Current Biology

Having Infants in the Family Group Promotes Altruistic Behavior of Marmoset Monkeys

Highlights

- We developed a novel rescue paradigm for studying altruistic behaviors in marmosets

- Marmoset parents and older siblings show strong motivation to rescue infants

- Having infants in the group promotes infant- and mate-rescue behaviors in marmosets

- Having infants alters infant-call-elicited brain activation in marmoset parents

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In Brief

Using a novel rescue paradigm, Huang et al. find that marmoset monkeys show altruistic behavior by rescuing trapped group members including young infants and mates. All these rescue behaviors depend on currently having young infants in the group. Furthermore, having infants alters infant-call-elicited brain activation in marmoset parents.

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Report

Having Infants in the Family Group Promotes Altruistic Behavior of Marmoset Monkeys

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SUMMARY

The common marmoset (*Callithrix jacchus*) has attracted much attention as a useful model for studying social behaviors [1–3]. They naturally live in a monogamous family group and exhibit cooperative breeding [4], in which parents and older siblings help to carry infants less than 2 months old [5–7]. Marmoset parents also transfer foods to their offspring, a process that may help them learn the food diet [8]. Furthermore, marmosets show spontaneous altruistic behaviors, such as providing food to non-reciprocating and genetically unrelated individuals [9]. These social habits indicate that marmosets may be a useful non-human primate model for studying parenting and altruistic behaviors, as well as underlying neural mechanisms. Using a novel rescue paradigm, we found that marmoset parents and older siblings showed strong motivation to rescue trapped young infants but not juvenile marmosets beyond 2 months of age, and infant calls alone could trigger these parents' rescue behaviors. The marmoset parents showed little rescue of each other, but young infants or infant calls could also induce such parents' mutual rescue. Moreover, all these infant- and mate-rescue behaviors depended on currently having young infants in the family group. Functional MRI studies on awake adult marmosets showed that calls from young infants, but not juvenile marmosets, elicited a large-scale activation of specific brain areas including auditory and insular cortices, and such activation was absent in marmosets not living with infants. Thus, such infant-induced modification of neural activity offers a window for examining the neural basis of altruistic behaviors in marmoset monkeys.

RESULTS

A Marmoset Infant Induces Parents' Rescue Behavior in A Novel Rescue Paradigm

To study altruistic behaviors of marmosets, we developed a novel paradigm in which a marmoset was trapped in a transparent restraining box on a platform surrounded by 50-cm-wide water pool, and another marmoset (rescuer) could jump to the platform, open the trap door (by pushing down a lever), and liberate the trapped marmoset (Figure 1A). An adjacent identical box on the platform containing an inert object (a ball) was used as a control. The percentage and latency of both jumping and opening events were used to quantify the rescue behavior (see STAR Methods). In the first set of experiments, a young infant less than 1 month old was used as the trapped marmoset, which usually made frequent calls in the restraining box. Its parents were tested together as potential rescuers, and the experiment ended when one of the parents performed the rescue. We found that marmoset parents showed a strong motivation to rescue their infants by jumping across the water pool, opening the door, and then carrying the infant back to the home cage (Figure 1B; Video S1). The tested 6

pairs of parents (2 trials each with and without an infant in the restraining box, 15 min per trial) performed the rescue in nearly all trials (100% jumping, 92% opening; Figure 1C), with a latency (124 ± 63 s, jumping; 245 ± 72 s, opening) in initiating the rescue (Figure 1D). No marmoset opened the adjacent control box (containing a ball) after making the jump. However, when the restraining box contained nothing (empty) or food, marmoset parents rarely exhibited jumping and door opening (Figures 1C and 1D), suggesting that jumping across the water pool represents a significant challenge for marmosets. Indeed, when we put the restraining box in the home cage, marmoset parents quickly opened the door for both food and the infant with a very short latency (opening, 80 ± 29 s for food; 17 ± 5 s for infant; n = 6 groups; Figure S1). Thus, our experimental paradigm represents a high-cost rescue task, and marmoset parents showed strong motivation for rescuing the infant, much higher than that for getting food.

