

Neurobiology of culturally common maternal responses to infant cry

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This report coordinates assessments of five types of behavioral responses in new mothers to their own infants' cries with neurobiological responses in new mothers to their own infants' cries and in experienced mothers and inexperienced nonmothers to infant cries and other emotional and control sounds. We found that 684 new primipara mothers in 11 countries (Argentina, Belgium, Brazil, Cameroon, France, Kenya, Israel, Italy, Japan, South Korea, and the United States) preferentially responded to their infants' vocalizing distress by picking up and holding and by talking to their infants, as opposed to displaying affection, distracting, or nurturing. Complementary functional magnetic resonance imaging (fMRI) analyses of brain responses to their own infants' cries in 43 new primipara US mothers revealed enhanced activity in concordant brain territories linked to the intention to move and to speak, to process auditory stimulation, and to caregive [supplementary motor area (SMA), inferior frontal regions, superior temporal regions, midbrain, and striatum]. Further, fMRI brain responses to infant cries in 50 Chinese and Italian mothers replicated, extended, and, through parcellation, refined the results. Brains of inexperienced nonmothers activated differently. Culturally common responses to own infant cry coupled with corresponding fMRI findings to own infant and to generic infant cries identified specific, common, and automatic caregiving reactions in mothers to infant vocal expressions of distress and point to their putative neurobiological bases. Candidate behaviors embedded in the nervous systems of human caregivers lie at the intersection of evolutionary biology and developmental cultural psychology.

maternal responsiveness | neurobiology | culture | infant cry | fMRI

When Charles Darwin had his firstborn son, William Erasmus ("Doddy"), he made extensive notes and eventually wrote in his "Biographical Sketch of an Infant" that "during the first 7 days... of course sucking and screaming, were well performed by my infant" (1). Human infants command precious few means of agency, and so their faces and voices serve signaling functions essential to their survival (2–4). The acoustic structure of infant distress vocalizations (cries) and caregiver responses appear to be conserved among mammals, including humans (2, 5). Infant cries reflect the coevolution of displays of progeny physiological state and caregiver psychobiological mechanisms designed to optimize strategic patterns of investment (6). From the moment of birth, certain signals from babies effectively influence parenting: Infant cries motivate adults to approach and to act (7, 8). That is, infant cries and caregiver responses to them constitute an integrated dyadic system that encompasses the infant production of cries as well as the adult anatomy (9–12), physiology (5, 13), and perception, processing, and response apparatus to cries (2, 4, 5, 14–17). Cries put both infant and caregiver in states of strong mutual nervous system activation and increase the probability of behavioral attunement (18).

How and why do caregivers respond to their infants' cries? Here, we report a confluence of results from two previously divergent approaches to understanding this fundamental and necessary act

of human caregiving. We hypothesize that, where evolutionary biology and developmental cultural psychology intersect, we might pinpoint universal behaviors and the structures that subserve them likely embedded in the nervous systems of human caregivers. The essential challenge of systems neuroscience is to identify and quantify brain activity underlying behavior. Specifically, human infants' altricial dependence on adult caregiving suggests that mechanisms associated with prompt and appropriate caregiver responsiveness ought to be automatic and deeply ingrained in the caregiver nervous system. From the perspective of evolutionary biology, the human brain evolved adaptive mechanisms to optimize decisions that enhance reproductive success (19), such as responding to the infant cry to sustain life. To test our general hypothesis, we undertook a series of interlocked complementary studies. In observations of maternal behavior in situ in 11 countries, we hypothesized preferred and common patterns of new mothers' responses to their own infants' cries. In three independent companion fMRI experiments in three countries, we sought to identify neurobiological underpinnings of the same behavioral responses in new mothers in the United States to their own young infants' cries, in experienced mothers in China to infant cries in comparison with noninfant cry emotional sounds, and in experienced mothers and inexperienced nonmothers in Italy to generic infant cries.

Care-soliciting vocalizations are common in the young of many species (2, 6, 16, 20, 21) and constitute a signal system that has been conserved throughout mammalian evolution (2, 22). Human infants effectively elicit parental attention, proximity, and solicitude by crying (23–29); in times of famine, for example, crying

Significance

We undertook an interdisciplinary exploration that unites evolutionary biology, neuroscience, and developmental cultural psychology. Based on extensive and detailed behavioral analyses of 684 new mothers in 11 countries and complementary functional magnetic resonance imaging (fMRI) analyses of brain responses in 43 first-time new US mothers to their own infants' cries, 44 experienced Chinese mothers to infant cries and control emotional sounds, and 12 Italian mothers and nonmothers to generic infant cries, we identified specific behavior repertoires and specific corresponding activated brain regions in human caregivers that constitute primary responses to infant distress. This study set will appeal to scientific and general audiences because it elucidates the foundations of core parenting practices in response to infant vocal distress.

