

Neurobiology of culturally common maternal responses to infant cry

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Edited by Charles Gross, Princeton University, Princeton, NJ, and approved September 6, 2017 (received for review July 7, 2017)

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.

Author contributions: M.H.B., P.R., G.E., J.T.D.S., and P.V. designed research; M.H.B., P.R., G.E., J.E.S., J.T.D.S., X.S., D.X., K.Z., L.R.C., N.D.P., and P.V. performed research; D.L.P., P.R., J.E.S., L.R.C., and N.D.P. analyzed data; and M.H.B., D.L.P., and P.R. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1712022114/-DCSupplemental.

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 pre-verbal 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

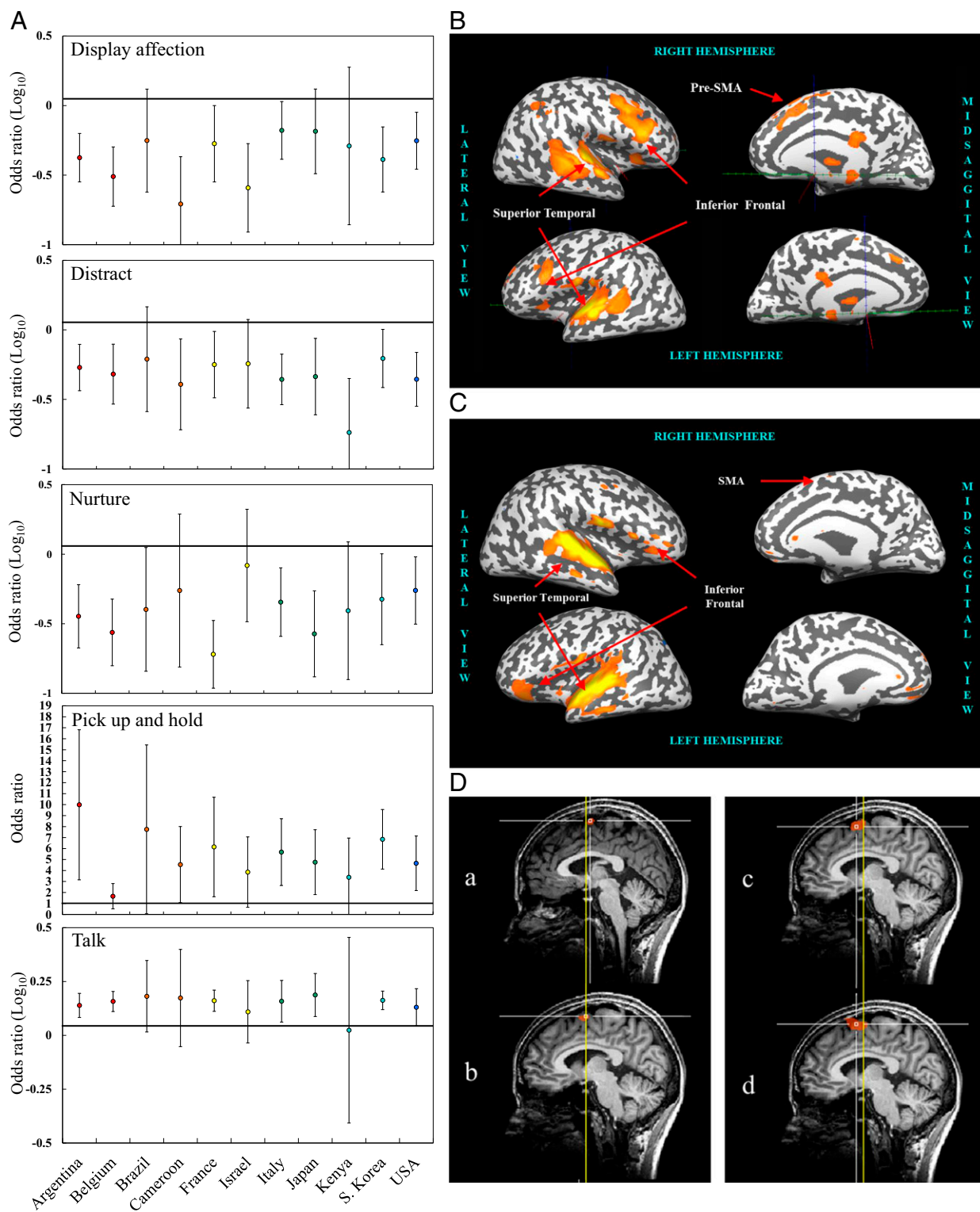


Fig. 1. Behavioral and fMRI responses to human infant cries. (A) Five types of maternal contingent responses to infant vocal distress in 11 countries. Display affection: Physical behaviors (kissing) or verbal statements (“I love you”). Distract: Encouraging the infant’s attention to a property, object, 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 the 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 non-verbal 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.

