 0.619 and 0.628, ps <
282	0.001, 95% CI = (0.449, 0.776) and (0.417, 0.775), Fig. 1d). We conducted mediation
283	analyses to further test an intermediate role of empathy between BOP and altruistic
284	behavior (see Methods). The first mediation analysis showed that rating scores of pain
285	intensity partially mediated the relationship between patient-identity change and
286	reduced amount of monetary donations (direct effect: $c' = -0.902$, $t(118) = -2.468$, $p =$
287	0.015, 95% CI = (-1.626, -0.178); indirect effect: a×b = -0.839, 95% CI = (-1.455,
288	-0.374), Fig. 1e, see Supplementary file 1 for statistical details). The second mediation
289	analysis showed evidence that the rating scores of pain intensity also mediated the
290	relationship between patient-identity repetition and increased amount of monetary
291	donations (direct effect: c'= 0.028, t(118) = 0.072, p = 0.943, 95% CI = (-0.727, 0.782),
292	indirect effect: $a \times b = 0.885$, 95% CI = (0.314, 1.563), Fig. 1f, see Supplementary file 2
293	for statistical details). These results indicate a key functional role of BOP in altruistic

behavior and suggest changes in subjective evaluation of others' pain as an intermediate
mechanism underlying the effect of BOP on monetary donations.

296 Experiment 2: Intrinsic BOP predicts subjective estimation of empathy and

297 altruistic behavior

298 In Experiment 1 BOP was manipulated by randomly assigning patient or actor/actress identities to faces and the results showed that experimentally manipulated 299 300 BOP changes caused variations of empathy and altruistic behavior. In Experiment 2 we 301 further investigated whether an individual's intrinsic BOP (i.e., various representations 302 of actual emotional states of different faces with pain expressions) can predict empathy 303 and altruistic behavior across different faces. Moreover, as a replication, we tested 304 whether changing the participants' intrinsic BOP causes changes in empathy and 305 altruistic behavior in directions similar to those observed in Experiment 1. In addition, 306 we assessed whether changing intrinsic BOP modulated sharing of others' pain — 307 another key component of empathy (Bieri et al., 1990; Jackson et al., 2005; Lamm et al., 308 2007; Fan and Han, 2008; Sheng and Han, 2012). Finally, we tested whether BOP 309 induced emotional sharing mediates the relationship between BOP and altruistic 310 behavior. To address these issues, we tested an independent sample (N = 60) using the stimuli 311 312 and procedure that were the same as those in Experiment 1 except the following. In the 313 1st_round test the participants were informed that they were to be shown with photos 314 with pain expressions taken from patients who suffered from a disease and received a

315 medical treatment. After the presentation of each photo the participants were asked to 316 estimate, based on perceived pain expression of each face, how effective they believed 317 the medical treatment was for each patient by rating on a Likert-type scale (0 = no effect 318 or 0% effective, 100 = fully effective or 100% effective). The rating scores were used to 319 estimate the participants' intrinsic BOP of each face with a higher rating score 320 (indicating more effective treatment) corresponding to a weaker BOP because a more 321 effective medical treatment reduces a patient's pain to a greater degree. In addition to 322 rating pain intensity of each face, the participants were asked to report how unpleasant 323 they were feeling when viewing each photo by rating on a Likert-type scale (0 = not)324 unpleasant at all, 10 = extremely unpleasant). The unpleasantness rating was performed to assess emotional sharing of others' pain. In the 2nd_round test the participants were 325 326 told that the medical treatment was actually fully effective for half patients but had no 327 effect for the others. Each photo was then presented again with information that the 328 medical treatment applied to the patient was 100% effective (to decrease the participants' 329 beliefs of the patients' painful states) or 0% effective (to enhance the participants' 330 beliefs of the patients' painful states). Thereafter, the participants were asked to perform 331 the rating tasks and to make monetary donation decisions, similar to those in the 1st round test. 332 333 To assess whether individuals' intrinsic BOP predicted their empathy and altruistic

behavior across different target faces, we conducted Pearson correlation analyses of the
 relationships between intrinsic BOP as indexed by the rating score of treatment

336	effectiveness and empathy rating scores/amounts of monetary donations across the
337	sixteen models in the 1st_round test in each participant. The correlation coefficients
338	were then transformed to Fisher's z values that were further compared with zero.
339	One-sample t-tests revealed that the z values were significantly smaller than zero
340	(correlations between intrinsic BOP and pain intensity/unpleasantness/monetary
341	donation: mean \pm s.d. = -0.631 \pm 0.531, -0.643 \pm 0.524 and -0.469 \pm 0.529; t(59) =
342	-9.213, -9.501 and -6.875; ps < 0.001; Cohen's d = 1.188, 1.227 and 0.887; 95% CI =
343	(-0.768, -0.494), (-0.778, -0.507), and (-0.606, -0.333), Fig. 2a-c), suggesting that a
344	larger score of treatment effectiveness (i.e., a weaker intrinsic BOP related to a face)
345	predicted weaker empathy and less monetary donations relate to that face. These results
346	provide evidence for associations between intrinsic BOP and empathy/altruism.



347

348 Fig. 2. Behavioral results in Experiment 2. The relationships between intrinsic BOP 349 (indexed by the rating score of effective medical treatments) and scores of pain intensity 350 (a), own unpleasantness (b), and monetary donations (c), respectively, across the sixteen 351 models in the 1st_round test in each participant. The regression line of each participant 352 is plotted in (a), (b), and (c). (d-f) Mean rating scores of pain intensity, own unpleasantness, and monetary donations in the 1st and 2nd round tests. (g) The 353 354 associations between rating scores of pain intensity and amounts of monetary donations for patients in the 1st round test and for 100%-effective patients in the 2nd round tests 355 356 across all the participants. (h) The associations between rating scores of own unpleasantness and amounts of monetary donations for patients in the 1st round test and 357 for-100% effective patients in the 2^{nd} -round tests across all the participants. (i) The 358 359 associations between rating scores of pain intensity and amounts of monetary donations for patients in the 1st_round test and for 0%-effective patients in the 2nd_round tests 360

361	across all the participants. (j) The associations between rating scores of own
362	unpleasantness and amounts of monetary donations for patients in the 1 st _round test and
363	for 0%-effective patients in the 2 nd _round tests across all the participants. (k) Rating
364	scores of pain intensity change partially mediate the relationship between decreased
365	BOP and changes in monetary donations. (1) Rating scores of pain intensity change fail
366	to mediate the relationship between enhanced BOP and changes in monetary donations.
367	Shown are group means (large dots), standard deviation (bars), measures of each
368	individual participant (small dots), and distribution (violin shape) in (d), (e), and (f).
369	The online version of this article includes the following source data for Figure 2: Figure
370	2-Source data 1.
271	Next we tested whether decreased (or increased) POP also predicts changes in
371	Next, we tested whether decreased (or increased) BOP also predicts changes in
372	empathy/altruistic behavior across different target faces for each participant. To do this,
373	we calculated belief changes (decreased BOP: 100%-effective minus the participants'
374	initial estimation; enhanced BOP: the participants' initial estimation minus
375	0%-effective), empathy changes (rating scores in the 2 nd _round vs. 1 st _round test), and
376	changes in altruistic behavior (the amount of monetary donation in the 2 nd _round vs.
377	1 st _round test) related to each model in each participant. Similarly, we conducted
378	Pearson correlation analyses to examine associations between changes in beliefs and
379	empathy/donation for decreased-BOP patients and enhanced-BOP patients, respectively,
380	in each participant. The correlation coefficients were then transformed to Fisher's z
381	values that were further compared with zero. One-sample t-tests showed that the z
382	values were significantly smaller than zero for decreased-BOP patients (the correlation
383	between changes in belief and pain intensity: z-value (mean \pm s.d.) = -0.304 \pm 0.370;
384	t(59) = -6.352, p < 0.001; Cohen's d = 0.822; 95% CI = (-0.400, -0.208); the correlation
385	between changes in belief and unpleasantness: z-value (mean \pm s.d.) = -0.277 \pm 0.455;
386	t(59) = -4.706, p < 0.001; Cohen's d = 0.609; 95% CI = (-0.394, -0.159); the correlation

387	between changes in belief and monetary donation: z-value (mean \pm s.d.) = -0.236 \pm
388	0.410; t(59) = -4.465, p < 0.001; Cohen's d = 0.576; 95% CI = (-0.342, -0.130)). These
389	results suggest that a greater decrease of BOP related to a face predicted greater reduced
390	empathy and less monetary donations. By contrast, one-sample t-tests showed that the z
391	values were significantly larger than zero for enhanced-BOP patients (the correlation
392	between changes in belief and pain intensity: z-value (mean \pm s.d.) = 0.286 \pm 0.488;
393	t(59) = 4.533, p < 0.001; Cohen's d = 0.586; 95% CI = (0.160, 0.412); the correlation
394	between changes in belief and unpleasantness: z-value (mean \pm s.d.) = 0.227 \pm 0.470;
395	t(59) = 3.735, p < 0.001; Cohen's d = 0.483; 95% CI = (0.105, 0.348); the correlation
396	between changes in belief and monetary donation: z-value (mean \pm s.d.) = 0.162 \pm 0.538;
397	t(59) = 2.332, $p = 0.023$; Cohen's $d = 0.301$; 95% CI = (0.023, 0.301)). These results
398	suggest that a greater increase of BOP predicted greater increased empathy and more
399	monetary donations across individual empathy targets. These results provide evidence
400	for associations between changes in BOP and empathy/altruism across different faces
401	for each participant.
402	To test whether the results in Experiment 2 replicated those in Experiment 1, we
403	conducted ANOVAs of the mean empathy scores and amounts of monetary donations

- 404 with Test Phase (1^{st} vs. 2^{nd} _round) and Belief Change (initial self-rated effectiveness to
- 405 informed 0%-effectiveness vs. initial self-rated effectiveness to informed
- 406 100%-effectiveness) as independent within-subjects variables. The results showed that
- 407 decreasing internal BOP (i.e., for 100% effective target faces) resulted in lower

408	subjective evaluation of others' pain and one's own unpleasantness and less monetary
409	donations in the 2 nd _vs. 1 st _round tests, whereas enhancing BOP (i.e., for 0% effective
410	target faces) produced opposite effects (Fig. 2d-f, see Supplementary file 3 for statistical
411	details). These results replicated those in Experiment 1 and provided further evidence
412	that changing BOP resulted in variations of empathy and altruistic behavior.
413	Pearson correlations analyses of the mean rating scores in the 1 st _round and
414	2 nd _round tests across the participants showed that, for '100%-effective' patients, the
415	1 st _round but not the 2 nd _round rating scores of empathy significantly predicted the
416	amount of monetary donations (Pain intensity rating: $r = 0.530$ and 0.184, $p < 0.001$ and
417	p = 0.159, 95% CI = (0.334, 0.698) and (-0.057, 0.425), Unpleasantness rating: $r =$
418	0.307 and 0.074, p = 0.017 and p = 0.576, 95% CI = (0.046, 0.541) and (-0.199, 0.358),
419	Fig. 2g and 2h). For '0%-effective' patients, however, both the 1 st _round and 2 nd _round
420	rating scores of empathy significantly predicted the amount of monetary donations (Pain
421	intensity rating: $r = 0.582$ and 0.476, ps < 0.001, 95% CI = (0.415, 0.725) and (0.287,
422	0.638); Unpleasantness rating: $r = 0.373$ and 0.280, $p = 0.006$ and 0.04, 95% CI =
423	(0.096, 0.590) and (0.011, 0.511), Fig. 2i and 2j).
424	Furthermore, the results of mediation analyses showed that rating scores of pain
425	intensity partially mediated the relationship between decreased BOP (i.e., for
426	'100%-effective' patients) and monetary donations (direct effect: $c' = -0.038$, $t(58) =$
427	-3.657, p < 0.001, 95% CI = (-0.059, 0.017); indirect effect: a×b = -0.016, 95% CI =
428	(-0.027, -0.005), Fig. 2k, see Supplementary file 4 for statistical details). However,