Marmoset Parents' Rescue Behavior Depends on the Offspring's Age

We then examined whether the parents' rescue behavior depends on the offspring's age. At 3-week intervals, we tested 6
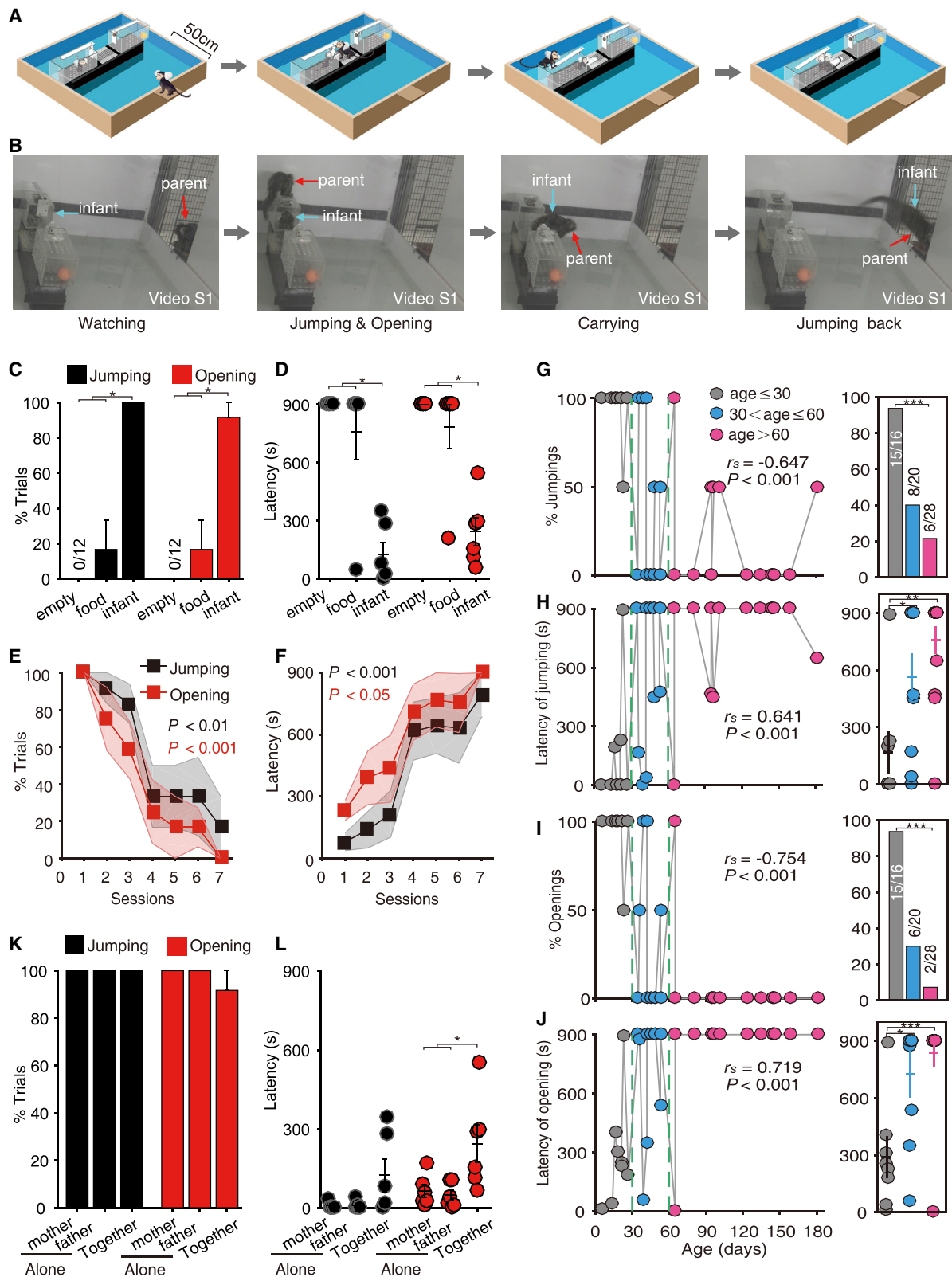
Figure 1. Young Marmoset Infants Could Induce Parents' Rescue Behavior

(A) Schematic drawing of the experimental apparatus. The rescuer marmoset could jump to the platform, then push down a lever to open the door, and liberate the trapped marmoset in a restraining box surrounded by water.