ACKNOWLEDGMENTS. We thank H. Azuma, R. Bakeman, S. Bali, E. Berti, A. De Houwer, C. de Zingman Galperin, M. Kabiru, K. Kwak, S. Maital, M. L. de Moura de Siedel, A. Bame Nsamenang, M.-G. Pêcheux, S. Toda, and A. Vyt. This research was supported by the Intramural Research Program of the NIH, Eunice Kennedy Shriver National Institute of Child Health and Human Development.

- Darwin CR (1877) A biographical sketch of an infant. *Mind* 2:285–294.
- Lingle S, Wyman MT, Kotrba R, Teichroeb LJ, Romanow CA (2012) What makes a cry a cry? A review of infant distress vocalizations. *Curr Zool* 58:698–726.
- Zeifman DM (2001) An ethological analysis of human infant crying: Answering Tinbergen's four questions. *Dev Psychobiol* 39:265–285.
- Lester BM, La Gasse LL (2008) Crying. *Encyclopedia of Infant and Early Childhood Development*, eds Haith MM, Benson JB (Academic, San Diego), pp 332–343.
- Newman JD (2007) Neural circuits underlying crying and cry responding in mammals. *Behav Brain Res* 182:155–165.
- Furlow FB (1997) Human neonatal cry quality as an honest signal of fitness. *Evol Hum Behav* 18:175–193.
- Ainsworth MDS, Blehar M, Waters CE, Wall S (1978) *Patterns of Attachment: A Psychological Study of the Strange Situation* (Erlbaum, Mahwah, NJ).
- Del Vecchio T, Walter A, O'Leary SG (2009) Affective and physiological factors predicting maternal response to infant crying. *Infant Behav Dev* 32:117–122.
- Ehret G, Haack B (1981) Categorical perception of mouse pup ultrasound by lactating females. *Naturwissenschaften* 68:208–209.
- Ehret G (1992) Categorical perception of mouse-pup ultrasounds in the temporal domain. *Anim Behav* 43:409–416.
- Aitkin L, Nelson J, Shepherd R (1996) Development of hearing and vocalization in a marsupial, the Northern Quoll, *Dasyurus hallucatus*. *J Exp Zool* 276:394–402.
- Bohn KM, Moss CF, Wilkinson GS (2006) Correlated evolution between hearing sensitivity and social calls in bats. *Biol Lett* 2:561–564.
- Nelson EE, Panksepp J (1998) Brain substrates of infant-mother attachment: Contributions of opioids, oxytocin, and norepinephrine. *Neurosci Biobehav Rev* 22:437–452.
- Parsons CE, Young KS, Parsons E, Stein A, Kringelbach ML (2012) Listening to infant distress vocalizations enhances effortful motor performance. *Acta Paediatr* 101:e189–e191.
- Zeskind PS (2013) Infant crying and the synchrony of arousal. *Evolution of Emotional Communication: From Sounds in Nonhuman Mammals to Speech and Music in Man*, Series in Affective Science, eds Altenmüller E, Schmidt S, Zimmerman E (Oxford Univ Press, Oxford), pp 155–172.
- Lingle S, Riede T (2014) Deer mothers are sensitive to infant distress vocalizations of diverse mammalian species. *Am Nat* 184:510–522.
- Newman JD (2004) The primate isolation call: A comparison with precocial birds and non-primate mammals. *Comparative Vertebrate Cognition: Are Primates Superior to Non-primates?*, eds Rogers LJ, Kaplan G (Kluwer Academic, New York), pp 171–187.
- Bornstein MH (2013) Mother-infant attunement: A multilevel approach via body, brain, and behavior. *The Infant Mind: Origins of the Social Brain*, eds Legerstee M, Haley DW, Bornstein MH (Guilford, New York), pp 266–298.