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infants are more properly cared for, enhancing their chances of survival (30, 31). Indeed, mothers react neurobiologically (32–39), autonomically (28, 39, 40), and hormonally (41–44), as well as behaviorally (45–48), to their babies' cries.

No study of a single society can reveal universals of childcare in our species. However, similarities in parenting practices across diverse cultural groups would supply unique evidence that responses to crying constitute culturally common, species-general, fundamental processes (49, 50). A central limitation of research in infancy and parenting to date is that it has described constructs, structures, functions, and processes largely deriving from Western, educated, industrialized, rich, and democratic societies (50, 51). Reviews of the literature consistently show that upwards of 80 to 90% of published psychological and developmental studies have been conducted in North America and Western Europe (the minority developed world) whereas only 10 to 20% of the world's literature represents the majority (developing) world (51). This limitation has impeded a comprehensive understanding of caregiving and child mental health (52), led to critiques of monocultural perspectives, and motivated consistent calls for enlarged multicultural study. Cross-cultural comparisons are especially valuable because they expose and deepen understanding of processes that likely generalize across disparate populations. Identifying what is culturally common biologically and psychologically is theoretically significant in social, behavioral, and neural science. For our behavioral observation, therefore, we recruited mother–infant dyads from one country in North America, two in South America, three in Western Europe, two in sub-Saharan Africa, one in the Middle East, and two in East Asia (see [Table S1](#)). For our companion neurobiological experiments, we recruited mothers (and nonmothers) from one country in North America, one in Western Europe, and one in East Asia.

What do new mothers naturally do when their infants cry and why? Mothers may display affection to the infant, distract the infant, nurture the infant, pick up and hold the infant, or talk to the infant (3, 5, 7, 18) (see [Fig. 1A](#) and [Supporting Information](#)). When infants cry, caregivers must balance empathy and approach motivations with the potential to cause harm (46). That is, infant cries draw a caregiver's attention and solicitude but sometimes invite neglect or maltreatment (53–55). Fundamental species-general responses to infant cries would suggest biological bases for generating appropriate caregiving behaviors as expressed by the nervous system. Understanding how mothers' brains respond to their infants' cries is therefore vital to optimizing care, as it is to diagnosing and obviating risk, to the next generation.

Results

Cross-Cultural Behavioral Observation of Infants and Mothers. Mothers in all countries showed within-country variation in all five response types but also demonstrated regular differences across response types ([Fig. 1A](#) and [Table S2](#)). Overall, combining countries, mothers were significantly unlikely to respond to infant distress by displaying affection, by distracting, and by nurturing, but mothers were significantly likely to respond to infant distress by picking up and holding and by talking to their infant. Some countries with smaller sample sizes ($n < 30$) of usable data (at least five infant distress vocalizations) did not reach significance for every behavior ([Supporting Information](#)). However, in every country, average odds ratios (ORs) for mothers' affection, distraction, and nurturance in response to their infants' vocal distress were below the transformed equivalent of 1, indicating that these responsive behaviors were unlikely. By contrast, average ORs for mothers to pick up and hold their infants and to talk to their infants in response to their infants' vocal distress were at or above 1 or its transformed equivalent, indicating that these responsive behaviors were likely. Looking across countries at maternal responses to infant vocal distress revealed culturally common parenting practices (i.e., virtually no country differences in ORs) ([Supporting Information](#)).

Mothers in 11 different countries around the world behaved with noteworthy consistency in promptly responding to their own infants' vocal distress by picking up and holding their infants and by talking to their infants as two likely contingent responses, and displaying affection, distraction, and nurturance as three unlikely contingent responses. In humans, infant cry is the earliest preverbal form of communication. Given their high biological relevance, infant-related stimuli capture adult attention and trigger physiological responses that prepare for action and speech (56). Evolutionary theories posit that parent responsiveness to infants plays a crucial role in child survival and so enhances reproductive success (24, 57). As evolutionary theorizing also appeals to the species-common genome, the shared biological heritage of some psychological processes presupposes their generality (58). We therefore reasoned that, because of their cross-cultural prevalence and significance for species survival, behaviorally common responses to infant cry may be subserved by neurobiological mechanisms embedded in mothers' nervous systems.