pairs of parents (2 trials each), whose offspring were 2–4 weeks of age at the beginning and 20–22 weeks at the end of the experiment. We found that the percentage of both jumping and opening declined and the latency of both jumping and opening increased with the age of the offspring (Figures 1E and 1F). To exclude the possibility that the age dependence was due to habituation after repetitive testing, we further examined 32 pairs of parents with the offspring's age ranging from 6 to 181 days, with each group tested only once (2 trials). We found that rescue behavior was observed in all groups with infants less than 1 month old (8/8) and in some groups with infants of age 1–2 months (4/10), whereas nearly none (1/14) performed the rescue when the offspring was older than 2 months ("juvenile") (Figures 1G–1J). Thus, the rescue behavior depended on the offspring's age, and the parents only rescued trapped young infants. In the above 13 groups that performed the rescue, the mother showed more openings in 9 groups (mother = father in 1 group; father > mother in 3 groups) in performing the rescue. However, when tested alone (in separate experiments), both mother and father showed 100% of both jumping and opening in all trials (Figure 1K, n = 6 for each), and the latency was much shorter (mother, 11 ± 5 s, jumping; 65 ± 25 s, opening; father, 11 ± 7 s, jumping; 49 ± 19 s, opening, Figure 1L), as compared to that observed when both parents were tested together (data from Figure 1D). Thus, the presence of the mate marmoset slowed down the rescue behavior, a phenomenon consistent with a previous report that adult marmosets who were alone with immature marmosets were more likely to share food than when other adult group members were also present [10].

Infant Calls Can Induce Parents' Rescue Behavior

In the second set of experiments, we examined the rescue behaviors of parents from 5 groups for 4 different trapped subjects in the transparent restraining box (Figure 2A): their own infant, "novel" infant from other family group, their own juvenile, and an inert object. All parents rescued their own infant and a great majority rescued the novel infant (100% jumping, 80% opening), but none rescued their own juvenile and the inert object (Figures 2B–2E). To determine whether the parents were responding to visual or auditory cues for rescue, the restraining box was covered on the side facing the potential rescuer with black tape (Figure 2F), and the parents could see the trapped subject only after jumping to the platform. We found that parents rescued both their own infant and novel infant at very high frequency but exhibit no rescue behavior for the inert object (20% jumping, no opening). However, for the trapped juvenile, the parents showed a high frequency of jumping (90%) but very few openings (10%) (Figures 2G–2J). The jumping could be triggered by the motion-induced noise from the restraining box, and no opening was performed after jumping and seeing the juvenile, consistent with the lack of rescue for trapped juveniles described above. Finally, we put a wireless speaker in the opaque restraining box for playback of pre-recorded calls of their own infant, the novel infant, or their juvenile. Parents also showed a high frequency of jumping in response to calls of their own infant (70%) and novel infant (50%) but not of their own juvenile (10%) (Figures 2K–2O). Thus, infant calls could induce the rescue behavior, although it is unclear whether the parents could distinguish the calls of their own infants.

Given the significant effects of infant calls on the rescue behavior, we then analyzed the difference of vocalizations between infants and juveniles when they were trapped. We recorded vocalizations from infants (age 15 ± 2 days, n = 10, Figures 2P–2R) and juveniles (age 201 ± 13 days, n = 10, Figure 2S) when they were trapped alone in a restraining box in the water pool for 15 min. Compared to trapped juveniles, trapped infants made more frequent calls and more variety of call types (Figure 2T), including several infant-specific calls such as Cry, Compound-Cry (Figure 2Q), and Trill-Twitter (Figure 2R), consistent with the findings in previous studies [3, 11]. The juveniles vocalized more Tsik (Figure 2T), a call type associated with anxiety and fear [12], in line with the previous finding that older marmosets showed higher anxiety [13]. Furthermore, the duration and dominant frequency of all marmoset calls and each typical type of calls (Trill, Phee, Trillphee, Tsik, and Twitter) were compared between infant and juvenile's calls. With the exception of Tsik, infant calls in general showed shorter duration and higher dominant frequency (Figure S2), consistent with developmental changes of marmoset vocalization reported in previous studies [3, 11]. Thus, these infant-specific calls produced when they were trapped could explain the infant-induced parents' rescue behavior.

Rescue Behavior Depends on Currently Having Young Infants in the Family Group

In the third set of experiments, we investigated the role of group structure in the rescue behavior. In the family group with both older siblings and young infants, older siblings (age 238 ± 34 days, n = 10) also rescued their younger siblings (age 16 ± 3 days) (Figures 3A and 3B) but not each other. Furthermore, compared with 5 pairs of parous couples currently having infants in the group ("PI") (data from Figure 2), infants from other groups did not induce the rescue by parous couples having only

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(B) Images from Video S1 showing the infant rescue by parents. Marmoset parents opened the door, and then carried the infant and jumped back to the home cage.