429	rating scores of unpleasantness did not mediate the relationship between decreased BOP
430	and monetary donations (indirect effect: $a \times b = -0.002$, 95% CI = (-0.009, 0.003)).
431	Neither pain intensity nor unpleasantness ratings mediated the relationship between
432	enhanced BOP (i.e., for '0%-effective' patients) and monetary donations (indirect effect:
433	a*b = 0.003 and -0.002, 95% CI = (-0.009, 0.013) and (-0.007, 0.004), Fig. 21, see
434	Supplementary files 5, 6, and 7 for statistical details). These behaviorsl results suggest
435	that decreased BOP influences altruistic decisions possibly via modulations of the
436	cognitive component of empathy (i.e., understanding others' pain) rather than the
437	affective component of empathy (i.e., sharing others' pain).
438	Experiment 3: Lack of BOP decreased empathic brain activity
439	Experiments 1 and 2 showed evidence that self-report measures of empathy for pain
440	were affected by BOP. In Experiment 3 we further investigated whether and how
441	changing BOP modulates brain activity in response to perceived cues signaling others'
442	pain as an objective estimation of empathy. If BOP provides a basis of empathy of
443	others' pain, lack of BOP should reduce empathic neural responses to visual stimuli
444	signaling others' pain. We tested this assumption by recording EEG to faces of 16
445	models from an independent sample ($N = 30$). The participants were first presented with
446	these faces with neutral expressions and were informed that these photos were taken
447	from 8 patients who suffered from a disease and from 8 actors/actresses. The
448	participants were asked to remember patient or actor/actress identity of each neutral face
449	and had to pass a memory test with a 100% recognition accuracy. Thereafter, the

450	participants were informed that they would be presented with photos of these faces with
451	either neutral or pain expressions, and photos of pain expressions were taken from the
452	patients who were suffering from the disease or from the actors/actresses who imitated
453	patients' pain. The participants were asked to make judgments on identity of each face
454	(i.e., patient vs. actor/actress) with a neutral or pain expression by pressing one of two
455	buttons while EEG was recorded. After EEG recording, the participants were asked to
456	rate pain intensity of each face with a pain or neutral expression on a Likert-type scale
457	(0 = not painful at all; 7 = extremely painful) and to what degree they believed in the
458	identity of each face with a pain expression on a 15-point Likert-type scale (-7 =
459	extremely believed as an actor/actress, $0 = not$ sure, $7 = extremely$ believed as a patient)
460	Because the same set of stimuli were perceived as patients or actors/actresses across the
461	participants, modulations of brain activity in response to pain expressions only reflected
462	the effects of BOP concomitant with the face identity (i.e., real pain for patients but fake
463	pain for actors/actresses).
464	The participants reported a positive mean belief score corresponding to faces with a
465	patient identity (2.496 \pm 2.51) but a negative mean belief score corresponding to faces
466	with an actors/actresses identity (-2.210 \pm 3.25) (t(29) = 4.932, p < 0.001, Cohen's d
467	= 0.900, 95% CI = $(2.755, 6.658)$), suggesting successes of our manipulations of face
468	identities. An ANOVA of the mean rating scores of pain intensity with Identity (patient

469 vs. actor/actress) and Expression (pain vs. neutral) as within-subject variables revealed a

470 significant Identity × Expression interaction (F(1,29) = 4.905, p = 0.035, $\eta_p^2 = 0.145$, 90%

471	CI = (0.006, 0.330), Fig. 3a), suggesting greater subjective feelings of pain intensity for
472	faces with patient compared to actor/actress identity. Moreover, a larger score of belief
473	of patient identities significantly predicted greater subjective feelings of pain intensity
474	related to patients' pain (vs. neutral) expressions (r = 0.384 , p = 0.036 , 95% CI = (0.074 ,
475	0.627)), whereas there was no significant association between belief scores and
476	subjective feelings of pain intensity related to actors/actresses' pain (vs. neutral)
477	expressions (r = 0.264, p = 0.159, 95% CI = (-0.162, 0.605)). These results provide
478	further evidence for a link between BOP and empathy for patients' pain.





480 Fig. 3. EEG results of Experiment 3. (a) Mean rating scores of pain intensity to pain 481 versus neutral expressions of faces with patient or actor/actress identities. (b) ERPs to 482 faces with patient or actor/actress identities at frontal electrodes. The voltage 483 topography shows the scalp distribution of the P2 amplitude with the maximum over the 484 central/frontal region. (c) Mean differential P2 amplitudes to pain versus neutral 485 expressions of faces with patient or actor/actress identities. The voltage topographies 486 illustrate the scalp distribution of the P2 difference waves to pain versus neutral 487 expressions of faces with patient or actor/actress identities, respectively. Shown are 488 group means (large dots), standard deviation (bars), measures of each individual 489 participant (small dots), and distribution (violin shape) in (a) and (c). The online version 490 of this article includes the following source data for Figure 3: Figure 3-Source data 1. 491 The participants responded to face identities with high accuracies during EEG 492 recording (>81% across all conditions, see Supplementary file 8 for details). ERPs to



494	ms (N1) and a positive activity at 175–195 ms (P2) at the frontal/central regions, which
495	were followed by two positive activities at 280-340 ms (P310) over the parietal region
496	and 500–700 ms (P570) over the frontal area (Fig. 3b). Previous ERP studies have
497	shown that empathic neural responses to pain expressions are characterized by an
498	increased P2 amplitude and the P2 amplitude to pain (vs. neutral) expressions predicts
499	self-report of affective sharing (Sheng and Han, 2012; Sheng et al., 2016; Luo et al.,
500	2018; Li and Han, 2019). Therefore, our ERP data analyses focused on whether BOP
501	modulates the P2 amplitude to pain (vs. neutral) expressions given the previous ERP
502	findings. ANOVAs of the P2 amplitudes with Identity (patient vs. actor/actress) and
503	Expression (pain vs. neutral) as within-subject variables revealed a significant Identity \times
504	Expression interaction (F(1,29) = 7.490, p = 0.010, $\eta_p^2 = 0.205$, 90% CI = (0.029,
505	0.391), see Supplementary file 9 for statistical details). Simple effect analyses verified
506	significantly greater P2 amplitudes to pain versus neutral expressions of patients' faces
507	$(F(1,29) = 18.059, p < 0.001, {\eta_p}^2 = 0.384, 90\% CI = (0.150, 0.546)),$ whereas the P2
508	amplitude did not differ significantly between pain and neutral expressions of
509	actors/actresses' faces (F(1,29) = 0.334, p = 0.568, $\eta_p^2 = 0.011$, 90% CI = (0.000, 0.135),
510	Fig. 3b and 3c). We further conducted Bayes factor analyses to examine the null effect
511	of pain expressions on the P2 amplitudes to actors/actresses' faces. The Bayes factor
512	represents the ratio of the likelihood of the data fitting under the alternative hypothesis
513	versus the likelihood of fitting under the null hypothesis. The results showed a Bayes
514	factor of 0.227 which provided further evidence for the null hypothesis. The results

515	indicate that, while the effect of pain (vs. neutral) expression on the P2 amplitudes to
516	patients' faces was similar to our previous findings that the P2 amplitudes increased to
517	pain (vs. neutral) expressions of face without patient identities (Sheng and Han, 2012;
518	Sheng et al., 2016), the P2 amplitude was less sensitive to pain versus neutral
519	expressions of faces with actor/actress identities. This finding indicate that lack of BOP
520	significantly weakens early empathic neural responses to others' pain within 200 ms
521	after stimulus onset.
522	Experiment 4: BOP is necessary for modulations of empathic brain activity
523	The learning and EEG recording procedures in Experiment 3 consisted of multiple
524	processes, including learning, memory and recognition of face identities, assignment to
525	different social groups (e.g., patient or actor groups), etc. The results of Experiment 3
526	left an open question of whether these processes, even without BOP changes induced
527	through these processes, would be sufficient to result in modulations of the P2
528	amplitude in response to pain (vs. neutral) expressions of faces with different identities.
529	In Experiment 4 we addressed this issue using the same learning and identity
530	recognition procedures as those in Experiment 3 except that the participants in
531	Experiment 4 had to learn and recognize identities of faces of two baseball teams and
532	that there is no prior difference in BOP associated with individual faces from the two
533	baseball teams. If the processes involved in the learning and reorganization procedures
534	rather than the difference in BOP were sufficient for modulations of the P2 amplitude in
535	response to pain (vs. neutral) expressions of faces, we would expect similar P2

536	modulations in Experiments 4 and 3. Otherwise, if the difference in BOP produced
537	during the learning procedure was necessary for the modulation of empathic neural
538	responses, we would not expect modulations of the P2 amplitude in response to pain (vs.
539	neutral) expressions in Experiment 4.
540	We clarified these predictions in an independent sample ($N = 30$) in Experiment 4.
541	We employed the stimuli and procedure that were the same as those in Experiment 3
542	except that, during the learning phase, the participants were informed that the 16 models
543	were from two baseball teams (half from a Tiger team and half from a Lion team) and
544	they suffered from a disease. After the participants had remembered team identity of
545	each neutral face in a procedure similar to that in Experiment 3, they performed identity
546	(i.e., Tiger vs. Lion team) judgments on the faces with neutral or pain expressions
547	during EEG recording. This manipulation built team identities should not influence
548	self-report and EEG estimation of empathy because the Tiger/Lion team identities did
549	not bring any difference in BOP between pain expressions of faces from the two teams.
550	The participants responded to face identities with high accuracies during EEG
551	recording (> 79% across all conditions). Rating scores of pain intensity did not differ
552	significantly between faces from the two teams (F(1,29) = 1.608, p = 0.215, $\eta_p^2 = 0.053$,
553	90% CI = $(0, 0.216)$, Bayes factors = 0.261, Fig. 4a, see Supplementary file 10 for
554	details). ANOVAs of the mean P2 amplitudes over the frontal electrodes revealed a
555	significant main effect of facial expression (F(1,29) = 12.182, P = 0.002, $\eta_p^2 = 0.296$, 90%
556	CI = (0.081, 0.473), Fig. 4b and 4c, see Supplementary file 11 for details), as the P2

557	amplitude was enlarged by pain compared to neutral expressions. However, this effect
558	did not differ significantly between faces from the two teams (F(1,29) = 0.040 , P =
559	0.843, $\eta_p^2 = 0.001$, 90% CI = (0, 0.053), Bayes factors = 0.258). The null interaction
560	effect on either self-report of empathy and the P2 amplitudes to pain (vs. neutral)
561	expressions in Experiment 4 was not simply due to an underpowered sample size
562	because the same sample size in Experiment 3 revealed reliable BOP effects on
563	self-report and EEG (i.e., the P2 amplitude) estimation of empathy. Together, the results
564	in Experiments 3 and 4 suggest a key role of BOP, but not other cognitive processes
565	involved in the experimental manipulations, in modulations of neural responses to
566	others' pain.



568 Fig. 4. EEG results of Experiment 4. (a) Mean rating scores of pain intensity to pain 569 versus neutral expressions of faces with Lion Team or Tiger Team identities. (b) ERPs 570 to faces with Lion/Tiger team identities at frontal electrodes. The voltage topography 571 shows the scalp distribution of the P2 amplitude with the maximum over the 572 central/frontal region. (c) Mean differential P2 amplitudes to pain versus neutral 573 expressions of faces with Lion/Tiger Team identities. The voltage topographies 574 illustrate the scalp distribution of the P2 difference waves to pain versus neutral 575 expressions of faces with the Lion/Tiger Team identities, respectively. Shown are group 576 means (large dots), standard deviation (bars), measures of each individual participant 577 (small dots), and distribution (violin shape) in (a) and (c). The online version of this 578 article includes the following source data for Figure 4: Figure 4-Source data 1.

579 Experiment 5: Empathic brain activity mediates relationships between BOP and

580 empathy/altruistic behavior

581	Given that Experiments 1 to 4 showed consistent evidence for BOP effects on
582	subjective feelings of others' pain, altruistic behavior, and empathic neural responses, in
583	Experiment 5, we further examined whether BOP-induced changes in empathic brain
584	activity plays a mediator role in the pathway from belief changes to altered subjective
585	feelings of others' pain and altruistic decisions. To this end, we conducted two-session
586	tests of an independent sample ($N = 30$). In the first session we employed the stimuli
587	and procedure that were identical to those in Experiment 1 to assess BOP effects on
588	empathy and altruistic behavior. In the second session we recorded EEG from the
589	participants using the same stimuli and procedure as those in Experiment 3 to examine
590	BOP effects on empathic neural responses. BOP-induced changes in empathic brain
591	activity, rating scores of pain intensity, and amounts of monetary donations recorded in
592	the two-session tests were then subject to mediation analyses.
593	To assure the participants' beliefs about patient and actor/actress identities of
594	perceived faces, after EEG recording, we asked the participants to complete an implicit
595	association test (IAT) (Greenwald et al., 1998) that measured reaction times to faces
596	with patient and actor/actress identities and words related to patients and
597	actors/actresses (see Methods). The D score was then calculated based on response
598	times (Greenwald et al., 2003) to assess implicit associations between patient and
599	actor/actress faces and the relevant words. One-sample t-test revealed that the D score
600	was significantly larger than zero (0.929 \pm 0.418, t(29) = 12.178, p < 0.001, Cohen's d =
601	2.223, 95% CI = $(0.773, 1.085)$), suggesting that patient faces were more strongly

associated with patient relevant words whereas actor/actress faces were more strongly
associated with actor/actress relevant words. The results indicate successful belief
manipulations during the two-session tests.