fMRI Experiments of Mothers' Brain Responses to Infant Cry. To uncover potential neurobiological underpinnings of specific maternal responses involving action and speech, we pursued a direct approach through fMRI in two main experiments, one of new primipara mothers' brain responses to their own infants' cry during the early postpartum period, and a second of more experienced mothers' brain responses to infant cries in contrast to other infant and adult emotional and control sounds. (In a third subsidiary fMRI experiment presented in [Supporting Information](#), we examined experienced mothers' and nonmothers' responses to generic infant cries.) fMRI allowed us to visualize locations of changes in brain metabolic activity that were correlated to the occurrence of stimuli linked to a young infant's vocal distress. Given our behavioral data, we hypothesized that infant cry (vs. other emotional and control sounds) would activate (*i*) the medial superior frontal gyrus, which includes the supplementary motor area (SMA) (59, 60) [known to be associated with two sets of functions especially relevant here: (*a*) preparing for movement and the conscious intention to move (61, 62), imagining to grasp (63), and experiencing an "urge" to move (64) and (*b*) as the "starting mechanism of speech" involved in preparing a verbal utterance and initiating vocal tract movement (65–69)]; (*ii*) the bilateral inferior prefrontal cortices (Broca's areas) associated with social speech processing (70); and (*iii*) the superior temporal gyri (STG) associated with processing complex sounds (71). (*iv*) We also hypothesized involvement of midbrain and striatum, known to play critical roles in maternal caregiving (72–74). To test these hypotheses about brain areas that would substantiate and presumably underlie universal observations from the cross-cultural behavioral observations, and to evaluate their generality, we studied mothers (and nonmothers) in three distinct cultures: the United States, China, and Italy. (For details about the participants, methods, and results of all fMRI experiments, see [Supporting Information](#).) Results with respect to the three main hypotheses are reported here (supplementary results for hypothesis *iv* are reported in [Supporting Information](#)).

fMRI experiment 1: New mothers in the United States. As hypothesized, we found one significant cluster of activation in the right pre-SMA, bilateral clusters of activation in the dorsolateral prefrontal cortex (includes Broca's areas) and in superior and middle temporal cortices, and one large bilateral cluster that included putamen, thalamus, and midbrain ([Fig. 1B](#)). For peaks of activity and cluster sizes, see [Table 1](#).

fMRI experiment 2: Experienced mothers in China. The main purposes of fMRI experiment 2 were to replicate, extend, and refine the results of fMRI experiment 1 in a second culture, to mothers who were more experienced with infants, and vis-à-vis emotional sounds other than infant cry. Results of fMRI experiment 2 replicated, extended, and refined results of fMRI experiment 1. The infant cry (IC) vs. noise control sound (NCS) contrast paralleled fMRI