- Gazzaniga MS (2000) Cerebral specialization and interhemispheric communication: Does the corpus callosum enable the human condition? *Brain* 123:1293–1326.
- MacLean PD (1990) *The Triune Brain in Evolution: Role in Paleocerebral Functions* (Plenum, New York).
- MacLean PD (1985) Brain evolution relating to family, play, and the separation call. *Arch Gen Psychiatry* 42:405–417.
- Newman JD (1985) The infant cry of primates: An evolutionary perspective. *Infant Crying: Theoretical and Research Perspectives*, eds Lester BM, Boukydis CFZ (Plenum, New York), pp 307–323.
- Ainsworth MDS (1969) Object relations, dependency, and attachment: A theoretical review of the infant-mother relationship. *Child Dev* 40:969–1025.
- Bowlby J (1969) *Attachment, Attachment and Loss* (Basic Books, New York), Vol 1.
- Christensson K, Cabrera T, Christensson E, Uvnäs-Moberg K, Winberg J (1995) Separation distress call in the human neonate in the absence of maternal body contact. *Acta Paediatr* 84:468–473.
- Hunziker UA, Barr RG (1986) Increased carrying reduces infant crying: A randomized controlled trial. *Pediatrics* 77:641–648.
- Michellson K, Christensson K, Rothgänger H, Winberg J (1996) Crying in separated and non-separated newborns: Sound spectrographic analysis. *Acta Paediatr* 85:471–475.
- Stallings J, Fleming AS, Corter C, Worthman C, Steiner M (2001) The effects of infant cries and odors on sympathy, cortisol, and autonomic responses in new mothers and nonpostpartum women. *Parenting* 1:71–100.
- Kim P, et al. (2011) Breastfeeding, brain activation to own infant cry, and maternal sensitivity. *J Child Psychol Psychiatry* 52:907–915.
- Basden GT (1966) *Among the Ibos of Nigeria* (Frank Cass and Co. Ltd., London).
- deVries MW (1984) Temperament and infant mortality among the Masai of East Africa. *Am J Psychiatry* 141:1189–1194.
- Kringelbach ML, et al. (2008) A specific and rapid neural signature for parental instinct. *PLoS One* 3:e1664.
- Ranote S, et al. (2004) The neural basis of maternal responsiveness to infants: An fMRI study. *Neuroreport* 15:1825–1829.
- Purhonen M, Pääkkönen A, Yppäriälä H, Lehtonen J, Karhu J (2001) Dynamic behavior of the auditory N100 elicited by a baby's cry. *Int J Psychophysiol* 41:271–278.
- Purhonen M, et al. (2001) Effects of maternity on auditory event-related potentials to human sound. *Neuroreport* 12:2975–2979.
- Purhonen M, Valkonen-Korhonen M, Lehtonen J (2008) The impact of stimulus type and early motherhood on attentional processing. *Dev Psychobiol* 50:600–607.
- Swain JE, Lorberbaum JP, Kose S, Strathearn L (2007) Brain basis of early parent-infant interactions: Psychology, physiology, and in vivo functional neuroimaging studies. *J Child Psychol Psychiatry* 48:262–287.
- Rodrigo MJ, et al. (2011) Brain and personality bases of insensitivity to infant cues in neglectful mothers: An event-related potential study. *Dev Psychopathol* 23:163–176.
- Barr RG (1990) The early crying paradox: A modest proposal. *Hum Nat* 1:355–389.
- Huffman LC, et al. (1998) Infant temperament and cardiac vagal tone: Assessments at twelve weeks of age. *Child Dev* 69:624–635.
- Fleming AS, Corter C, Stallings J, Steiner M (2002) Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Horm Behav* 42:399–413.
- McNeilly AS, Robinson IC, Houston MJ, Howie PW (1983) Release of oxytocin and prolactin in response to suckling. *Br Med J (Clin Res Ed)* 286:257–259.
- Riem MME, et al. (2011) Oxytocin modulates amygdala, insula, and inferior frontal gyrus responses to infant crying: A randomized controlled trial. *Biol Psychiatry* 70:291–297.
- Riem MME, Pieper S, Out D, Bakermans-Kranenburg MJ, van Ijzendoorn MH (2011) Oxytocin receptor gene and depressive symptoms associated with physiological reactivity to infant crying. *Soc Cogn Affect Neurosci* 6:294–300.