605	The behavioral results in the first-session test replicated the findings of Experiment
606	1. In particular, decreasing BOP (i.e., changing patient identity in the 1 st _round test to
607	actor/actress identity in the 2 nd _round test) significantly reduced self-report of others'
608	pain and monetary donations (Test Phase \times Identity Change interactions on rating
609	scores of pain intensity and amounts of monetary donations: $(F(1,29) = 59.654 \text{ and}$
610	129.696, ps < 0.001, $\eta_p^2 = 0.673$ and 0.817, 90% CI = (0.479, 0.764) and (0.694, 0.868);
611	Effects of patient-to-actor/actress identity change on rating scores of pain intensity and
612	amounts of monetary donations: F(1,29) = 58.196 and 180.022, ps < 0.001, $\eta_p^2 = 0.667$
613	and 0.861, 90% CI = (0.472, 0.760) and (0.765, 0.900), Fig. 5a and 5b). However,
614	patient-identity repetition failed to significantly increase rating scores of pain intensity
615	and amounts of monetary donations (F(1,29) = 0.016 and 0.209 , p = 0.901 and 0.651 ,
616	$\eta_p^2 = 0.001$ and 0.007, 90% CI = (0, 0.022) and (0, 0.119)), possibly due to ceiling
617	effects of our measures in the participants (i.e., larger mean rating scores of pain
618	intensity and mean amounts of monetary donations in the 1 st _round test in Experiment 5
619	than in Experiment 1).



620

Fig. 5. Behavioral and EEG results of Experiment 5. (a) Mean rating scores of pain intensity in the 1^{st} and 2^{nd} round tests. (b) Mean amounts of monetary donations in the 1^{st} and 2^{nd} round tests. (c) ERPs to faces with patient or actor/actress identities at frontal electrodes. The voltage topography shows the scalp distribution of the P2 amplitude with the maximum over the central/frontal region. (d) Mean differential P2

626 amplitudes to pain versus neutral expressions of faces with patient or actor/actress 627 identities. The voltage topographies illustrate the scalp distribution of the P2 difference 628 waves to pain versus neutral expressions of faces with patient or actor/actress identities, 629 respectively. (e) Illustration of the serial mediation model of the relationship between 630 decreased BOP and changes in monetary donations. Shown are group means (large 631 dots), standard deviation (bars), measures of each individual participant (small dots), 632 and distribution (violin shape) in (a), (b) and (d). The online version of this article 633 includes the following source data for Figure 5: Figure 5-Source data 1. 634 The participants responded to face identities with high accuracies during EEG 635 recording (> 83% across all conditions). The EEG results replicated those in Experiment 636 3 by showing significantly deceased P2 amplitudes to pain (vs. neutral) expressions of 637 actor/actress compared to patient faces (Identity \times Expression interaction: F(1,29) = 9.494, p = 0.004, $\eta_p^2 = 0.247$, 90% CI = (0.050, 0.429), Fig. 5c and 5d, see 638 639 Supplementary file 12 for statistical details). Simple effect analyses verified 640 significantly greater P2 amplitudes to pain vs. neutral expressions for patients' faces $(F(1,29) = 17.409, p < 0.001, \eta_p^2 = 0.375, 90\%$ CI = (0.142, 0.539)) but not for faces of 641 actors/actresses (F(1,29) = 0.270, p = 0.607, $\eta_p^2 = 0.009$, 90% CI = (0, 0.127), Bayes 642 643 factor = 0.220). These behavioral and EEG results are consistent with those in 644 Experiments 1 and 3 and provide repeated evidence for BOP effects on subjective 645 feelings of others' pain, altruistic behavior, and empathic brain activity in the same 646 sample. 647 Next, we tested a serial mediation model of the relationship between decreased 648 BOP (i.e., identity change from patient to actor/actress) and changes in monetary 649 donations with two mediator variables including empathic neural responses (as indexed 650 by the differential P2 amplitude to pain versus neutral expressions) and changes in

651	subjective feelings of others' pain (as indexed by differential rating scores of pain
652	intensity) (see Methods for details). This model includes three paths: (1) the indirect
653	effect of patient-identity change on monetary donation via the P2 amplitude ($a_1 \times b_1 =$
654	0.219, 95% CI = $(-0.141, 0.745)$; (2) the indirect effect of patient-identity change on
655	monetary donation via pain intensity ($a_2 \times b_2 = -1.182, 95\%$ CI = (-2.048, -0.510)); (3)
656	the indirect effect of patient-identity change on monetary donation via P2 amplitude \times
657	pain intensity ($a_1 \times d_{21} \times b_2 = -0.261$, 95% CI = (-0.584, -0.059), Fig. 5e, see
658	Supplementary file 13 for statistical details). The total indirect effect of patient-identity
659	change on the monetary donation after controlling all indirect effect was $c' = -1.223, 95\%$
660	CI = (-2.145, -0.400), which explained 26.14% variance of total effect of
661	patient-identity change on monetary donation. The effect sizes of the indirect path (2)
662	and (3) were 25.26% and 5.58%, respectively, indicating that subjective feelings of
663	others' pain mediated the association between patient-identity change and reduced
664	monetary donations. Moreover, this mediator role was partially mediated by BOP
665	induced variations of empathic brain activity in response to others' pain expressions.
666	Together, the results of these mediation analyses suggest a pathway from changes in
667	BOP to varied empathic brain activity and changes in subjective report of empathy for
668	other's pain (i.e., the degree of perceived pain in others), which further accounted for
669	BOP-induced changes in monetary donations.

Experiment 6: Neural structures underlying BOP effects on empathy

671 While our EEG results revealed evidence for modulations of empathic neural 672 responses by BOP, neural structures underlying these modulation effects remain unclear. 673 In particular, it is unknown whether brain responses underlying cognitive and affective 674 components of empathy are similarly sensitive to the influence of BOP. Therefore, in 675 Experiment 6, we used fMRI to record BOLD signals from an independent sample (N =676 31) to examine neural architectures in which empathic activities are modulated by BOP. 677 Similarly, the participants were first shown with photos of neutral faces of 20 models 678 and had to remember their patient (10 models) or actor/actress (10 models) identities. 679 After the participants had performed 100% correct in a memory task to recognize the 680 models' identities, they were scanned using fMRI when viewing video clips of the 681 models whose faces received painful (needle penetration) stimulation and showed pain 682 expressions or received non-painful (cotton swab touch) stimulation and showed neutral 683 expressions, similar to those used in the previous studies (Han et al., 2009; Luo et al., 684 2014; Han et al., 2017). Before scanning the participants were informed that these video 685 clips were recorded from 10 patients who were receiving medical treatment and 10 686 actors/actresses who practiced to imitate patients' pain expressions. The participants 687 responded to face identity (patient vs. actor/actress) of each model after viewing each 688 video clip by pressing one of two buttons with high accuracies (> 80% across all 689 conditions, see Supplementary file 14 for details). 690 After fMRI scanning the participants were presented with each video clip again and

had to rate the model's pain intensity and their own unpleasantness. The participants

692	were also asked to rate the degree to which they believed in the models' patient or
693	actor/actress identities in painful video clips on a 15-point Likert-type scale (-7 =
694	extremely believed as an actor/actress, $0 = not$ sure, $7 = extremely$ believed as a patient)
695	(see Method, Supplementary file 14 for results). The mean rating scores confirmed
696	significant differences in beliefs of patient and actors/actresses identities (2.776 ± 3.20
697	vs4.890 ± 1.44; t(30) = 10.526, p < 0.001, Cohen's d = 1.890, 95% CI = (6.178,
698	9.153)), indicating successful identity manipulations.
699	We first localized empathic neural responses by conducting a whole-brain analysis
700	of BOLD responses to perceived painful versus non-painful stimuli applied to targets
701	(collapsed faces with patient and actor/actress identities). This analysis revealed
702	significant activations in the cognitive, affective, and sensorimotor nodes of the
703	empathy network, including the bilateral anterior insula/inferior frontal cortex (MNI
704	peak coordinates $x/y/z = -45/17/-5$ and $45/26/-8$), bilateral inferior and superior
705	temporal gyri (-48/-70/-2 and 51/-58/-5), mPFC (3/56/25), left inferior parietal lobe
706	(-63/-25/31), right superior parietal lobe (30/-58/55), and right post-central gyrus and
707	posterior insula (58/-25/26, Fig. 6a; all activations were identified using a combined
708	threshold of voxel level $p < 0.001$, uncorrected, and cluster level $p < 0.05$, FWE
709	corrected). These brain activations are similar to those observed in previous research
710	(e.g., Luo et al., 2014). To examine brain activity engaged in representing facial
711	identities independent of perceived painful stimulation and pain expressions, we
712	conducted a whole-brain analysis of the contrast of the stimuli showing non-painful
- stimulations to patient versus actor/actress. This analysis showed significant activations
- 714 in the mPFC (-6/59/25) and bilateral TPJ (-54/-58/28 and 57/-67/31, Fig. 6b, all
- activations were identified using a combined threshold of voxel level p < 0.001,
- 716 uncorrected, and cluster level p < 0.05, FWE corrected).



717

Fig. 6. fMRI results of Experiment 6. (a) Brain activations in response to perceived
 painful (vs. non-painful) stimuli applied to targets (collapsed faces with patient and

720 actor/actress identities). (b) Brain activations in response to non-painful stimuli to 721 patients compared to actors/actresses. (c) Illustration of the behavioral dissimilarity 722 matrix derived from the rating scores of pain intensity across all participants. Each cell 723 in the dissimilarity matrix represents the mean difference in rating scores of pain 724 intensity between each pair of conditions. (d) Brain activations that were correlated with 725 the behavioral dissimilarity matrix revealed in the searchlight RSA. (e) Illustration of 726 the vicarious pain signature (defined by response to perceived noxious stimulation of 727 body limbs) responses to patients' and to actors/actresses' pain. (f) Illustration of the 728 general vicarious signature (defined by response to perceived noxious stimulation of 729 body limbs and painful facial expressions) responses to patients' and actors/actresses' 730 pain. AI = Anterior Insula; IPL = Inferior Parietal Lobe; ITG = Inferior Temporal Gyrus; 731 mPFC = medial Prefrontal Cortex; SPL = Superior Parietal Lobe; PoCG = Post-Central 732 Gyrus; FG = Frontal Gyrus; STS = Superior Temporal Sulcus; MFC = Middle Frontal 733 Cortex; TPJ = Temporoparietal Junction. The online version of this article includes the 734 following source data for Figure 6: Figure 6-Source data 1.

735

We conducted a whole-brain univariate analysis to examine the interaction effect

736 (patient vs. actor x pain vs. neutral) on brain activities in response to video clips but did

not find a significant effect. Therefore, we further conducted multivariate analyses of

738 BOLD signals to assess neural correlates of BOP effects on subjective feeling of others'

pain. Specifically, we conducted a representational similarity analysis (RSA) (Nili et al.,

740 2014) of brain activity using a dissimilarity matrix (DM) constructed from scores of

pain intensity in different conditions. The RSA sought to find patterns of brain activities

in the empathy neural network which can predict the pattern of subjective feeling of

others' pain that varied due to BOP. To do this, we first conducted ANOVAs of the

mean rating scores and found a significant Identity (patient vs. actor/actress) ×

Expression (pain vs. neutral) interaction on the rating scores of pain intensity (F(1,30) =

746 5.370, p = 0.027, $\eta_p^2 = 0.152$, 90% CI = (0.029, 0.391)) but not on the rating scores of

747 unpleasantness (F(1,30) = 3.945, p = 0.056, $\eta_p^2 = 0.116$, 90% CI = (0, 0.296), see

748 Supplementary file 14 for statistical details). Simple effect analyses showed

110	significantly larger scores of pain intensity for pain expressions of patients (vs.
750	actors/actresses) (F(1,30) = 9.823, p = 0.004, $\eta_p^2 = 0.247, 90\%$ CI = (0.053, 0.427)),
751	whereas scores of pain intensity did not differ significantly between neutral faces with
752	patient and actor/actress identifies (F(1,30) = 2.829, p = 0.103, $\eta_p^2 = 0.086$, 90% CI = (0,
753	0.260)). The results suggested a clear boundary between subjective feelings of pain
754	intensity in different conditions. Thus we constructed a 4×4 DM for each participant
755	with each cell in the DM representing the mean difference in rating scores of pain
756	intensity between each pair of conditions, as illustrated in Fig. 6c.
757	Next, we conducted a searchlight RSA to identify brain regions in which the
758	pairwise similarity of neural responses in the 4 conditions (2 Expressions \times 2 Identities)
759	corresponded to the behavioral DM in each participant (see Methods for details). We
760	first conducted a whole-brain searchlight RSA for each participant. The searchlight
761	results of all participants were then subject to a second group-level analysis to examine
762	the voxels in the empathy network, defined based on the results of the whole-brain
763	contrast of painful vs. non-painful stimuli applied to targets, that passed a threshold of
764	voxel level $p < 0.05$, FWE corrected. The results revealed significant activations in the
765	left anterior insula (MNI peak coordinates $x/y/z = -39/20/8$) and inferior parietal cortex
766	(-60/-19/29), and the right anterior insula/frontal cortex (36/23/11), superior temporal
767	gyrus (54/-37/11), inferior post-central gyrus (63/-40/26), and superior parietal cortex
768	(39/-49/50) (Fig. 6d).

significantly larger scores of pain intensity for pain expressions of patients (vs.