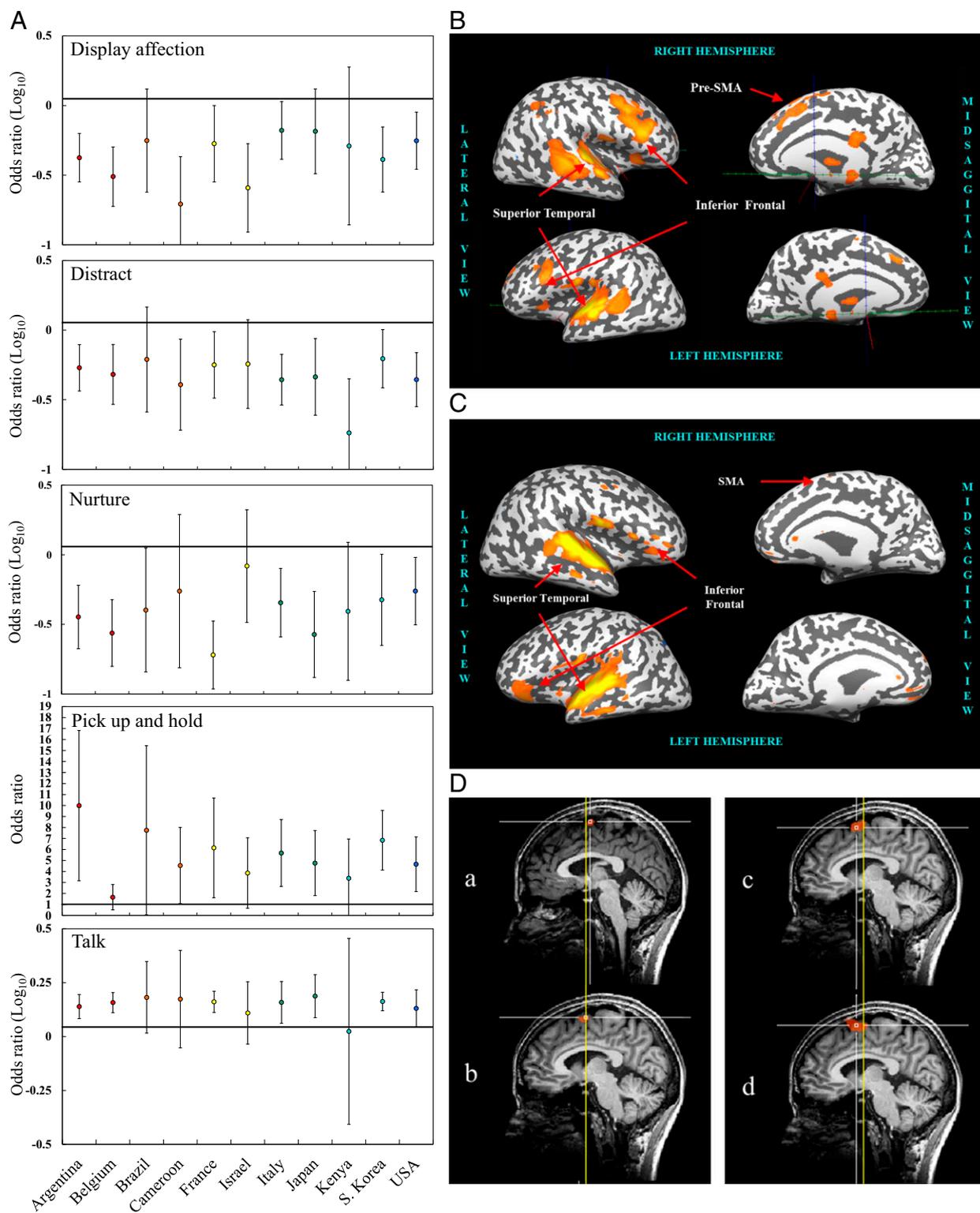


Fig. 1. Behavioral and fMRI responses to human infant cries. (A) Five types of maternal contingent responses to infant vocal distress in 11 countries. Display affection: Physical behaviors (kissing) or verbal statements (“I love you”). Distract: Encouraging the infant’s attention to a property, object, or event in the environment physically or verbally. Nurture: Feeding, burping, wiping the infant’s face or hands, or diapering the infant. Pick up and hold: Lifting and supporting some or all of the infant’s weight with the body. Talk: Vocalizing directed toward the infant. Reference lines for statistical significance are drawn. Except for talk, which has an absolute minimum of -1 , abscissae mark the absolute minima for transformed ORs. Means and 97.5% CIs. (B) US mothers. Graphical representation of brain regions resulting from the contrast own-infant cry vs. control noise in the whole group of new mothers at 3.5 mo postpartum. The top of the figure refers to the right hemisphere, the bottom to left hemisphere, the left to lateral views, and the right to midsagittal views. (C) Chinese mothers. Graphical representation of brain regions resulting from the contrast infant cry vs. control noise in the whole group of mothers at 7 mo postpartum. The top of the figure refers to the right hemisphere, the bottom to the left hemisphere, the left to lateral views, and the right to midsagittal views. (D) Chinese mothers. Sagittal brain views of pre-SMA and SMA-proper activation peaks (white squares) in the following contrasts (and coordinates): (a) IC vs. NCS ($x = 3, y = -4, z = 64$), (b) IB vs. NCS ($x = 6, y = -1, z = 61$), (c) AC vs. NCS ($x = 6, y = 5, z = 58$), and (d) IL vs. NCS ($x = 6, y = 5, z = 61$). The vertical anterior commissure (VAC) line ($y = 0$) is indicated in yellow.

Table 1. US mothers, own-infant cry vs. control noise

Region	Brodman area	Peak x	Peak y	Peak z	t	Voxels at q(FDR) < 0.01
Left <u>superior</u> and middle temporal gyri	41/42/22/21	-52	-20	9	9.75	20,705
Right <u>superior</u> and middle temporal gyri/insula	41/42/21/22/13	53	-20	6	8.57	21,803
Right <u>middle</u> frontal gyrus, precentral gyrus/insula	6/9/46/44/45/13	32	1	39	6.98	18,618
Left <u>putamen</u> /right putamen/thalamus (bilateral medial dorsal and ventral anterior nuclei)/bilateral midbrain (subthalamic nuclei)		-22	1	9	5.87	17,194
Right <u>pre-supplementary motor area</u> /bilateral medial frontal gyrus	6/8	2	4	63	5.83	6,558
Left <u>middle</u> and inferior frontal gyrus	9/44/46	-40	13	33	5.43	4,132
Left anterior insula	13	-31	22	9	5.25	744
<u>Left</u> and right ventral posterior cingulate cortex	23	-1	-32	27	5.11	1,122
Cerebellum (pyramis)		-16	-65	-30	5.09	2,067
Right supramarginal gyrus	40	47	-50	42	5.05	713
Right intraparietal sulcus	40	32	-53	36	4.75	870
Cerebellum (uvula)		8	-65	-30	4.61	547
Left <u>superior</u> and middle frontal gyri	9/10	-28	43	30	4.44	741

Brain regions (cluster peaks of activity are underlined), Brodmann area specifications, Talairach coordinates, *t* values, and cluster sizes resulting from the contrast own-infant cry vs. control noise in the whole group of participants (see Fig. 1B for graphical representation). Brodmann areas are missing for regions that fall outside the cerebral cortex (e.g., subcortical and cerebellar regions). qFDR, *P* value adjusted for the false discovery rate.

experiment 1 most closely and revealed increased activation in the right SMA and in two large bilateral clusters centered in the STG that extended to the inferior frontal gyrus [including Brodmann area (BA) 44 and 45], the insula, and the globus pallidus. Activation was also observed in one right cluster centered in the putamen (Fig. 1C). For peaks of brain activity and cluster size, see Table 2.