- Konner MJ (2010) *The Evolution of Childhood: Relationships, Emotion, Mind* (Harvard Univ Press, Cambridge, MA).
- Soltis J (2004) The signal functions of early infant crying. *Behav Brain Sci* 27:443–458, discussion 459–490.
- van Anders SM, Tolman RM, Volling BL (2012) Baby cries and nurturance affect testosterone in men. *Horm Behav* 61:31–36.
- Wood W, Eagly AH (2002) A cross-cultural analysis of the behavior of women and men: Implications for the origins of sex differences. *Psychol Bull* 128:699–727.
- Bornstein MH (2010) *The Handbook of Cultural Developmental Science* (Psychology Press, New York).
- Henrich J, Heine SJ, Norenzayan A (2010) The weirdest people in the world? *Behav Brain Sci* 33:61–83, discussion 83–135.
- Tomlinson M, Bornstein MH, Marlow M, Swartz L (2014) Imbalances in the knowledge about infant mental health in rich and poor countries: Too little progress in bridging the gap. *Infant Ment Health J* 35:624–629.
- Bornstein MH (2013) Parenting and child mental health: A cross-cultural perspective. *World Psychiatry* 12:258–265.
- Kurth E, Kennedy HP, Spichiger E, Hösl I, Stutz EZ (2011) Crying babies, tired mothers: What do we know? A systematic review. *Midwifery* 27:187–194.
- Lee C, Barr RG, Catherine N, Wicks A (2007) Age-related incidence of publicly reported shaken baby syndrome cases: Is crying a trigger for shaking? *J Dev Behav Pediatr* 28:288–293.
- Cavanagh K, Dobash RE, Dobash RP (2007) The murder of children by fathers in the context of child abuse. *Child Abuse Negl* 31:731–746.
- Brosch T, Sander D, Scherer KR (2007) That baby caught my eye... attention capture by infant faces. *Emotion* 7:685–689.
- Darwin CR (1872) *The Expression of the Emotions in Man and Animals* (John Murray, London).
- Norenzayan A, Heine SJ (2005) Psychological universals: What are they and how can we know? *Psychol Bull* 131:763–784.
- Zhang S, Ide JS, Li CSR (2012) Resting-state functional connectivity of the medial superior frontal cortex. *Cereb Cortex* 22:99–111.
- Schwartz M, Rothermich K, Kotz SA (2012) Functional dissociation of pre-SMA and SMA-proper in temporal processing. *Neuroimage* 60:290–298.
- Haggard P (2008) Human volition: Towards a neuroscience of will. *Nat Rev Neurosci* 9:934–946.
- Nachev P, Kennard C, Husain M (2008) Functional role of the supplementary and pre-supplementary motor areas. *Nat Rev Neurosci* 9:856–869.
- Filimon F, Nelson JD, Hagler DJ, Sereno MI (2007) Human cortical representations for reaching: Mirror neurons for execution, observation, and imagery. *Neuroimage* 37:1315–1328.
- Fried I, et al. (1991) Functional organization of human supplementary motor cortex studied by electrical stimulation. *J Neurosci* 11:3656–3666.

65. Ackermann H, Riecker A (2010) Functional brain imaging of speech motor control. *Speech Motor Control: New Developments in Basic and Applied Research*, eds Maassen B, van Lieshout PHHM (Oxford Univ Press, Oxford), pp 85–111.
66. Ackermann H, Ziegler W (2010) Brain mechanisms underlying speech motor control. *The Handbook of Phonetic Sciences*, eds Hardcastle WJ, Laver J, Gibbons F (Blackwell Publishing Ltd, Oxford), 2nd Ed, pp 202–250.
67. Brendel B, et al. (2010) The contribution of mesiofrontal cortex to the preparation and execution of repetitive syllable productions: An fMRI study. *Neuroimage* 50: 1219–1230.
68. Riecker A, et al. (2005) fMRI reveals two distinct cerebral networks subserving speech motor control. *Neurology* 64:700–706.
69. Shamay-Tsoory SG, Aharon-Peretz J, Perry D (2009) Two systems for empathy: A double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain* 132:617–627.
70. Horwitz B, et al. (2003) Activation of Broca's area during the production of spoken and signed language: A combined cytoarchitectonic mapping and PET analysis. *Neuropsychologia* 41:1868–1876.