769	Finally, we estimated BOP effects on neural responses in a vicarious pain signature
770	(VPS) map that was identified to be sensitive to perceived painful stimulations applied
771	to others but not to self-experienced pain (Krishnan et al., 2016). We calculated the VPS
772	pattern responses to video clips showing patient or actor/actress faces that received
773	painful (needle penetration) or non-painful (cotton swab touch) stimulation using both
774	the body-specific VPS map in response to perceived noxious stimulation of body limbs
775	(Krishnan et al., 2016) and the general VPS in response to both perceived noxious
776	stimulation of body limbs and painful facial expressions (Zhou et al., 2020). We tested
777	the hypothesis of decreased VPS responses to actors/actresses' compared to patients'
778	pain (i.e., lack of BOP reduces empathic brain activities) by conducting t-tests of BOLD
779	signals in VPS maps. The results showed that activities in the VPS pattern were
780	significantly decreased in response to video clips showing actors/actresses' compared to
781	patients' pain (Fig. 6e and 6f, body-specific VPS: mean \pm s.d. = 41.487 \pm 28.794 vs.
782	46.548 ± 32.051 , t(30) = -2.059, p _(one-tailed) = 0.024, BF_{+0} = 2.361; general VPS: mean \pm
783	s.d. = 1.188 ± 6.058 vs. 2.462 ± 6.997 , t(30) = -2.447, p _(one-tailed) = 0.010, BF ₊₀ = 4.820).
784	These results provide further evidence for decreased empathic brain activities due to
785	lack of BOP for actors/actresses' pain in the empathic neural network.
786	Discussion
787	We conducted six experiments to investigate psychological and neural mechanisms
788	underlying BOP impacts on empathy and altruistic behavior in humans. We
789	manipulated individuals' BOP by randomly assigning patient or actor/actress identities

790	to faces as there was a lack of BOP for actors/actresses' faces but not for patients' faces.
791	We also estimated individuals' intrinsic BOP by asking the participants to estimate
792	effectiveness of medical treatments of patients to trigger BOP as an effective medical
793	treatment reduces a patient's pain. We further measured brain activity using EEG and
794	fMRI to examine BOP effects on empathic neural responses with high temporal and
795	spatial resolutions, respectively. Our behavioral and neuroimaging findings showed
796	evidence for a functional role of BOP in modulations of the
797	perception-emotion-behavior reactivity by illustrating how BOP predicted and affected
798	self-reports of empathy, empathic brain activities, and monetary donations. Our findings
799	suggest that BOP may provide a cognitive basis for empathy and altruistic behavior in
800	humans.
801	Experiments 1 and 2 showed behavioral evidence that manipulated changes in BOP
802	caused subsequent variations of self-report of empathy and altruistic behavior along the
803	directions as predicted. Specifically, decreasing BOP concomitant with changes in face
804	identities (from patient to actor/actress) or changes in effective medical treatments
805	(from suffering due to a disease to recovery due to medical treatment) significantly
806	reduced self-report of both cognitive (perceived intensity of others' pain) and affective
807	(own unpleasantness induced by perceived pain in others) components of empathy.
808	Decreasing BOP also inhibited following altruistic behavior that was quantified by the
809	amount of monetary donations to those who showed pain expressions. By contrast,
810	reassuring patient identities in Experiment 1 or by noting the failure of medical

811 treatment related to target faces in Experiment 2 increased subjective feelings of others' 812 pain and own unpleasantness and prompted more monetary donations to target faces. 813 The increased monetary donations might be due to that repeatedly confirming patient 814 identity or knowing the failure of medical treatment increased the belief of authenticity 815 of targets' pain and thus enhanced cognitive and affective components of empathy. Alternatively, repeatedly confirming patient identity or knowing the failure of medical 816 817 treatment might activate other emotional responses to target faces such as pity or 818 helplessness, which might also influence altruistic decisions. The increased empathy 819 rating scores and monetary donations might also reflect a contrast effect due to rating 820 patient and actor/actress targets alternately. These possible accounts can be clarified in 821 future work by asking participants to report their emotions and performing rating tasks 822 on patient and actor/actress targets in separate blocks of trials. In consistent with the 823 effects of manipulated BOP on empathy and altruism across the participants, the results 824 of Experiment 2 showed that individuals' intrinsic BOP related to each target face 825 predicted their self-report of empathy and altruistic behavior across different target 826 faces. Moreover, decreased (or increased) intrinsic BOP also predicted changes in 827 empathy/altruistic behavior across different target faces. These converging behavioral 828 findings across different participants and across different target faces provide evidence 829 for causal relationships between BOP and empathy/altruism. 830 Our results showed that self-reports of others' pain intensity and own

831 unpleasantness elicited by perception of others' pain were able to positively predict

832	altruistic behavior across individuals. Previous research using questionnaire measures of
833	empathy ability found that empathy as a trait is positively correlated with the amount of
834	money shared with others in economic games (Edele et al., 2013; Li et al., 2019).
835	Together, these findings are consistent with the proposition that empathy, as either an
836	instant emotional response to others' suffering (e.g., estimated in our study) or a
837	personality trait (e.g., estimated in Edele et al. (2013) and Li et al. (2019)), plays a key
838	role in driving altruistic behavior (Batson, 1987; Batson et al., 2015; Eisenberg et al.,
839	2010; Hoffman, 2008; Penner et al., 2005). Our mediation analyses of the behavioral
840	data in both Experiments 1 and 2 further revealed that the effects of decreased BOP on
841	monetary donations were mediated by self-report of others' pain intensity. These results
842	further suggest empathy as an intermediate mechanism of the BOP effects on altruistic
843	behavior.
844	Our neuroimaging experiments went beyond subjective estimation of the
845	relationships between BOP and empathy/altruism by investigating neural mechanisms
846	underlying BOP effects on empathy for others' pain. It is necessary to conduct objective
847	estimation of empathy to examine BOP effects because self-report measures of empathy
848	can be influenced by social contexts and are unable to unravel brain mechanisms
849	underlying BOP effects on empathy (e.g., Sheng and Han, 2012). Our EEG results in
850	Experiments 3 and 5 repeatedly showed that neural responses to pain (vs. neutral)
851	expressions over the frontal regions within 200 ms after face onset (indexed by the P2
852	amplitude over the frontal/central electrodes) were significantly reduced to faces with

853	actor/actress identities compared to those with patient identities. The results in
854	Experiments 3 and 4 indicate that BOP concomitant with face identity (i.e., patients'
855	pain expressions manifest their actual painful emotional states whereas actors/actresses'
856	pain expressions do not) rather than face identity (e.g., Tiger or Lion team identities)
857	alone resulted in modulations of the P2 amplitudes to pain expressions in the direction
858	as expected. Numerous EEG studies have shown that the frontal P2 component
859	responds with enlarged amplitudes to various facial expressions such as fear, anger,
860	happy (Williams et al. 2006; Luo et al. 2010; Calvo et al. 2013) and pain (Sheng and
861	Han, 2012; Sheng et al., 2013; 2016) expressions compared to neutral faces. These
862	findings uncovered early affective processing by differentiating emotional and neutral
863	expressions. ERPs to others' pain within 200 ms post-stimulus occur regardless of task
864	demands and are associated with spontaneous empathy for pain (Fan and Han, 2008).
865	Our ERP results indicate that BOP may provide a cognitive basis for early spontaneous
866	neural responses to others' suffering reflected in pain expressions. Moreover, the results
867	in Experiment 5 showed that the early spontaneous empathic neural responses in the P2
868	time window mediated the BOP effect on self-report of others' pain intensity, which
869	further mediated the relationship between the P2 empathic responses and the amount of
870	monetary donations. These results highlight both early spontaneous neural responses to
871	others' pain and subjective feelings of others' pain as intermediate mechanisms by
872	which BOP influences altruistic behavior.

873	To identify neural architectures underlying BOP effects on empathy, we recorded
874	BOLD responses, using fMRI, to perceived painful and non-painful stimuli applied to
875	individuals with patient or actor/actress identities in Experiment 6. We showed that the
876	contrast of perceived painful (vs. non-painful) stimulations activated the sensory (i.e.,
877	post-central gyrus), affective (i.e., insula), and cognitive (i.e., mPFC) nodes of the
878	empathy network, similar to the findings of previous studies (Singer et al., 2004;
879	Jackson et al., 2005; Saarela et al., 2007; Shamay-Tsoory et al., 2009; Han et al., 2009;
880	Fan et al., 2011; Lamm et al., 2011; Zhou and Han, 2021; Luo et al., 2014). Viewing
881	non-painful stimulations applied to neutral faces with patient versus actor/actress
882	identities revealed increased activity in the mPFC and bilateral TPJ, suggesting possible
883	neural representation of facial identities in the brain regions. Most importantly, the
884	results of searchlight RSA that was sensitive to both stimuli and subjective feelings
885	evoked by the stimuli revealed significant variations of activities in the insula,
886	post-central gyrus, and lateral frontal cortex in correspondence with the patterns of
887	self-reports of empathy for patients and actors/actresses' pain. In other words, the
888	patterns of the activities in the insula, post-central gyrus, and lateral frontal cortex were
889	able to predict distinct subjective feelings of patients' and actors/actresses' pain.
890	Moreover, the results of our VPS analyses showed consistent evidence for decreased
891	neural activities in the empathy-related neural network due to lack of BOP. These fMRI
892	results together suggest that activities in the brain regions supporting affective sharing
893	(e.g., insula, Shamay-Tsoory et al., 2009; Fan et al., 2011; Lamm et al., 2019), empathic

894	sensorimotor resonance (e.g., post-central gyrus, Avenanti et al., 2005; Zhou and Han,
895	2021), and emotion regulation (e.g., lateral frontal cortex, Ochsner and Gross, 2005;
896	Etkin et al., 2015) may provide intermediate mechanisms underlying variations of
897	subjective feelings of others' pain intensity due to lack of BOP.
898	Numerous studies have shown evidence for modulations of empathy by social
899	contexts. Contextual variables that influence perception of others' pain and empathy
900	include empathy targets' posture (Martel et al., 2008), identifiable pain pathology
901	(Twigg and Byrne, 2015), moral valence (Cui et al., 2016; Nicolardi et al., 2020), etc.
902	Empathizers' prior exposure to pain (Prkachin and Rocha, 2010), socioeconomic status
903	(Varnum et al., 2015), and cultural experiences (Wang et al., 2015; Hampton and
904	Varnum, 2018) also influence empathy and its underlying brain activities. Perceived
905	information about social relationships between observers and empathy targets also
906	modulates empathic neural responses such that, relative to viewing own-race or
907	own-team individuals' pain, viewing other-race or opponent-team individuals' pain
908	decreased empathic neural responses in the affective (e.g., ACC, AI), cognitive (e.g.,
909	mPFC, TPJ), and sensorimotor (e.g., motor cortex) nodes of the empathy network (Xu
910	et al., 2009; Avenanti et al., 2010; Hein et al., 2010; Mathur et al., 2010; Sheng and Han,
911	2012; Sheng et al., 2014; 2016; Han, 2018; Zhou and Han, 2021). The perceived
912	intergroup (racial) relationships between empathizers and empathy targets also
913	influenced altruistic behavior such as medical treatment (Drwecki et al., 2011). These
914	findings uncovered how social information perceived from stimuli and social experience

915	modulate empathic neural responses to others' suffering and subsequent social behavior.
916	The results of our current work complemented the findings of previous studies by
917	uncovering how beliefs, as preexisting internal mental representations of something that
918	is not immediately present to the scenes (Fuentes, 2019), also modulate people's
919	empathy and following altruistic behavior. Specifically, in the current study,
920	participants' beliefs (i.e., pain expressions of patients manifest their actual feelings
921	whereas pain expressions performed by actors/actresses do not) weakened the
922	participants' empathy for others' pain and reduced their monetary donations to those
923	who appeared suffering. BOP effects on empathy and altruistic behavior can be
924	understood as modulations of empathy by preexisting internal information (e.g., beliefs)
925	whereas previous findings revealed modulations of empathy by instantly perceived
926	social information in a specific social context. These findings together help to construct
927	neurocognitive models of empathy that take into consideration of both perceived social
928	information and preexisting internal information and their interactions that lead to
929	modulations of empathy and altruistic behavior during real-life social interactions.
930	It should be noted that our experimental manipulations changed the participants'
931	mind about the models' identities (e.g., patient vs. actor/actress) rather than explicitly
932	asking them to alter their BOP. BOP altered implicitly with target persons' identities due
933	to observers' knowledge about individuals with different identities (e.g., painful stimuli
934	applied to actors/actresses do not really hurt them and they show facial expressions to
935	pretend a specific emotional state). Therefore, the BOP effects on empathy and altruistic