(C and D) Marmoset parents showed higher percentage (C) and shorter latency (D) of both jumping and opening for the restraining box containing their infant than that containing nothing (empty) or food. Mean ± SEM, n = 6; *p < 0.05, Friedman test.

(E and F) The percentage of both jumping and opening declined (E) and the latency of both jumping and opening increased (F) with the offspring's age. Square point: mean, shade: SEM, n = 6; Friedman test.

(G–J) Data from 32 groups (with offspring at different ages) showing the percentage (G) and latency (H) of jumping, and also the percentage (I) and latency (J) of opening to rescue their offspring (Spearman rank correlation). Average data of three groups were shown in right panels. Mean ± SEM; *P < 0.05, **P < 0.01, ***p < 0.001, Kruskal-Wallis test.

(K and L) When tested alone, marmoset mothers and fathers showed 100% percentage of both jumping and opening to rescue their infant (K). The latency of both jumping and opening of mothers and fathers when tested alone was shorter than that when tested together (L). Data of "Together" were the same used in (C and D). Mean ± SEM, n = 6; *p < 0.05, Kruskal-Wallis test. See also Video S1 and Figure S1.
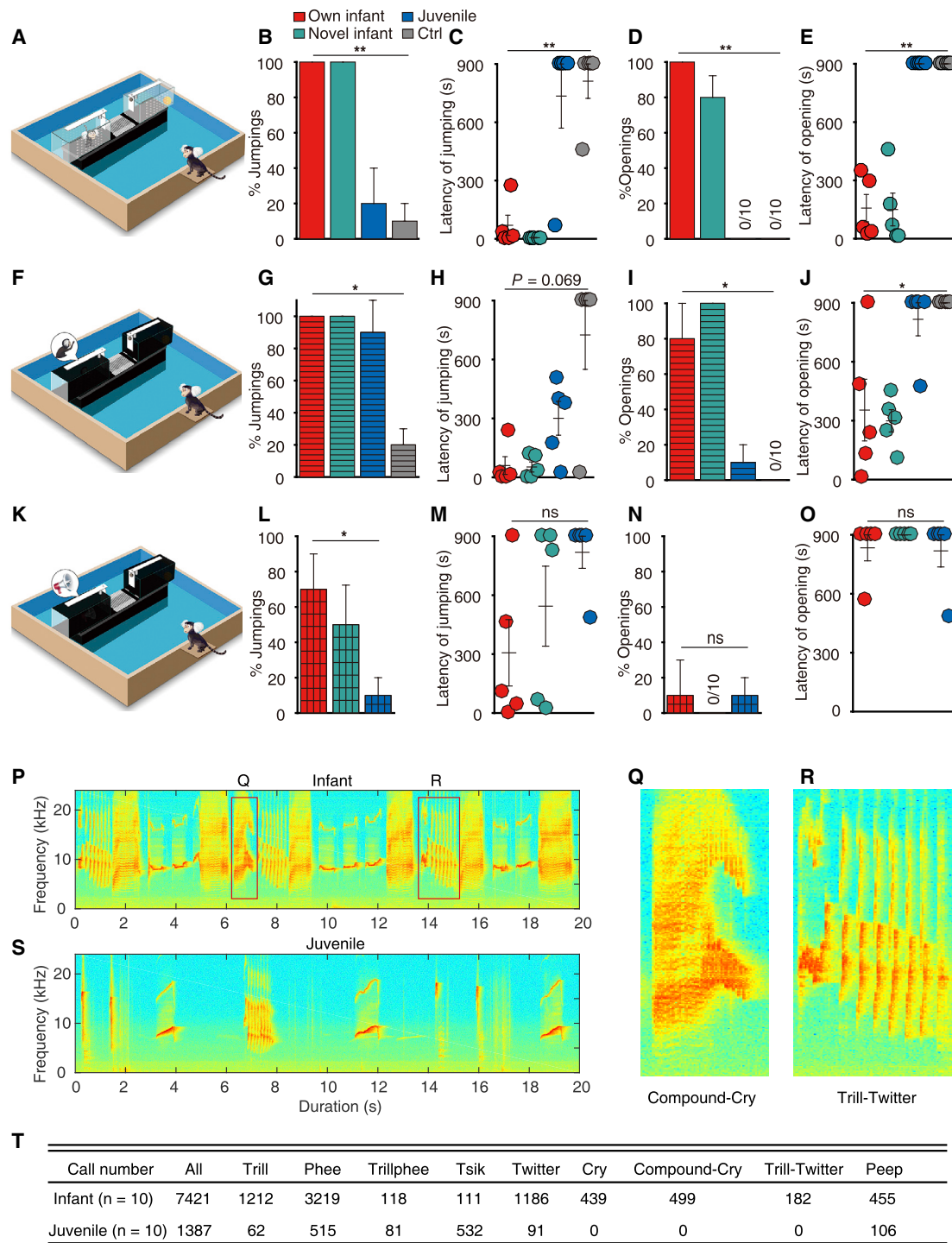
Figure 2. Infant Calls Could Induce Parents' Rescue Behavior