The infant laugh (IL) vs. NCS contrast revealed increased activation in the bilateral pre-SMA and in two large bilateral clusters centered in the STG. The left cluster extended to the middle temporal gyrus, the inferior frontal gyrus, and the insula. The anterior part of the right cluster included the temporal pole, the inferior (including BA 44 and 45) and middle frontal gyrus, the precentral gyrus, and the insula, whereas the posterior part of the same cluster extended to the supramarginal gyrus. Another peak of cerebral activation was observed in the clusters centered in the right inferior gyrus. Cerebral activation was also found in the left lateral globus pallidus, the right caudate body, and the right thalamus (the cluster extended to the lentiform nucleus) (Fig. S1). For peaks of brain activity and cluster size, see Table S3.

The infant babble (IB) vs. NCS contrast revealed peaks of cerebral activations at the right edge between pre-SMA and SMA-proper, in the right inferior frontal gyrus, and in two large clusters centered in the left STG—which extended to the middle and transverse temporal gyri, the inferior frontal gyrus (including BA 44), the postcentral gyrus and the insula—and the right STG that included the middle temporal gyrus, the inferior frontal gyrus (including BA 44 and 45), and the insula. We also observed subcortical activity in the bilateral thalamus and the left medial globus pallidus (Fig. S2). For peaks of brain activity and cluster sizes, see Table S4.

The adult female cry (AC) vs. NCS contrast revealed cerebral activations in the right pre-SMA and in one large cluster centered in the right STG that extended to the inferior and the middle frontal gyri, the insula, the thalamus, the putamen, and the midbrain in both hemispheres and to the globus pallidus and the amygdala in the right hemisphere (Fig. S3). For peaks of brain activity and cluster sizes, see Table S5.

Summary, fMRI experiment 3, and activation peaks analysis. The fMRI results from one Western and one Eastern culture confirm that new mothers hearing their own infants' vocal distress as well as

Table 2. Chinese mothers, infant cry vs. control noise

Region	Brodman area	Peak x	Peak y	Peak z	t	Voxels at q(FDR) < 0.05
Left superior <u>temporal</u> gyrus, inferior frontal gyrus, insula, globus pallidus	22/21/42/44/46/13	-48	-13	7	9.95	40,269
Right superior <u>temporal</u> gyrus, inferior frontal gyrus, insula, globus pallidus	22/21/44/45/13	57	-13	7	10.29	33,898
Left cerebellar declive		-15	-64	-20	6.03	9,002
Left anterior <u>cingulate</u> , medial frontal gyrus	32/10	-3	41	-5	4.78	1,711
Left superior frontal gyrus	9	-12	53	28	4.39	712
Right precentral gyrus	6	45	-1	46	4.18	867
Right putamen		21	2	13	4.15	847
Right cerebellar uvula		15	-85	-26	3.99	862
Right supplementary motor area	6	3	-4	64	3.88	302
Right inferior frontal gyrus	45	51	17	19	3.73	143
Left inferior semi-lunar lobule		-12	-64	-42	3.62	529
Left precuneus	7	-24	-64	31	-3.55	319
Left precentral gyrus	6	-63	-4	31	-3.56	201

Brain regions (cluster peaks of activity are underlined), Brodmann area specifications, Talairach coordinates, *t* values, and cluster sizes resulting from the contrast infant cry vs. control noise in the whole group of participants (see Fig. 1C for graphical representation). Brodmann areas are missing for regions that fall outside the cerebral cortex (e.g., subcortical and cerebellar regions). qFDR, *P* value adjusted for the false discovery rate.

experienced mothers hearing infant vocal distress generally activate brain areas linked to the intention (*i*) to move and to grasp (SMA), (*ii*) to speak (inferior frontal regions, SMA), and (*iii*) to process auditory stimulation (superior temporal regions). (*iv*) In addition, we found strong activity in other brain areas known to be associated with caregiving (midbrain, basal ganglia, cingulate, and insula) (75). Furthermore, we found similar results in a third fMRI experiment with experienced Italian mothers (Fig. S4 and Table S6). See [Supporting Information](#) for full details of fMRI experiment 3.