936	behavior identified in our study might take place implicitly. This is different from the
937	placebo effects on first-hand pain experiences that are produced by explicitly perceived
938	verbal, conditioned, and observational cues that induce expectations of effective
939	analgesic treatments (Meissner et al., 2011). Similar explicit manipulations of making
940	individuals believe receiving oxytocin also promotes social trust and preference for
941	close social distances (Yan et al., 2018). Moreover, the placebo treatment relative to a
942	control condition significantly attenuated activations in the ACC, AI, and subcortical
943	structures (e.g., the thalamus) in response to painful electric shocks but increased the
944	prefrontal activity during anticipation of painful stimulations possibly to inhibit activity
945	in pain processing regions (Wager et al., 2004; 2015). The brain regions in which
946	empathic neural responses altered due to BOP (e.g., the lateral frontal cortex) as
947	unraveled in the current study do not overlap with those in which activities are
948	modulated by placebo analgesia (Atlas and Wager, 2014). These results suggest there
949	may be distinct neural underpinnings of BOP effects on empathic brain activity and
950	placebo effects on brain responses to first-hand pain experiences.
951	Do beliefs also provide a cognitive basis for the widely documented ingroup bias in
952	empathy for pain? Previous studies suggest that multiple neurocognitive mechanisms
953	are involved in ingroup bias in empathy for pain such as lack of attention (Sheng and
954	Han, 2012) and early group-based categorization of outgroup faces (Zhou et al., 2020,
955	see Han, 2018 for review). There has been behavioral evidence that white individuals
956	who more strongly endorsed false beliefs about biological differences between blacks

957	and whites (e.g., "black people's skin is thicker than white people's skin") reported
958	lower pain ratings for a black (vs. white) target and suggested less accurate treatment
959	recommendations (Hoffman et al., 2016). These behavioral findings suggest that other
960	beliefs may also provide a basis for modulations of empathy for others' pain and
961	relevant altruistic behavior. The underlying brain mechanisms, however, remain
962	unknown. The paradigms developed in the current study may be considered in future
963	research to examine neural underpinnings of the effects of false beliefs on empathy for
964	pain.
965	Another question arising from the findings of the current study is whether the belief
966	effect is specific to neural underpinnings of empathy for pain or is also evident for
967	neural responses to other facial expressions. To address this issue, we conducted an
968	additional EEG experiment in which we tested (1) whether beliefs of authenticity of
969	others' happiness influence brain responses to perceived happy expressions, and (2)
970	whether lack of beliefs of others' happiness also modulate neural responses to happy
971	expressions in the P2 time window, similar to the BOP effect on ERPs to pain
972	expressions (see Appendix 1 for methods). Similar to the paradigm used in Experiment
973	3, participants in the additional experiment had to first remember face identities
974	(awardees or actors/actresses). Thereafter these faces with happy or neutral faces were
975	presented with contextual information that the awardees showed happy expressions
976	when receiving awards whereas actors/actresses imitated others' happy expressions. The
977	participants also performed identity judgments on the faces while EEG was recorded.

978	Behavioral results in this experiment showed that participants reported less feelings of
979	actors' happiness compared to awardees' happiness. ERP results in this experiment
980	showed that lack of beliefs of authenticity of others' happiness (e.g., actors simulating
981	others' happy expressions vs. awardees smiling when receiving awards) reduced the
982	amplitudes of a long-latency positive component (i.e., P570) over the frontal region in
983	response to happy expressions. However, the face identities did not affect the P2
984	amplitudes in response to happy (vs. neutral) expressions (see Appendix 1 for statistical
985	details). These findings suggest that belief effects are evident for subjective feelings and
986	brain activities in response to happy expressions. However, beliefs of others' pain or
987	happiness affect neural responses to facial expressions in different time windows after
988	face onset. Future research should examine neural mechanisms underlying belief effects
989	on neural responses to other emotions to deep our understanding of general belief
990	effects on neural processes of others' emotional states.
991	Our behavioral and neuroimaging findings have implications for how we
992	understand the general functional role of beliefs in social cognition and interaction.
993	Empathy is supposed to originate from an evolved adaptation to quickly and
994	automatically respond to others' emotional states during parental care that is necessary
995	for offspring survival in humans and other species (De Waal, 2008; Decety, 2011). In
996	most cases of interactions among family members (i.e., between parents and offspring
997	or between siblings) perceived cues signaling pain in a person manifest his/her actual
998	emotional states that urge help from other family members. Such life experiences may

999 set up a default belief that perceived painful stimulation to others and their facial 1000 expressions reflect individuals' actual emotional states. This default belief provides a 1001 fundamental cognitive basis of reflexive and automatic empathy and empathic brain 1002 activity that further generates autonomic and somatic responses, as suggested by the 1003 perception-action model of empathy (Preston and de Waal, 2002). Nevertheless, when social interactions expand beyond family members to non-kin members and even 1004 1005 strangers, perceived pain expressions or painful stimuli applied to others may not 1006 always manifest others' actual emotional states because perceived painful cues may be 1007 fake in some cases. BOP in such situations may function as cognitive gate-control to 1008 modulate neural responses to perceived pain in others. This is necessary for monitoring 1009 social interactions to determine whether to help or to coordinate with those who appear 1010 suffering. Our findings illustrate how the perception-emotion-behavior reactivity occurs 1011 under the cognitive constraint of BOP to keep empathy and altruistic decision/behavior 1012 for the right target who is really in need of help. In this sense, BOP also provides an 1013 important cognitive basis for survival and social adaption during social interactions. 1014 Some limitations of the current work create future research opportunities. For 1015 example, a recent approach to hierarchical Bayesian models of cognition assumes that 1016 the brain represents information probabilistically and people represent a state or feature 1017 of the world not using a single computed value but a conditional probability density 1018 function (Knill and Pouget, 2004; Friston, 2005; Clark, 2013; Tappin and Gadsby, 1019 2019). Our manipulations of BOP, however, had only two conditions (patient vs.

1020	actor/actress) and thus lack a model of effects of probability-based belief-updating on
1021	empathy and relevant altruistic behavior. Future research should examine how empathy
1022	and relevant altruistic behavior vary as a function of the degree of BOP. Other
1023	interesting research questions arising from our work include how the brain represents
1024	BOP. It has been proposed that different types of beliefs (e.g., empirical beliefs,
1025	conceptual beliefs, relational beliefs) exist in human mind and may have distinct neural
1026	underpinnings (Harris et al., 2009; Seitz and Angel, 2020). To address neural
1027	representations of BOP will allow researchers to further explore and construct neural
1028	models of the interaction between beliefs and empathic brain activity in the key nodes
1029	of the empathy network. Another interesting issue related to our findings is individual
1030	differences in BOP and BOP effects on empathy and altruism. Since specific degrees of
1031	beliefs differ widely across individuals (Ais et al. 2016), it is crucial to examine what
1032	personality/psychopathic traits or biological factors make individuals hold strong or
1033	weak BOP and exhibit large or small BOP effects on empathy and altruistic behavior. It
1034	is also important to clarify what environmental factors modify individuals' default BOP
1035	and consequently change their motivations to help those who appear suffering. To
1036	clarify these issues will advance our understanding of individual and contextual factors
1037	that shape the functional role of BOP in modulations of empathy and altruistic behavior.
1038	Finally, a general issue arising from the current work is whether beliefs affect the
1039	processing of other emotions such as fear, sad, and happy, and, if yes, whether there are
1040	common underlying psychological and neural mechanisms.

1041	Concl	lusion

1042 Our behavioral and neuroimaging findings provide a new cognitive framework for 1043 understanding human empathy and altruism. Our findings indicate that lack of BOP or 1044 decreasing BOP weakened human empathy and altruistic behavior. Changing BOP 1045 affected both subjective feelings of others' emotional states and the underlying brain 1046 activity. BOP effects on altruistic behavior were mediated by two serial mediators, i.e., 1047 empathic neural responses and subjective feelings of others' pain. Our behavioral and 1048 brain imaging findings suggest that BOP provides a cognitive basis of the 1049 perception-emotion-behavior reactivity that underlies human altruism. The methods 1050 developed in our study open a new avenue for testing functional roles of beliefs as 1051 cognitive-gate control of other emotion processing and relevant social behavior. 1052 **Methods** 1053 **Participants** Sixty Chinese students were recruited in Experiment 1 as paid volunteers (29 males, 1054 1055 mean age \pm s.d. = 21.15 \pm 2.31 years). The sample size was estimated using G*Power 1056 (Faul et al., 2007) with a middle effect size of 0.25. To test the difference in pain intensity rating scores or monetary donations between the 1st and 2nd round tests, we 1057 conducted ANOVAs with Test Phase (1st vs. 2nd round) and Identity Change (patient to 1058 1059 actor/actress vs. patient to patient) as independent within-subjects variables. To detect a 1060 significant Test x Identity interaction requires a sample size of 36 with an error 1061 probability of 0.05 and a power of 0.95, given the correlation among repeated measures

1062	(0.5) and the nonsphericity correction (1). Sixty Chinese students were recruited in
1063	Experiment 2 as paid volunteers (30 males, 21.55 ± 2.45 years). Thirty Chinese students
1064	were recruited in Experiment 3 (all males, 22.23 ± 2.51 years) as paid volunteers. The
1065	sample size was determined based on our previous EEG research on empathy for pain
1066	using the same set of stimuli (Sheng and Han, 2012). We recruited only male
1067	participants to exclude potential effects of gender difference in empathic neural
1068	responses. Thirty-one Chinese students were recruited in Experiment 4 as paid
1069	volunteers. One participant was excluded from data analyses due to his lower response
1070	accuracy during EEG recording (< 50%). This left 30 participants (all males, 20.70 \pm
1071	1.97 years) for behavioral and EEG data analyses. Thirty Chinese students were
1072	recruited in Experiment 5 (all males, 20.60 ± 1.75 years). Thirty-two Chinese students
1073	were recruited in Experiment 6 as paid volunteers. One participant was excluded from
1074	data analyses due to excessive head movement during fMRI scanning. There were 31
1075	participants left (all males, 22.23 ± 2.59 years) for behavioral and fMRI data analyses.
1076	The sample size in Experiment 6 was determined based on our previous fMRI research
1077	using similar stimuli (Luo et al., 2014). All participants had normal or
1078	corrected-to-normal vision and reported no history of neurological or psychiatric
1079	diagnoses. This study was approved by the local Research Ethics Committee of the
1080	School of Psychological and Cognitive Sciences, Peking University. All participants
1081	provided written informed consent after the experimental procedure had been fully

1082 explained. Participants were reminded of their right to withdraw at any time during the1083 study.

1084 **Experiment 1: Lack of BOP reduces subjective estimation of empathy and**

- 1085 altruistic behavior
- 1086 Stimuli and procedure

1087 The stimuli were adopted from our previous work (Sheng and Han, 2012), which 1088 consisted of photos of 16 Chinese models (half males) with each model contributing one 1089 photo with pain expression and one with neutral expression.

1090 After reporting demographic information, the participants were informed that they

1091 would be paid with ¥10 as a basic payment for their participation. They would be able

1092 to obtain an extra bonus payment as much as \$2 depending on their decisions in the

1093 following procedure. In the 1st_round test the participants were informed that they

1094 would be shown photos with pain expressions taken from patients who suffered from a

serious disease. After the presentation of each photo the participants were asked to

1096 evaluate intensity of each patient's pain based on his/her expression by rating on a

1097 Likert-type scale ("How painful do you think this person is feeling?", 0 = not painful at

1098 all; 10 = extremely painful). This rating task was adopted from previous research (Bieri

1099 et al., 1990; Jackson et al., 2005; Lamm et al., 2007; Fan and Han, 2008; Sheng and

1100 Han, 2012) to assess the participants' understanding of others' pain feeling — a key

1101 component of empathy. The instructions of the rating tasks focused on emotional states

1102 of faces and had nothing to do with face identities (i.e., patients or actors/actresses).