71. Wessinger CM, et al. (2001) Hierarchical organization of the human auditory cortex revealed by functional magnetic resonance imaging. *J Cogn Neurosci* 13:1–7.
72. Swain JE, Mayes LC, Leckman JF (2004) The development of parent-infant attachment through dynamic and interactive signaling loops of care and cry. *Behav Brain Sci* 27:472–473.
73. Swain JE, et al. (2014) Approaching the biology of human parental attachment: Brain imaging, oxytocin and coordinated assessments of mothers and fathers. *Brain Res* 1580:78–101.
74. Swain JE, et al. (2012) Parenting and beyond: Common neurocircuits underlying parental and altruistic caregiving. *Parent Sci Pract* 12:115–123.
75. Swain JE (2008) Baby stimuli and the parent brain: Functional neuroimaging of the neural substrates of parent-infant attachment. *Psychiatry (Edgmont)* 5:28–36.
76. Kim JH, et al. (2010) Defining functional SMA and pre-SMA subregions in human MFC using resting state fMRI: Functional connectivity-based parcellation method. *Neuroimage* 49:2375–2386.
77. Picard N, Strick PL (1996) Motor areas of the medial wall: A review of their location and functional activation. *Cereb Cortex* 6:342–353.
78. Alario FX, Chainay H, Lehericy S, Cohen L (2006) The role of the supplementary motor area (SMA) in word production. *Brain Res* 1076:129–143.
79. Kohn N, et al. (2014) Neural network of cognitive emotion regulation—An ALE meta-analysis and MACM analysis. *Neuroimage* 87:345–355.
80. Glasser MF, et al. (2016) A multi-modal parcellation of human cerebral cortex. *Nature* 536:171–178.
81. Luppino G, Matelli M, Rizzolatti G (1990) Cortico-cortical connections of two electrophysiologically identified arm representations in the mesial agranular frontal cortex. *Exp Brain Res* 82:214–218.
82. Gowen E, Miall RC (2007) Differentiation between external and internal cuing: An fMRI study comparing tracing with drawing. *Neuroimage* 36:396–410.
83. Jenkins IH, Jahanshahi M, Jueptner M, Passingham RE, Brooks DJ (2000) Self-initiated versus externally triggered movements. II. The effect of movement predictability on regional cerebral blood flow. *Brain* 123:1216–1228.
84. Chainay H, et al. (2004) Foot, face and hand representation in the human supplementary motor area. *Neuroreport* 15:765–769.
85. Mitz AR, Wise SP (1987) The somatotopic organization of the supplementary motor area: Intracortical microstimulation mapping. *J Neurosci* 7:1010–1021.
86. Sadato N, Yonekura Y, Waki A, Yamada H, Ishii Y (1997) Role of the supplementary motor area and the right premotor cortex in the coordination of bimanual finger movements. *J Neurosci* 17:9667–9674.
87. Krainik A, et al. (2001) Role of the supplementary motor area in motor deficit following medial frontal lobe surgery. *Neurology* 57:871–878.
88. Zentner J, Hufnagel A, Pechstein U, Wolf HK, Schramm J (1996) Functional results after resective procedures involving the supplementary motor area. *J Neurosurg* 85: 542–549.
89. Messina I, et al. (2016) Sex-specific automatic responses to infant cries: TMS reveals greater excitability in females than males in motor evoked potentials. *Front Psychol* 6:1909.
90. Cunningham F, et al. (2010) *Williams Obstetrics* (McGraw-Hill, New York), 23rd Ed.
91. Kringelbach ML, Stark EA, Alexander C, Bornstein MH, Stein A (2016) On cuteness: Unlocking the parental brain and beyond. *Trends Cogn Sci* 20:545–558.
92. Alley TR (1981) Head shape and the perception of cuteness. *Dev Psychol* 17:650–654.
93. Alley TR (1983) Infantile head shape as an elicitor of adult protection. *Merrill Palmer Q* 29:411–427.
94. Lorenz KZ (1971) *Studies in Animal and Human Behavior* (Methuen & Co., London), Vol 2.
95. Glocker ML, et al. (2009) Baby schema modulates the brain reward system in nulliparous women. *Proc Natl Acad Sci USA* 106:9115–9119.