In fMRI experiment 2, SMA activated to all emotional sounds (IC, IL, IB, and AC) when contrasted with a control sound (NCS). However, each sound has a distinctive emotional valence, recruited different resources of the SMA, and activated different parts of the SMA (Fig. 1D). SMA is subdivided into pre-SMA and SMA-proper. The *y* coordinates of peak activations of the sounds used in fMRI experiment 2 lay along the anterior–posterior axis and ranged from $y = -4$ to $+5$. Pre-SMA is the portion of the SMA anterior to the vertical line intersecting the vertical anterior commissure (VAC or $y = 0$), and SMA-proper is posterior to the VAC (60). SMA-proper and pre-SMA, located in the medial superior frontal gyrus, are involved in motor and cognitive control and play active roles from motor planning to motor output and action (62, 76–78). Passive listening to nonverbal emotional vocalizations, such as crying, laughter, and speech, evokes responses in pre-SMA and SMA-proper, which in turn promotes action responses. Each is also involved in affective processing in emotion regulation (79).

However, pre-SMA and SMA-proper control motor behaviors (reach and speech) at different levels. Functional connectivity (80) reveals that the more rostral pre-SMA is involved in higher level cognitive processing of motor behaviors whereas the more caudal SMA-proper is involved in motor output of different kinds. Pre-SMA and SMA-proper also connect to different brain regions, which helps to explain functional differences between them. The pre-SMA is associated with brain regions that underlie cognitive and affective processing, such as the prefrontal cortex (81), the anterior premotor area, the cingulate cortex, and the medial prefrontal cortex (59). Pre-SMA is recruited in top-down integration subserving actions, plans, and motivation in volitional processes (62), as well as self-initiated actions, and is not triggered by external cues (82, 83). By contrast, the SMA-proper is connected with the primary motor cortex, the posterior premotor areas, the cingulate cortex, and parietal areas. SMA-proper is itself somatotopically organized (60) with cortical representation from the face (anterior) to the foot (posterior) (84, 85). The anterior portion of the SMA-proper (close to the border with pre-SMA) is involved in producing orofacial movements, vocalizations, and speech (65) and in bimanual coordination of finger movements (86). SMA-proper is therefore activated in conjunction with overt articulation and movement of the lips and hands (78). In accord, clinical data reveal that lesions of the SMA-proper produce language and motor impairments (87, 88), and transcranial magnetic stimulation confirms enhanced hand motor-evoked potentials to infant cry in women (89). Moreover, in contrast to the pre-SMA, the SMA-proper is activated by external triggers (83) and is involved with sequential processes (60). Our analysis revealed that only infant cry activated the (anterior) SMA-proper; other emotional sounds (IL, IB, and AC) activated the pre-SMA or the border between pre-SMA and SMA-proper (Fig. 1D).

Discussion

Some characteristics of children likely affect parents everywhere, perhaps in similar ways. By the end of the first trimester, fetuses are felt to move in utero (“quickening”) (90), a significant marker in the life of the child and in the lives and psyches of parents. Soon after birth, physiognomic features of the infant (a large head

dominated by a disproportionately large forehead, widely spaced sizable eyes, a small snub nose, an exaggeratedly round face, and a small chin) (91–93) prompt adults to express nurturance and solicitude (94–96). Moreover, many adult responses to infants are culturally common, such as the special vocal register of child-directed speech (97). Infant cries and maternal responses to them appear to function in the same way.

Distress vocalizations emitted when infants are separated from their mothers, hungry, or physically ill at ease (3, 15, 17, 98–100) are similar in many mammals, including humans. Infant cries interrupt cognition (101). Hearing infant cries, mothers (or other caregivers) promptly move to retrieve or establish contact and communication with offspring (2, 3, 5, 15, 17) and to nourish or defend them against predators (102–104). Indeed, caregivers in different species even display strong emotional and physiological responses to cries of nonoffspring (3, 28). For example, deer (*Odocoileus hemionus* and *Odocoileus virginianus*) mothers will approach a speaker playing distress vocalizations of infant marmots (*Marmota flaviventris*), seals (*Neophoca cinerea* and *Arctocephalus tropicalis*), domestic cats (*Felis catus*), bats (*Lasiorycteris noctovagans*), humans (*Homo sapiens*), and other mammals as though they were going to assist a fawn in distress. Does also emit contact calls when near that speaker, as they do when responding to their own fawns (16). Chimpanzees are the primate species closest to humans. Chimpanzee infants emit distress vocalizations rarely and only following physical separation from their mothers. In response to their infants’ distress vocalizations, chimpanzee mothers move to restore physical proximity and retrieve their infants (105). Thus, mothers in many species respond to their infants’ calls by orienting, approaching, retrieving, and vocalizing (106, 107).

In *The Expression of the Emotions*, Darwin highlighted the significance of infant distress signals (57), and, in detailing attachment theory, Bowlby underscored that “crying... plays an important part in the earliest phases of social interaction” between parent and child (24). Parental caregiving blends tuition and intuition. Some aspects of parenting are learned, as through culture, but parents also rely on their instincts in caregiving. The long evolutionary history of altricial human infant dependency on requisite adult caregiving suggests that some mechanisms associated with adult attentiveness and responsiveness to infants ought to be automatic and deeply ingrained in caregivers’ nervous systems. For example, parents have specific implicit cognitive (108), autonomic (109, 110), and CNS (111) reactions to human infant faces that differ from their responses to faces of human adults and faces of in-frahuman mammal infants and adults.