1103 Therefore, BOP effects on empathy, if observed, occurred implicitly and automatically. 1104 Immediately after the pain intensity rating, the participants were asked to decide how 1105 much from the extra bonus payment they would like to donate to the patient (0 to 10 1106 points, 1 point = ± 0.2). The participants were informed that the amount of one of their 1107 donation decisions would be selected randomly and endowed to a charity organization 1108 to help those who suffered from the same disease. After the 1st_round test the participants were asked to perform a short (5 mins) 1109 1110 calculation task (10 arithmetic calculations, e.g. $25-3\times7=?$) to clean their memory of the 1st_round ratings. Thereafter, the participants were told that the photos were actually 1111 1112 taken from 8 patients and 8 actors/actresses and this experiment actually tested their 1113 ability of recognizing social identities by examination of facial expressions. Faces 1114 assigned with patient or actor/actress identities were counterbalanced across the participants. The participants were then asked to conduct the 2nd round test in which 1115 1116 each photo was presented again with a word below to indicate patient or actor/actress

1117 identity of the face in the photo. The participants had to report again pain intensity of

1118 each face and how much they would like to donate to the person shown in the photo.

1119 The participants were informed that an amount of money would be finally selected

1120 randomly from their 2nd_round decisions and donated to one of the patients through the

same charity organization. After the experiments had been finished, the total amount of

1122 the participants' donations were subject to a charity organization.

1123	We conducted ANOVAs of rating scores of pain intensity and amounts of monetary
1124	donations with Test Phase (1^{st} vs. 2^{nd} _round) × Identity Change (patient to actor/actress
1125	vs. patient to patient) as independent within-subjects variables to assess whether and
1126	how beliefs of others' pain (BOP) influenced empathy and altruistic behavior toward
1127	those who suffered. Finally, the participants completed two questionnaires to estimate
1128	individual differences in trait empathy (Davis, 1983) and interpersonal trust (Wright and
1129	Tedeschi, 1975). We analyzed the relationship between our empathy/altruistic measures
1130	and individuals' trait empathy/interpersonal trust but failed to find significant results
1131	and thus were not reported in the main text.
1132	Mediation analysis
1133	We performed mediation analyses to examine whether pain intensity mediates the
1134	pathway from BOP to monetary donation. To do this, we first dummy coded
1135	patient-identity change (i.e., 0 (patient identity in the 1 st _round test) and 1 (actor/actress
1136	in the 2 nd _round test) or patient-identity repetition (i.e., as 0 (patient identity in the
1137	1 st _round test) and 1 (patient identity in the 2 nd _round test). Then, we estimated four
1138	regression models: 1) whether the independent variable (BOP) significantly accounts
1139	for the dependent variable (monetary donation) when not considering the mediator (e.g.,
1140	Path c); 2) whether the independent variable (BOP) significantly accounts for the
1141	variance of the presumed mediator (pain intensity) (e.g., Path a); 3) whether the
1142	presumed mediator (pain intensity) significantly accounts for the variance of the
1143	dependent variable (monetary donation) when controlling the independent variable

1144	(BOP) (e.g., Path b); 4) whether the independent variable (BOP) significantly accounts
1145	for the variance of the dependent variable (monetary donation) when controlling the
1146	presumed mediator (pain intensity) (e.g., Path c'). To establish the mediation, the path c
1147	is not required to be significant. The only requirement is that the indirect effect a×b is
1148	significant. Given a significant indirect effect, if Path c is not significant, the mediation
1149	is classified as indirect-only mediation which is the strongest full mediation (Kenny et
1150	al., 1998; Zhao et al., 2019). A bootstrapping method was used to estimate the
1151	mediation effect. Bootstrapping is a nonparametric approach to estimate effect-sizes and
1152	hypotheses of various analyses, including mediation (Shrout and Bolger, 2002;
1153	Mackinnon et al., 2004). Rather than imposing questionable distributional assumptions,
1154	a bootstrapping analysis generates an empirical approximation of the sampling
1155	distribution of a statistic by repeated random resampling from the available data, which
1156	is then used to calculate p-values and construct confidence intervals. 5,000 resamples
1157	were taken for our analyses. Moreover, this procedure supplies superior confidence
1158	intervals (CIs) that are bias-corrected and accelerated (Preacher et al., 2007; Preacher
1159	and Hayes, 2008a, 2008b). The analyses were performed using Hayes's PROCESS
1160	macro (Model 4, Hayes, 2017).
1161	Statistical comparison
1162	Behavioral data were assumed to have a normal distribution but this was not
1163	formally tested. 95% Confidence intervals (95% CIs) were reported for t-tests of the

1164 mean difference between two conditions and for correlation analyses of correlation

1165 coefficients. 90% CIs were reported for effect sizes (η_p^2) of ANOVA analyses.

1166 According to Steiger (2004), the general rule of thumb to use CIs to test a statistical

1167 hypothesis (H0) is to use a $100 \times (1-\alpha)\% / 100 \times (1-2\alpha)\%$ CI when testing a two-sided /

- 1168 one-sided hypothesis at alpha level. We thus reported 90% CIs of η^2 in ANOVAs
- 1169 because η^2 is always positive.

1170 Experiment 2: Intrinsic BOP predicts subjective estimation of empathy and

1171 altruistic behavior

1172 The face stimuli and the procedure were the same as those in Experiment 1 except

1173 the following. The participants were informed that they were to be shown photos with

1174 pain expressions taken from patients who had suffered from a serious disease and

1175 received medical treatment. After the presentation of each photo the participants were

asked to estimate how effective the medical treatment was for each patient by rating on

1177 a Likert-type scale (0 = no effective or 0% effective, 100 = fully effective or 100%

1178 effective). Besides rating pain intensity of each face in the 1st_round test, the

1179 participants were asked to report how unpleasant they were feeling when they viewed

1180 the photo (i.e., own unpleasantness) by rating on a Likert-type scale ("How unpleasant

1181 do you feel when viewing this person?" 0 = not unpleasant at all, 10 = extremely

1182 unpleasant). The unpleasantness rating was performed to evaluate emotional sharing of

1183 others' pain — another key component of empathy (Jackson et al., 2005; Fan and Han,

1184 2008; Sheng and Han, 2012). The order of the two empathy rating tasks was

1185 counterbalanced across the participants. Immediately after the empathy rating tasks, the

participants were asked to decide how much from the extra bonus payment they would like to donate to the patient (0 to 10 points, 1 point = ± 0.2).

In the 2^{nd} _round test the participants were told that the medical treatment was actually effective for only half of the patients. Each photo was then presented again with information that the medical treatment applied to the patient was 100% effective or 0% effective. Thereafter, the participants were asked to perform the rating tasks and monetary donations as those in the 1^{st} _round test. The participants were told that an amount of money would be finally selected from their 2^{nd} _round decisions and donated to one of the patients.

1195 Mediation analysis

1196 This was the same as that in Experiment 1 except that we tested whether changes of 1197 pain intensity mediate the pathway from decreased BOP or enhanced BOP to changes of 1198 monetary donation. To do this, we first calculated belief update (decreased BOP: 1199 100%-effect minus the participants' initial estimation; enhanced BOP: the participants' 1200 initial estimation minus 0%-effect). Then, we estimated four regression models: 1) 1201 whether the independent variable (BOP) significantly accounts for the dependent 1202 variable (changes of monetary donation) when not considering the mediator (e.g., Path 1203 c); 2) whether the independent variable (BOP) significantly accounts for the variance of 1204 the presumed mediator (changes of pain intensity) (e.g., Path a); 3) whether the 1205 presumed mediator (changes of pain intensity) significantly accounts for the variance of 1206 the dependent variable (changes of monetary donation) when controlling the

independent variable (BOP) (e.g., Path b); 4) whether the independent variable (BOP)
significantly accounts for the variance of the dependent variable (changes of monetary
donation) when controlling the presumed mediator (changes of pain intensity) (e.g.,
Path c').

1211 Experiment 3: Lack of BOP decreased empathic brain activity

1212 Stimuli and procedure

Face stimuli were adopted from our previous work (Sheng and Han, 2012) and used in Experiments 3, 4 and 5 in this study. The stimuli consisted of 32 faces of 16 Chinese models (half males) with each model contributed one photo with pain expression and one with neutral expression. During behavioral tests or EEG recording, each photo was presented in the center of a gray background on a 21-inch color monitor, subtending a visual angle of $3.8^{\circ} \times 4.7^{\circ}$ (width × height: 7.94×9.92 cm) at a viewing distance of 60 cm.

1220 Before EEG recording the participants were asked to perform an identity memory 1221 task in which faces with neutral expressions were presented. Eight faces were marked as 1222 patients and 8 faces as actors/actresses. After viewing photos with marked identity for 1223 15 minutes, the participants performed a discrimination task in which each neutral face 1224 was displayed for 200 ms and the participants had to press the left or right button using 1225 the left or right index finger to indicate identity of each face (i.e., patient or actor/actress) 1226 within two seconds. After their response accuracies reached 100%, the participants were 1227 moved into an acoustically- and electrically-shielded booth for EEG recording.

1228	During EEG recording each trial consisted of a painful or neutral face with a
1229	duration of 200 ms, which was followed by a fixation cross with a duration varying
1230	randomly between 800 and 1400 ms. There were 8 blocks of 64 trials (each of the 32
1231	photographs was presented twice in a random order in each block). The participants
1232	were asked to press the left or right button using the left or right index finger to indicate
1233	the identity of the face (i.e., patient or actor/actress) as fast and accurately as possible.
1234	The relation between responding hand and face identity was counterbalanced across
1235	different blocks of trials.
1236	After EEG recording, the participants were presented with each face again with a
1237	neutral or pain expression and asked to rate how painful the person is feeling (i.e., pain
1238	intensity) by rating on a Likert-type scale (1 = not painful at all; 7 = extremely painful).
1239	To estimate the participants' BOP, they were also asked to answer the question of "To
1240	what extent do you believe the identity of this model (either patient or actor/actress)?"
1241	on a 15-point Likert-type scale (-7 = extremely believed as an actor/actress, $0 = not$ sure,
1242	7 = extremely believed as a patient).
1243	EEG data acquisition and analysis
1244	A NeuroScan system (CURRY 7, Compumedics Neuroscan) was used for EEG
1245	recording and analysis. EEG was continuously recorded from 32 scalp electrodes and

- 1246 was re-referenced to the average of the left and right mastoid electrodes offline.
- 1247 Impedances of individual electrodes were kept below 5 k Ω . Eye blinks and vertical eye
- 1248 movements were monitored using electrodes located above and below the left eye. The

1249	horizontal electro-oculogram was recorded from electrodes placed 1.5-cm lateral to the
1250	left and right external canthi. The EEG signal was digitized at a sampling rate of 1,000
1251	Hz and subjected to an online band-pass filter of 0.01–400 Hz. EEG data were filtered
1252	with a low-pass filter at 30 Hz offline. Artefacts related to eye movement or eye blinks
1253	were removed using the covariance analysis tool implemented in CURRY 7 (Semlitsch
1254	et al., 1986). Only trials with correct responses to face identity were included for data
1255	analyses (see Supplementary file 15 for the numbers of trials included for data analyses
1256	in Experiments 3-5). ERPs in each condition were averaged separately offline with an
1257	epoch beginning 200 ms before stimulus onset and continuing for 1200 ms. Trials The
1258	baseline for all ERP measurements was the mean voltage of a 200-ms prestimulus
1259	interval and the latency was measured relative to the stimulus onset.
1260	Face stimuli in the identity judgment task elicited an early negative activity at
1261	95-115 ms (N1) and a positive activity at 175-195 ms (P2), followed by a positive
1262	activity at 280-340 ms (P310) and a long-latency positivity at 500-700 ms (P570) over
1263	the frontal area. The mean ERP amplitudes were subject to ANOVAs with Identity
1264	(patient vs. actor/actress) and Expression (pain vs. neutral) as within-subject variables.
1265	To avoid potential significant but bogus effects on ERP amplitudes due to multiple
1266	comparisons (Luck and Gaspelin, 2017), the mean values of the amplitudes of the N1,
1267	P2, P310, and P570 components were calculated at frontocentral electrodes (i.e., F3, Fz,
1268	F4, FC3, FCz and FC4).