96. Sanefuji W, Ohgami H, Hashiya K (2007) Development of preference for baby faces across species in humans (*Homo sapiens*). *J Ethol* 25:249–254.
97. Soderstrom M (2007) Beyond babytalk: Re-evaluating the nature and content of speech input to preverbal infants. *Dev Rev* 27:501–532.
98. Charrier I, Mathevon N, Jouventin P (2002) How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocepalus tropicalis*. *J Exp Biol* 205: 603–612.
99. Insley SJ, Phillips AV, Charrier I (2003) A review of social recognition in pinnipeds. *Aquat Mamm* 29:181–201.
100. Torriani MVG, Vannoni E, McElligott AG (2006) Mother-young recognition in an ungulate hider species: A unidirectional process. *Am Nat* 168:412–420.
101. Dudek J, Fares A, Bornstein MH, Haley DW (2016) Infant cries rattle adult cognition. *PLoS One* 11:e0154283.
102. Chaiken M (1992) Individual recognition of nestling distress screams by European starlings *Sturnus vulgaris*. *Behaviour* 120:139–150.
103. Benedict L (2007) Offspring discrimination without recognition: California towhee responses to chick distress calls. *Condor* 109:79–87.
104. Lingle S, Rendall D, Wilson WF, DeYoung RW, Pellis SM (2007) Altruism and recognition in the predator defense of deer: Why mule deer help nonoffspring fawns. *Anim Behav* 73:907–916.
105. Mizuno Y, Takeshita H, Matsuzawa T (2006) Behavior of infant chimpanzees during the night in the first 4 months of life: Smiling and suckling in relation to behavioral state. *Infancy* 9:221–240.
106. Jovanovic T, Megna NL, Maestripietri D (2000) Early maternal recognition of offspring vocalizations in rhesus macaques *Macaca mulatta*. *Primates* 41:421–428.
107. Rendall D, Notman H, Owren MJ (2009) Asymmetries in the individual distinctiveness and maternal recognition of infant contact calls and distress screams in baboons. *J Acoust Soc Am* 125:1792–1805.
108. Senese VP, et al. (2013) Human infant faces provoke implicit positive affective responses in parents and non-parents alike. *PLoS One* 8:e80379.
109. Esposito G, et al. (2014) Baby, you light-up my face: Culture-general physiological responses to infants and culture-specific cognitive judgements of adults. *PLoS One* 9: e106705.
110. Esposito G, et al. (2014) Using infrared thermography to assess emotional responses to infants. *Early Child Dev Care* 185:438–447.
111. Caria A, et al. (2012) Species-specific response to human infant faces in the premotor cortex. *Neuroimage* 60:884–893.
112. Seifritz E, et al. (2003) Differential sex-independent amygdala response to infant crying and laughing in parents versus nonparents. *Biol Psychiatry* 54:1367–1375.
113. Swain JE, Kim P, Ho SS (2011) Neuroendocrinology of parental response to baby-cry. *J Neuroendocrinol* 23:1036–1041.
114. Bornstein MH, Arterberry ME, Mash C (2013) Differentiated brain activity in response to faces of "own" versus "unfamiliar" babies in primipara mothers: An electrophysiological study. *Dev Neuropsychol* 38:365–385.
115. Esposito G, Valenzi S, Islam T, Mash C, Bornstein MH (2015) Immediate and selective maternal brain responses to own infant faces. *Behav Brain Res* 278:40–43.
116. Atzil S, Hendler T, Feldman R (2011) Specifying the neurobiological basis of human attachment: Brain, hormones, and behavior in synchronous and intrusive mothers. *Neuropsychopharmacology* 36:2603–2615.
117. Strathearn L, Li J, Fonagy P, Montague PR (2008) What's in a smile? Maternal brain responses to infant facial cues. *Pediatrics* 122:40–51.
118. Noriuchi M, Kikuchi Y, Senoo A (2008) The functional neuroanatomy of maternal love: Mother's response to infant's attachment behaviors. *Biol Psychiatry*, 63, pp 415–423.
119. Montoya JL, et al. (2012) Regional brain responses in nulliparous women to emotional infant stimuli. *PLoS One* 7:e36270.
120. Venuti P, et al. (2012) Differential brain responses to cries of infants with autistic disorder and typical development: An fMRI study. *Res Dev Disabil* 33:2255–2264.