We expected that some types of maternal responsiveness to infant cry would be common across cultures. In accord with this expectation, we explored contingencies between their own infants’ vocal distress and maternal affection, distraction, nurturance, movement/contact, and speech, along with the neurobiological bases of those responses, in a wide variety of societies. Nearly 700 mother–infant dyads in nearly a dozen countries were observed in situ and closely analyzed. Across these social groups, new mothers preferentially and systematically responded to their infants’ vocal distress by picking up and holding and by speaking to their infants. Corresponding fMRI results confirmed that new mothers, hearing their own infant’s distress, and more experienced mothers, hearing infant cries, generally activate the SMA associated with the intention to move and speak, inferior frontal regions involved in the production of speech, and superior temporal regions linked to processing auditory stimuli (61–63, 78, 111). These automatic responses in brain and behavior appear to occur in advance of conscious awareness, as the brain evolved adaptive circuits in the service of reproductive success (19). SMA is associated with the programming, generation, and control of relevant motor action and speech sequences.

Notably, the neurobiological findings obtained for mothers but not for nonmothers ([Supporting Information](#)). These results accord

with others in the extant literature: Mothers exhibit more pronounced neural responses in brain areas involved in emotional processing in response to infant cry than do nonmothers (75, 112, 113), suggesting that mothers may experience the cry as an emotionally important signal which requires their attention. This result points to rapid plasticity in the maternal brain (29, 74, 114, 115). With as little as 3 mo postpartum experience, mothers' brains become responsive to particular infant facial and vocal stimuli.

The behavioral observations study recruited mothers from different parts of the world, but the three imaging experiments recruited mothers only from the United States, China, and Italy. Is there evidence that, following the cry of their child, similar brain structures that promote similar responsive behaviors are activated in mothers in still other countries? Imaging experiments from Israel, Japan, and the United Kingdom reveal involvement of the motor cortex in mothers listening to their own infants' crying, as well as looking at pictures of their own infants' faces or watching video registrations of their own children (112, 116–120).

We do not contend that mothers' behavioral responses to infant cry differ from their responses to other infant stimuli, but rather that mothers in different cultures preferentially respond to infant cry in certain ways (picking up and talking to their infants) and not other ways (distracting, showing affection, or nurturing) and that their prominent motor and vocal responses are supported by specific matching brain responses.

In the spirit of systems neuroscience, the convergence of behavioral and neurobiological modalities increases the validity of results and the added value of applying both methodologies, here in investigating parent sensitivity to infant cries. That conjunction is reinforced by related independent findings from the emerging neuroscience of parenting. Other methodologies [for example, event-related potentials (ERPs)] that address the timing and stages of neural responsiveness to infant cues complement fMRI data focused on neural architecture (121).

Caregiver responsiveness is vital to infant survival and hence continuation of the species, parent–infant bonding, and the wholesome development of the child. It has been argued that, whether experience-expectant or experience-dependent, hard-wired responses to newborn distress vocalizations exemplify an adaptive speed–accuracy trade-off (121, 122), in which responding to the infant in distress is preferred to delaying action because hesitation increases the risk of the infant suffering harm (123). Another evolved function of the human infant cry is to communicate phenotypic quality (fitness) to caregivers (6) because cries signal infant health status (4, 46, 123). Finally, responsiveness to infant distress, and not nondistress, is critical for infants' attachment security with parents, and prosocial behavior has long-lasting impact on children's well-being (3, 124, 125).

Studying offspring solicitation vocalizations and caregiver responsiveness contributes to understanding animal communication systems and caregiver investment and also speaks to the etiology, prediction, and prevention of child neglect and abuse. Caregiver reactions to infant crying are not always benevolent. Cries sometimes trigger caregiver maltreatment (126–128). Our results encourage further research on caregivers who may be at-risk for problematic responsiveness to infants. The data reported here reveal a propensity to act and to speak in response to infant vocal distress. However, whether the action and speech are positive and growth-promoting or negative and harmful may depend on idiosyncratic characteristics of the caregiver. Using brain imaging, it may be possible to identify caregivers who are unaware or reluctant to disclose such risks (38). For example, depressed mothers compared with nondepressed mothers (129–131), and mothers who abuse drugs compared with mothers with no such dependencies (132), show altered brain involvement (subcortical limbic regions, prefrontal cortex including SMA, and superior temporal cortex) and altered behavior in response to negative emotions expressed

by their own infants. Altered cerebral activations in specific brain circuits might compromise parental motivation or the implementation of behaviors attuned to the needs of the child. Screening and diagnosis could be combined with early intervention to sensitize parents and to enhance their understanding of the importance and meaning attached to infant cries. Such a multimodal therapeutic approach could lead to the introduction of an array of tools for parents to respond appropriately to optimize child care and manage negative feelings tantamount to child maltreatment.