1269	To further assess the null hypothesis regarding the difference in the P2 amplitude in
1270	response to pain and neutral expressions of actors/actress' faces, we conducted Bayes
1271	factor analyses for repeated-measures ANOVA and paired t-tests. We calculated the
1272	Bayes factor in the program R v.3.5.1 (www.r-project.org) using the function anovaBF
1273	and ttestBF from the package BayesFactor (Morey and Rouder, 2015). We conducted
1274	Bayes factor analyses based on the default priors for ANOVA and paired t-test design
1275	(scale r on an effect size of 0.707). A Bayes factor indicates how much more likely each
1276	alternative model is supported compared with the null hypothesis.
1277	Experiment 4: BOP is necessary for modulations of empathic brain activity
1278	Stimuli and procedure
1279	These were the same as those in Experiment 3 except the following. Before EEG
1280	recording, the participants were informed that all the 16 faces were patients and they
1281	were from two baseball teams (half from Tiger team and half from Lion team). After the
1282	identity memory task, they performed identity judgments on faces with neutral or pain
1283	expressions by pressing one of two buttons while EEG was recorded.
1284	EEG data acquisition and analysis
1285	These were the same as those in Experiment 3.
1286	Experiment 5: Empathic brain activity mediates relationships between BOP and
1287	empathy/altruistic behavior
1288	Stimuli and procedure

- 1289 The stimuli and behavioral tests were the same as those in Experiment 1 to assess
- 1290 BOP effects on self-report of perceived pain intensity and altruistic decisions.
- 1291 Thereafter, the participants went through the EEG session that was the same as that in
- 1292 Experiment 3 to examine BOP effects on empathic brain activity. These designs
- allowed us to test whether BOP induced changes of empathic brain activity plays a
- 1294 mediator role in the pathway from belief changes to altered subjective feelings of others'
- 1295 pain and altruistic decisions.
- 1296 Behavioral and EEG data recording and analyses
- 1297 These were the same as those in Experiments 1 and 3.
- 1298 Multiple mediation model analysis
- We constructed a serial mediation model to test the hypothesis that BOP (dummy coded as 0 for patients and 1 for actors/actresses) effect on monetary donations was
- 1301 sequentially mediated by two chain mediators, i.e., empathic neural responses and
- 1302 subjective feelings of others' pain. This model includes three indirect paths: (1) indirect
- 1303 effect of BOP on monetary donation via empathic neural responses (i.e. P2 amplitude);
- 1304 (2) indirect effect of BOP on monetary donation via subjective feelings of others' pain
- 1305 (pain intensity); (3) indirect effect of BOP on monetary donation via P2 amplitude \times
- 1306 pain intensity. To do this, we estimated seven regression models: 1) whether the
- 1307 independent variable (BOP) significantly accounts for the dependent variable (monetary
- 1308 donation) when not considering the mediator (e.g., Path c); 2) whether the independent
- 1309 variable (BOP) significantly accounts for the variance of the presumed mediator (P2

1327	Implicit association test
1326	test the hypothesis.
1325	intensity. Similarly, the bootstrapping method was used to estimate the effect-size and
1324	indirect effect ($a_1 \times d_{21} \times b_2$) of BOP on monetary donation via P2 amplitude \times pain
1323	amplitude; indirect effect $(a_2 \times b_2)$ of BOP on monetary donation via pain intensity;
1322	significance of indirect effect $(a_1 \times b_1)$ of BOP on monetary donation via the P2
1321	To test the significance of the three paths, we separately conducted to examine the
1320	(monetary donation) when controlling the presumed the two mediators (e.g., Path c').
1319	variable (BOP) significantly accounts for the variance of the dependent variable
1318	controlling the independent variable (BOP) (e.g., Path b ₂); 7) whether the independent
1317	accounts for the variance of the dependent variable (monetary donation) when
1316	(BOP) (e.g., Path b ₁); 6) whether the presumed mediator (pain intensity) significantly
1315	dependent variable (monetary donation) when controlling the independent variable
1314	presumed mediator (P2 amplitude) significantly accounts for the variance of the
1313	variance of the second mediator (pain intensity) (e.g., Path d_{21}); 5) whether the
1312	whether the first independent mediator (P2 amplitude) significantly accounts for the
1311	accounts for the variance of the presumed mediator (pain intensity) (e.g., Path a ₂); 4)
1310	amplitude) (e.g., Path a ₁); 3) whether the independent variable (BOP) significantly

1328To assure our experimental manipulation of patient and actor/actress identities, after1329the EEG recording, participants were asked to complete a modified implicit association1330test (IAT, Greenwald et al., 1998). The participants were asked to respond to faces with

1331 patient identifies and patient related words (e.g. ache, weak) with one key and to faces 1332 with actor/actress identities and actor/actress related words (e.g. imitation) with another 1333 key in two blocks of trials (60 trials in each block). They were then asked to respond to 1334 faces with patient identities and actor/actress related words with one key and to faces 1335 with actor/actress identities and patient related words with another key in two additional 1336 blocks of trials. A D score was then calculated based on response times according to the 1337 established algorithm (Greenwald et al., 2003). A positive D score significantly larger 1338 than zero would suggest that patient faces were more strongly associated with patient 1339 (vs. actor/actress) relevant words whereas actor/actress faces were more strongly 1340 associated with actor/actress (vs. patient) relevant words. 1341 **Experiment 6: Neural structures underlying BOP effects on empathy** 1342 Stimuli and procedure 1343 We adopted 24 video clips from 6 models from our previous work (Luo et al., 2014) 1344 and recorded 56 video clips from 14 Chinese models (half males) in Experiment 6. Each 1345 model contributed four video clips, in which a face with pain expressions receiving 1346 painful stimulation (needle penetration) or with neutral expressions receiving 1347 non-painful stimulation (cotton swab touch) applied to the left or right cheeks. Each 1348 video subtended a visual angle of $21^{\circ} \times 17^{\circ}$ (width \times height) at a viewing distance of 80 1349 cm during fMRI scanning. 1350 A photo of each model with a neutral expression was obtained from each video clip.

1351 These photos were then used in the identity memory task, which was the same as that in

1352	Experiment 3. After the identity memory task the participants underwent fMRI scanning
1353	An event-related design was employed in 6 functional scans. Each scan consisted of 20
1354	video clips (half patients (5 pain and 5 neutral expressions) and half actors/actresses (5
1355	pain and 5 neutral expressions)) that were presented in a random order. Each video clip
1356	lasted for 3 s. There was a 9-s interstimulus interval between two successive video clips
1357	when the participants fixated at a central cross and had to judge the identity (patient or
1358	actor/actress) of each model in the video clip by pressing one of two buttons using the
1359	right index or middle finger. The relation between responding finger and face identity
1360	was counterbalanced across participants.

1361 After fMRI scanning, the participants were presented with each video clip again

1362 outside the scanner. They were asked to rate pain intensity of each model (1 = not

painful at all; 7 = extremely painful) and own unpleasantness (1 = not unpleasant at all,

1364 7 = extremely unpleasant). Finally, we assessed the participants' beliefs of models'

1365 identities by asking them to answer the question of "To what extent do you believe the

1366 identity of this model (either patient or actor/actress)?" on a 15-point Likert-type scale

1367 (-7 = extremely believed to be an actor/actress, 0 = not sure, 7 = extremely believed to1368 be a patient).

1369 **fMRI data acquisition and analysis**

1370 Imaging data were acquired using a 3.0 T Siemens scanner with a standard head

1371 coil. Head motion was controlled to the maximum extent by using foam padding.

1372 Functional images were acquired by using T2-weighted, gradient-echo, echo-planar

1373imaging (EPI) sequences sensitive to Siemens scanner contrast ($64 \times 64 \times 32$ matrix with1374 $3.75 \times 3.75 \times 5$ mm³ spatial resolution, repetition time = 2000 ms, echo time = 30 ms, flip1375angle = 90°, field of view = 24×24 cm). Anatomical images were subsequently obtained1376using a standard 3D T1-weighted sequence ($256 \times 256 \times 144$ matrix with a spatial1377resolution of $1 \times 1 \times 1.33$ mm3, TR = 2530 ms, TE = 3.37 ms, inversion time (TI) = 11001378ms, FA = 7°).

1379 Functional images were preprocessed using SPM12 software (the Wellcome Trust 1380 Centre for Neuroimaging, London, UK, http://www.fil.ion.ucl.ac.uk/spm). Functional 1381 scans were first corrected for within-scan acquisition time differences between slices 1382 and then realigned to the first volume to correct for inter-scan head motions. This 1383 realigning step provided a record of head motions within each fMRI run. Head 1384 movements were corrected within each run and six movement parameters (translation; x, 1385 y, z and rotation; pitch, roll, yaw) were extracted for further analysis in the statistical model. The functional images were resampled to $3 \times 3 \times 3$ mm³ voxels, normalized to 1386 1387 the MNI space using the parameters of anatomical normalization and then spatially 1388 smoothed using an isotropic of 8 mm full-width half-maximum (FWHM) Gaussian 1389 kernel. 1390 Whole-brain analyses was conducted to examine brain regions in which activities 1391 increased in response to pain versus neutral stimuli regardless of patient or actor/actress

identities. This contrast pooled video clips of patient and actor/actress models together

1392

1393 to focus on BOLD responses to painful versus neutral stimuli. The general linear model

1394	(GLM) had four regressors including patients receiving pain stimuli, patients receiving
1395	neutral stimuli, actors/actresses receiving pain stimuli, and actors/actresses receiving
1396	neutral stimuli. The GLM also included the realignment parameters to account for any
1397	residual movement-related effect. A box-car function was used to convolve with the
1398	canonical hemodynamic response in each condition. Random-effect analyses were
1399	conducted based on statistical parameter maps from each participant to allow population
1400	inference. The contrast values were compared using whole-brain paired t-tests to
1401	identify activations, which were defined using a threshold of voxel-level $p < 0.001$,
1402	uncorrected, cluster-level $p < 0.05$, FWE corrected. We also conducted a whole-brain
1403	analysis to calculate the contrast of patient versus actor/actress non-painful stimuli to
1404	test whether BOP may motivate inference of patients' mental states independently of
1405	any perceived painful cues.
1406	Representational similarity analysis
1407	We conducted a representational similarity analysis (RSA) of brain activity (Nili et
1408	al., 2014) to examine neural correlates to BOP effects on subjective feelings of others'
1409	pain. We constructed a 4×4 dissimilarity matrix (DM) for each participant with each
1410	cell in the DM represents the mean difference in rating scores of pain intensity between

- 1411 each pair of conditions. The DM was then used for a whole-brain searchlight RSA to
- 1412 identify brain regions in which the pairwise similarity of neural responses in the 4
- 1413 conditions (2 Expressions \times 2 Identities) corresponded to the behavioral DM of
- 1414 condition dissimilarity in each participant. To do this, functional images were similarly

1415	preprocessed using a GLM but were not smoothed and normalized. We then estimated a
1416	GLM for each participant with Identity (patient vs. actor/actress) and Expression (pain
1417	vs. neutral) as experimental regressors. The estimated beta images corresponding to
1418	each condition were then averaged across runs at each voxel and were used as activity
1419	patterns in the RSA toolbox (Nili et al., 2014). We compared the neural-pattern
1420	similarity (i.e., the neural DM) with the behavioral DM in each voxel of the brain using
1421	the searchlight procedure (Kriegeskorte et al., 2006). The neural DM was constructed
1422	by 1 minus the correlation coefficient between the pattern vectors of each condition pair.
1423	The Spearman rank correlations between the neural DM and behavioral DMs were
1424	computed and assigned to the central voxel of the sphere. As such, the searchlight
1425	procedure produced Spearman p values on each voxel for each participant, which were
1426	then subject to Fisher's z transformation for statistical tests. The resulting z maps were
1427	then normalized to standard space (resampled to 3 x 3 x 3 mm ³ voxels), smoothed
1428	(FWHM= 8mm), and entered into a random effect analysis using one-sample t tests
1429	against zero. The searchlight results of all participants were then subject to a second
1430	group-level analysis to examine the voxels in the empathy network, defined based on
1431	the results of the whole-brain contrast of painful versus non-painful stimuli applied to
1432	targets, that passed a threshold of voxel level $p < 0.05$, FWE corrected.

1433 Neural signature analysis

We conducted vicarious pain signature (VPS) analyses (Krishnan et al., 2016) to
further assess BOP effects on empathic brain activity. We first calculated contrast

1436	images in the condition of patient-pain (or actor/actress-pain) versus an implicit baseline
1437	(e,g., using a design matrix of [1, 0, 0, 0]) since the test-retest reliability was higher
1438	when examining brain activations to painful stimulation using an implicit baseline than
1439	using a control condition (Han et al., 2021). The VPS map, which was sensitive to
1440	perceived painful stimulations applied to others' body limbs but not to self-experienced
1441	pain (Krishnan et al., 2016), was then converted into the image space using the ImCalc
1442	function of SPM. Thereafter, the VPS map was dot-multiplied with the contrast of
1443	patient-pain versus baseline and the contrast of actor/actress-pain versus baseline,
1444	respectively. These yielded a scalar VPS response value in each condition. The VPS
1445	response values were then subject to a one-tailed t-test to test the hypothesis of
1446	decreased VPS responses related to actor/actress-pain relative to patient-pain. To further
1447	validate the results of VPS analyses, we conducted a similar analysis using the general
1448	vicarious pain signature, which was identified to respond to both perceived noxious
1449	stimulation of body limbs and painful facial expressions (Zhou et al., 2020).
1450	Supplementary File legends
1451	• Source code 1. Scripts for plotting Figure 1a, 1b, 2d, 2e, 2f, 3a, 4a, 5a, 5b.
1452	• Source code 2. Scripts for plotting Figure 3c, 4c, 5d.
1453	• Source code 3. Scripts for the whole-brain analysis in Figure 6a and 6b.
1454	• Source code 4. Scripts for plotting Figure 6c.