121. Trimmer PC, et al. (2008) Mammalian choices: Combining fast-but-inaccurate and slow-but-inaccurate decision-making systems. *Proc Biol Sci* 275:2353–2361.
122. Chittka L, Skorupski P, Raine NE (2009) Speed-accuracy tradeoffs in animal decision making. *Trends Ecol Evol* 24:400–407.
123. LaGasse LL, Neal AR, Lester BM (2005) Assessment of infant cry: Acoustic cry analysis and parental perception. *Ment Retard Dev Disabil Res Rev* 11:83–93.
124. McElwain NL, Booth-Laforce C (2006) Maternal sensitivity to infant distress and nondistress as predictors of infant-mother attachment security. *J Fam Psychol* 20: 247–255.
125. Leerkes EM, Nayana Blankson A, O'Brien M (2009) Differential effects of maternal sensitivity to infant distress and nondistress on social-emotional functioning. *Child Dev* 80:762–775.
126. Carbaugh SF (2004) Understanding shaken baby syndrome. *Adv Neonatal Care* 4: 105–117, quiz 15–17.
127. Keenan HT, Runyan DK, Marshall SW, Nocera MA, Merten DF (2004) A population-based comparison of clinical and outcome characteristics of young children with serious inflicted and noninflicted traumatic brain injury. *Pediatrics* 114:633–639.
128. Miehle NJ (2005) Shaken baby syndrome. *J Forensic Nurs* 1:111–117.
129. Laurent HK, Ablow JC (2012) A cry in the dark: Depressed mothers show reduced neural activation to their own infant's cry. *Soc Cogn Affect Neurosci* 7:125–134.
130. Pearson RM, Cooper RM, Penton-Voak IS, Lightman SL, Evans J (2010) Depressive symptoms in early pregnancy disrupt attentional processing of infant emotion. *Psychol Med* 40:621–631.
131. Pearson RM, Lightman SL, Evans J (2011) Attentional processing of infant emotion during late pregnancy and mother-infant relations after birth. *Arch Women Ment Health* 14:23–31.
132. Landi N, et al. (2011) Maternal neural responses to infant cries and faces: Relationships with substance use. *Front Psychiatry* 2:32.
133. Esposito G, et al. (2013) Infant calming responses during maternal carrying in humans and mice. *Curr Biol* 23:739–745.
134. Bakeman R, Deckner DF, Quera V (2005) Analysis of behavioral streams. *Handbook of Research Methods in Developmental Science*, ed Teti DM (Blackwell, Oxford), pp 394–420.
135. Wickens TD (1993) Analysis of contingency tables with between-subjects variability. *Psychol Bull* 113:191–204.
136. Parsons CE, Young KS, Craske MG, Stein AL, Kringelbach ML (2014) Introducing the Oxford Vocal (OxVoc) sounds database: A validated set of non-acted affective sounds from human infants, adults, and domestic animals. *Front Psychol* 5:562.

137. Byers-Heinlein K, Burns TC, Werker JF (2010) The roots of bilingualism in newborns. *Psychol Sci* 21:343–348.
138. May L, Byers-Heinlein K, Gervain J, Werker JF (2011) Language and the newborn brain: Does prenatal language experience shape the neonate neural response to speech? *Front Psychol* 2:222.
139. Moon C, Cooper RP, Fifer WP (1993) Two-day-olds prefer their native language. *Infant Behav Dev* 16:495–500.
140. Tabachnick BG, Fidell LS (2007) *Using Multivariate Statistics* (Allyn & Bacon, Boston), 5th Ed.
141. Bronfenbrenner U (1979) The ecology of human development: Experiments by nature and design. *Am Psychol* 32:513–531.
142. Connors E, Glenn SM (1996) Methodological considerations in observing mother-infant interactions in natural settings. *Psychological Research: Innovative Methods and Strategies*, ed Haworth J (Routledge, London), pp 139–152.
143. McCune-Nicolich L, Fenson L (1984) Methodological issues in studying early pretend play. *Child's Play: Developmental and Applied*, eds Yawley TD, Pellegrini AD (Erlbaum, Mahwah, NJ), pp 81–124.
144. Stevenson MB, Leavitt LA, Roach MA, Chapman RS, Miller JF (1986) Mother's speech to their 1-year-old infants in home and laboratory settings. *J Psycholinguist Res* 15: 451–461.