Healthy human mothers are likely to pick up and hold and to speak to their infants in response to their infants' cry, and this specific complex of behavioral responsiveness is known to calm infants (133). A survey of more than 180 societies showed that infants cried less when they were responded to in this way (4), and a randomized controlled trial (RCT) demonstrated the effectiveness of this same response (26). Perhaps because of their evolutionary advantage, these reactions toward infants are specific and automatic, widespread culturally, and embedded neurobiologically in mothers.

Materials and Methods

Cross-Cultural Behavioral Observation of Infants and Mothers. All study procedures and consent documents were approved by the Institutional Review Board of the Eunice Kennedy Shriver National Institute of Child Health and Human Development, and mothers provided written informed consent. We first recruited, observed, and recorded 1 h of home-based naturalistic mother–infant interactions in 684 dyads in 11 countries, including Argentina, Belgium, Brazil, Cameroon, France, Kenya, Israel, Italy, Japan, South Korea, and the United States. Only primipara mothers and firstborn singleton healthy awake full-term 5.5-mo-olds participated, with approximately equal numbers of girls and boys in each country sample. (Detailed sociodemographic information for all participants appears in Table S1.) Next, we carefully operationalized infant cries (distress vocalizations that indicated protest, complaint, anger, or upset and encompassed whining, fretting, fussing, whimpering, and full-blown distress) and five maternal response types (affection, distraction, nurturance, action, and speech) and coded video records of infants and mothers using mutually exclusive and exhaustive schemes to mark all behavior onsets and offsets to the nearest 0.10 s (for details of behavior durations, coding, and reliability see *Supporting Information*). Finally, we analyzed behavioral contingencies between maternal responses and infant cries in terms of odds ratios (ORs) (*Supporting Information*). Separately for each dyad, time units were tallied in two-by-two tables for each behavioral sequence, and ORs were computed for each table (134, 135). Odds ratios indicate the likelihood of mothers' responding to infant distress within a 5-s time window of the onset of a cry, with each response type compared with the likelihood of their initiating the same five behaviors outside of those time windows. This microanalytic strategy allowed us to examine in quantitative detail lead–lag sequences of infant cry–mother response, taking into consideration the timing of their interactions at the level of in-the-moment lived experiences.

fMRI Experiment 1: New Mothers in the United States. All study procedures and consent documents were approved by the Yale University School of Medicine Human Investigations Committee, and deidentified data were used in this study. Participants provided informed consent. We recruited 43 new primipara healthy European American middle-class mothers and their 3.5-mo-olds (56% male). Acoustic stimuli consisted of each mother's own-infant cry and own-infant noise (matched in pattern, intensity, and frequency range to their own infant's cry). Because each own-infant cry varied according to each infant's individual characteristics, the own-infant cry and matched control sounds were necessarily unique to each mother. Mothers underwent two fMRI scanning sessions at 3 tesla in a Siemens Trio full-body scanner. They heard 10 blocks of stimuli. Each block of 30 s was composed of own-infant cry or own-infant control sound. Imaging data analyses were performed with BrainVoyager QX version 2.0 (Brain Innovation; www.BrainVoyager.com) (see *Supporting Information* for preprocessing details). Using general linear models (GLMs), we analyzed whole-brain blood oxygenation level-dependent (BOLD) activity and contrasted activity during exposure to own-infant cry to activity during exposure to the own-infant control sound.

fMRI Experiment 2: Experienced Mothers in China. All study procedures and consent documents were approved by the East China Normal University Committee on Human Research. Participants provided written informed consent. We recruited 44 healthy Shanghai Chinese middle-class mothers of 7.6-mo-olds (57% male). Acoustic stimuli consisted of infant cries (ICs), infant

laughs (ILs), infant babbles (IBs), adult female cries (ACs), and noise control sounds (NCSs) (derived from and matched to ICs). ICs and ILs were retrieved from Oxford Vocal (OxVoc) Sounds (136) and public online databases. IBs, which can have characteristic sounds of the native language (137–139), were collected from native Chinese infants. ICs, ILs, and IBs came from children in the first year of life. Mothers underwent two fMRI scanning sessions at 3 tesla in a Siemens Trio Tim system. They heard 48 blocks of stimuli. Each block of 15 s consisted of one of the five sounds: IC or IL or IB or AC or NCS. Imaging data analyses were performed with BrainVoyager QX version 2.8 (Brain Innovation; www.BrainVoyager.com) (see [Supporting Information](#) for preprocessing details).

Using GLM, we analyzed whole-brain BOLD activity and created one statistical whole-brain map for each of the following contrasts: IC vs. NCS, IL vs. NCS, IB vs. NCS, and AC vs. NCS.

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