1455 • Source code 5. Scripts for plotting Figure 6d.
1456	• Supplementary File 1. Statistical results of the mediation analysis (pain intensity
1457	mediated the relationship between decreased BOP and monetary donations) in
1458	Experiment 1.
1459	• Supplementary File 2. Supplementary file 2. Statistical results of the mediation
1460	analysis (pain intensity mediated the relationship between enhanced BOP and monetary
1461	donations) in Experiment 1.
1462	• Supplementary File 3. Pain intensity, unpleasantness, and monetary donation (mean
1463	± SD) in Experiment 2.
1464	• Supplementary File 4. Statistical results of the mediation analysis (pain intensity
1465	mediated the relationship between decreased BOP and monetary donations) in
1466	Experiment 2.
1467	• Supplementary File 5. Statistical results of the mediation analysis (pain intensity
1468	mediated the relationship between enhanced BOP and monetary donations) in
1469	Experiment 2.
1470	• Supplementary File 6. Statistical results of the mediation analysis (unpleasantness
1471	mediated the relationship between decreased BOP and monetary donations) in
1472	Experiment 2.
1473	• Supplementary File 7. Statistical results of the mediation analysis (unpleasantness
1474	mediated the relationship between enhanced BOP and monetary donations) in
1475	Experiment 2.

1476	• Supplementary file 8. Statistical results of reaction times, accuracies, and rating
1477	scores (mean \pm SD) in Experiment 3.
1478	• Supplementary file 9. Statistical results of mean ERP amplitudes (mean \pm SD) in
1479	Experiment 3.
1480	• Supplementary file 10. Statistical results of reaction times, accuracies, and rating
1481	scores (mean \pm SD) in Experiment 4.
1482	• Supplementary file 11. Statistical results of mean ERP amplitudes (mean \pm SD) in
1483	Experiment 4.
1484	• Supplementary file 12. Statistical results of reaction times, accuracies, and mean
1485	ERP amplitudes (mean \pm SD) in Experiment 5.
1486	• Supplementary file 13. Results of the serial mediation analysis in Experiment 5.
1487	• Supplementary file 14. Statistical results of reaction times, accuracies and rating
1488	scores (mean \pm SD) in Experiment 6
1489	• Supplementary file 15. Number of ERP trials for analyses (mean ± SD) in
1490	Experiments 3-5.
1491	Data availability
1492	All data generated or analyzed for figures of this study are included in the manuscript
1493	and supporting files. Source data files have been provided for Figures 1-6 and Appendix
1494	1 Figure 1.
1495	Code availability

1496 Code files used to analyze the data and to generate the figures that support the findings

1497 of this study have been uploaded.

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- 1875 **Competing interests**
- 1876 The authors declare no competing interests.

1 Appendix 1

2	Our results in Experiments 1 to 6 showed consistent evidence for modulations of
3	both subjective (self-report) and objective (EEG/fMRI) measures of empathy for others'
4	suffering. An interesting question arising from these findings is whether the belief
5	effects are specific to neural underpinnings of empathy for pain. We addressed this issue
6	by examining belief effects on neural responses to other facial expressions in an
7	additional experiment. Specifically, in this experiment, we sought to test (1) whether
8	beliefs of authenticity of others' happiness influence brain responses to perceived happy
9	expressions, and (2) whether beliefs also modulate neural responses to happy
10	expressions in the P2 time window, similar to the BOP effect on ERPs to pain
11	expressions. The paradigm used in the additional experiment was the same as that used
12	in Experiment 3 except the following. We asked an independent sample of participants
13	to remember identities (awardees or actors/actresses) of neutral faces. Thereafter, EEG
14	signals to happy and neutral expressions of awardees or actors/actresses were recorded
15	after informing the participants that photos of happy faces were taken from awardees
16	who were smiling when receiving awards whereas actors/actresses imitated others'
17	smiling and showed happy expressions. We predicted that beliefs that actors/actresses'
18	expressions do not reflect their actual emotional states would decrease brain response to
19	happy expressions. We tested this prediction by comparing ERPs to happy/neutral faces
20	with awardee or actor/actress identities.

We recorded EEG signals from an independent sample of healthy young adults (N = 30 males, mean age \pm s.d. = 22.30 \pm 2.73 years). Face stimuli with happy or neutral expressions were adopted from the previous study (Wang and Han, 2021). There were photos of 16 Chinese models (half males) and each model contributed one photo with happy expression and one with neutral expression.

26 The participants were first presented with the faces with neutral expressions and 27 were informed that these photos were taken from 8 awardees who recently obtained 28 awards and from 8 actors/actresses. After the identity memory task, in which the 29 participants were able to correctly recognize all faces with awardee or actor/actress 30 identities, they were asked to perform identity judgments on faces with neutral or happy 31 expressions by pressing one of two buttons while EEG was recorded. After EEG 32 recording, the participants were presented with each happy face again and had to rate 33 how happy the person is feeling (i.e., happiness intensity) by rating on a Likert-type 34 scale (1 = not happy at all; 7 = extremely happy).



41	1-table 1 for details). The results suggest weaker subjective feelings of happiness
42	intensity for faces with actor/actress identities compared to awardee identities.
43	The participants responded to face identities with high accuracies during EEG
44	recording (>88% across all conditions, see Appendix 1-table 1 for details). Similarly,
45	ERPs to face stimuli in this experiment were characterized by an early negative activity
46	at 90-120 ms (N1) and a positive activity at 175-195 ms (P2) at the frontal/central
47	regions, which were followed by two positive activities at 280-340 ms (P310) over the
48	parietal region and 500–700 ms (P570) over the frontal area (Appendix 1-Figure 1b).
49	ANOVAs of the P2 amplitudes with Identity (awardee vs. actor/actress) and Expression
50	(happy vs. neutral) as within-subject variables did not reveal a significant Identity \times
51	Expression interaction (F(1,29) = 0.441, P = 0.512, $\eta_p^2 = 0.015$, 90% CI = (0, 0.145),
52	Bayes factors = 0.303).
53	Importantly, ANOVAs of the later P570 amplitudes showed a significant Identity \times
54	Expression interaction (F(1,29) = 4.832, P = 0.036, $\eta_p^2 = 0.143$, 90% CI = (0.005,
55	0.328), Appendix 1-Figure 1b and 1c, see Appendix 1-table 1 for statistical details).
56	Simple effect analyses indicated significantly larger P570 amplitudes in response to
57	happy versus neutral expressions of awardees' faces (F(1,29) = 20.880, $p < 0.001$, η_p^2 =
58	0.419, 90% CI = (0.181, 0.573)), but not of actors/actresses' faces (F(1,29) = 3.375, p =
59	0.076, $\eta_p^2 = 0.104$, 90% CI = (0, 0.285), Bayes factor = 0.858).



Appendix 1-Figure 1. EEG results of the additional experiment. (a) Mean rating scores 61 62 of happy intensity related to happy and neutral expressions of faces with awardee or 63 actor/actress identities. (b) ERPs to faces with awardee or actor/actress identities at 64 frontal electrodes. The voltage topography shows the scalp distribution of the P570 65 amplitude with the maximum over the central/parietal region. (c) Mean differential P570 amplitudes to happy versus neutral expressions of faces with awardee or 66 67 actor/actress identities. The voltage topographies illustrate the scalp distribution of the 68 P570 difference waves to happy (vs. neutral) expressions of faces with awardee or 69 actor/actress identities, respectively. Shown are group means (large dots), standard 70 deviation (bars), measures of each individual participant (small dots), and distribution 71 (violin shape) in (a) and (c). The online version of this article includes the following 72 source data for Appendix 1-Figure 1: Appendix 1-Figure 1-Source data 1. 73

75	Our behavioral and ERP results in this experiment suggest reduced subjective
76	feelings and brain responses to happy (vs. neutral) expressions of actors/actresses' faces
77	compared to awardees' faces. These results support the prediction that beliefs that
78	actors/actresses' expressions do not reflect their actual emotional states decrease brain
79	response to happy expressions. However, belief effects on brain responses to happy
80	expressions were observed on the P570 amplitudes but not on the P2 amplitudes. This is
81	different from our ERP results in in Experiments 3-5, in which we showed evidence that
82	BOP modulated the P2 amplitudes. These results suggest general belief modulation
83	effects on brain activities involved in processing of facial expressions. In addition, our

84	results suggest that the time window in which beliefs modulate brain responses to facial
85	expressions depends on the nature of facial expressions (e.g., pain or happiness
86	expressions).
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90	(2021).

		Awardee			Actor/Actress		
		Neutral	Нарру		Neutral	Нарру	
RT (ms)		654±63	657±60		666±64	680±66	
Accuracy (%)	1	92±4.9	90±7.5		92±5.4	88±8.7	
Happy Intensity		2.525±0.94	5.638±0.64		2.146±0.94	4.95±0.96	
N1 amplitude (μV) P2 amplitude (μV) P310 amplitude (μV)		-2.267±1.69	-2.606±1.75		-2.297±1.43	-2.620±1.5	
		2.544±2.64	2.375±2.30		2.940±2.56	2.593±2.56	
		3.449±3.45	3.445±3.30		3.492±3.38	3.376±3.38	
P570 amplitud	de (µV)	4.677±2.22	5.379±2.15		4.696±2.16	4.950±2.11	
ERP trials		114±10	110±13		113±11	108±12	
	Statist	-	ANOVA		Simple eff	Simple effect (Identity)	
	Voluo	Idontity	Evennession	Idontity*Fynnog	sion Awardaa	A ator/A atr	
	value F	12 220	11.256			12 220	
	г D	0.001	0.002	4.755	0.915	0.001	
RT (ms)	r n ²	0.001	0.002	0.038	0.031	0.001	
	ղ _թ 000/	(0.004.0.488)	(0.071, 0.450)	(0.004, 0.326)	(0, 0, 180)	(0.094.0.4	
	90 70 E	0.406	(0.071, 0.439)	0.505	(0, 0.180)	(0.094, 0.4	
• • • • • • • • • •	r D	0.490	40.390	0.393			
	r ²	0.467	< 0.001	0.447			
(%)	ղ _թ ոու	(0, 0, 150)	(0.262, 0.608)	(0, 0, 158)			
	90%	(0, 0.150)	(0.362, 0.698)	(0, 0.158)	122 261	202 129	
TT	r	19.512	422.774	0.010	433.304	<0.001	
Нарру	P 2	<0.001	< 0.001	0.010	< 0.001	<0.001	
Intensity	η _p -	0.402	0.936	0.186	(0.802.0.055)	0.912	
	90%	(0.166, 0.560)	(0.889, 0.953)	(0.021, 0.372)	(0.892, 0.955)	(0.849, 0.9	
274	f D	0.031	9.890	0.005			
NI (05.115	P 2	0.802	0.004	0.944			
(95-1151118)	ղ _թ ոու	0.001	(0.055, 0.426)	(0, 0,007)			
	90 70 E	(0, 0.041)	0.055, 0.450)	(0, 0.007)			
D2	г D	0.470	2.822	0.441			
r2 (175–105mg)	r n ²	0.017	0.104	0.015			
(175-1951118)	ղ _թ ոոջ/	0.105	(0, 0, 266)	(0, 0, 145)			
	90%	(0.019, 0.309)	(0, 0.200)	(0, 0.143)			
D210	г D	0.012	0.140	0.232			
(280 240mg)	r m ²	0.915	0.711	0.019			
(200-340MS)	η _р 0∩0∕	(0, 0, 0, 0, 1, 7)	(0, 0, 106)	(0, 0, 125)			
D57 0	90%) E	(0, 0.017)	(0, 0.100)	(0, 0.125)	20.880	2 275	
r5/U	r	1.948	20.752	4.832	20.880	3.373	
(500-700ms)	Р	0.173	< 0.001	0.036	< 0.001	0.076	

92 Appendix 1-table 1. RTs, accuracies, rating scores, numbers of ERP trials, and ERP amplitudes (mean ±

$\eta_p^{\ 2}$	0.063	0.417	0.143	0.419	0.104
90%	(0, 0.232)	(0.180, 0.572)	(0.005, 0.328)	(0.181, 0.573)	(0, 0.285)

94 Note: Effect size is indexed as the partial eta-squared value. The 90% CIs are reported for partial

95 eta-squared value.