145. Brislin RW (1980) Translation and content analysis of oral and written material. *Handbook of Cross-Cultural Psychology*, eds Triandis HC, Berry JW (Allyn & Bacon, Boston), Vol 1, pp 389–444.
146. Brislin RW (1986) The wording and translation of research instruments. *Field Methods in Cross-Cultural Research*, eds Lonner WJ, Berry JW (Sage, Thousand Oaks, CA), Vol 8, pp 137–164.
147. Peña ED (2007) Lost in translation: Methodological considerations in cross-cultural research. *Child Dev* 78:1255–1264.
148. Huffman LC, et al. (1994) Infant cry acoustics and maternal ratings of temperament. *Infant Behav Dev* 17:45–53.
149. Bornstein MH, Cote LR, Haynes OM, Suwalsky JT, Bakeman R (2012) Modalities of infant-mother interaction in Japanese, Japanese American immigrant, and European American dyads. *Child Dev* 83:2073–2088.
150. Gratier M (2003) Expressive timing and interactional synchrony between mothers and infants: Cultural similarities, cultural differences, and the immigration experience. *Cogn Dev* 18:533–554.
151. Van Egeren LA, Barratt MS, Roach MA (2001) Mother-infant responsiveness: Timing, mutual regulation, and interactional context. *Dev Psychol* 37:684–697.
152. Bornstein MH, et al. (1992) Maternal responsiveness to infants in three societies: The United States, France, and Japan. *Child Dev* 63:808–821.
153. Cohen J (1960) A coefficient of agreement for nominal scales. *Educ Psychol Meas* 20: 37–46.
154. Cohen J (1968) Weighted kappa: Nominal scale agreement with provision for scaled disagreement or partial credit. *Psychol Bull* 70:213–220.
155. Fleiss JL (1981) *Statistical Methods for Rates and Proportions* (Wiley, New York), 2nd Ed, pp 38–46.
156. Bakeman R, Quera V (2011) *Sequential Analysis and Observational Methods for the Behavioral Sciences* (Cambridge Univ Press, New York).
157. Faul F, Erdfelder E, Lang AG, Buchner A (2007) G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav Res Methods* 39:175–191.
158. McCartney K, Burchinal MR, Bub KL (2006) Best practices in quantitative methods for developmentalists. *Monogr Soc Res Child Dev* 71:1–145.
159. De Pisapia N, et al. (2013) Sex differences in directional brain responses to infant hunger cries. *Neuroreport* 24:142–146.
160. Genovese CR, Lazar NA, Nichols T (2002) Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage* 15:870–878.
161. Chang LJ, Yarkoni T, Khaw MW, Sanfey AG (2013) Decoding the role of the insula in human cognition: Functional parcellation and large-scale reverse inference. *Cereb Cortex* 23:739–749.
162. Shackman AJ, McMennamin BW, Maxwell JS, Greischar LL, Davidson RJ (2009) Right dorsolateral prefrontal cortical activity and behavioral inhibition. *Psychol Sci* 20: 1500–1506.
163. Ho SS, Konrath S, Brown S, Swain JE (2014) Empathy and stress related neural responses in maternal decision making. *Front Neurosci* 8:152.
164. Saxe R (2006) Uniquely human social cognition. *Curr Opin Neurobiol* 16:235–239.
165. Frewen PA, et al. (2011) Neuroimaging social emotional processing in women: fMRI study of script-driven imagery. *Soc Cogn Affect Neurosci* 6:375–392.
166. Bernhardt BC, Singer T (2012) The neural basis of empathy. *Annu Rev Neurosci* 35: 1–23.
167. Carr L, Iacoboni M, Dubeau MC, Mazziotta JC, Lenzi GL (2003) Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proc Natl Acad Sci USA* 100:5497–5502.
168. Zeng H, Constable RT (2002) Image distortion correction in EPI: Comparison of field mapping with point spread function mapping. *Magn Reson Med* 48:137–146.
169. Nishitani S, Doi H, Koyama A, Shinohara K (2011) Differential prefrontal response to infant facial emotions in mothers compared with non-mothers. *Neurosci Res* 70: 183–188.
170. Poldrack RA (2011) Inferring mental states from neuroimaging data: From reverse inference to large-scale decoding. *Neuron* 72:692–697.