(A) The own infant, "novel" infant from other family group, own juvenile, or an inert object was trapped in a transparent restraining box.

(B–E) Parents showed higher percentage (B) and shorter latency (C) of jumping, and also higher percentage (D) and shorter latency (E) of opening to rescue their own infant or a novel infant than that of their own juvenile or an inert object.

(F) The restraining box was covered on the side facing the potential rescuer with black tapes.

(G–J) Parents showed higher percentage (G) and shorter latency (H) of jumping, and also higher percentage (I) and shorter latency (J) of opening to rescue their own infant or a novel infant than that of an inert object in the dark restraining box. In the case for trapped juvenile in the dark restraining box, parents showed high percentage of jumping (G) but did not open the door after jumping (I).

(K) A wireless speaker was put in the dark restraining box to playback the calls from their own infant, a novel infant and their own juvenile.

(legend continued on next page)

juveniles ("PJ," n = 6) and barely induced the rescue by nulliparous couples ("NP," 17% of both jumping and opening, n = 6) (Figures 3C and 3D). Thus, the rescue behavior of adult marmosets depends on the current presence of young infants in the family group. We also examined the rescue behavior between the parents themselves in 9 couples with no infant ("NI") and 7 parous couples with infants ("PI") and found that adult marmosets in both NI and PI groups showed very few rescues of their mates (NI: 11% opening; PI: 18% opening) (Figures 3E and 3F). Interestingly, the presence of infant calls during the test could induce significant mutual rescue between mates only in the PI group. This was revealed by the following test. We put an infant from other family group or a wireless speaker playing infant calls behind an opaque screen (to ensure their invisibility to the tested adult marmoset, Figure 3G). In the presence of a hidden infant, parents in the PI group showed significantly more mate rescue behavior (68% jumping, 43% opening) than adult marmosets in the NI group (25% jumping; 8% opening, Figures 3H and 3I). Similar results were found in the presence of a hidden speaker playing infant calls (Figures 3H and 3I). In addition, to exclude the possibility that the rescue was due to searching for the infant instead of rescuing the mate, the trapped adult mate marmoset was replaced by a similar-size toy, and adult marmosets rarely opened the box containing the toy in both conditions with the presence of an infant and a speaker (Figures 3H and 3I). Thus, the presence of young infants in the family group induced rescue of not only the infant but also the adult mate. Moreover, infant calls alone could trigger these rescue behaviors of adult marmosets living with infants in the group (see both Figures 2 and 3).

Infant Calls Activate Specific Cortical Areas in Marmosets Having Young Infants

The above findings suggest that having infants in the family group may alter neural circuit functions underlying the responsiveness to infant calls. This was explored further by using functional MRI (fMRI) on awake marmosets with or without infants in the group. In 7 marmosets with young infants ("PI" group), we found that infant-call stimuli (a 28-second sound clip cut from the infant calls used above, Figure 4A), compared to its scrambled version, elicited significant blood-oxygen-level-dependent (BOLD) activation in many brain areas (Figure 4B), including the auditory system (auditory core area, medial and lateral auditory belt area, rostral and caudal auditory parabelt area, superior temporal rostral area), insular and parainsular cortex (Figure 4B, middle panel; false discovery rate [FDR]-corrected $p < 0.05$, n = 7). Interestingly, no significant brain activation was detected in response to the same infant-call stimuli in marmosets currently having no infant in the group ("NI" group) (Figure 4B, bottom panel, FDR-corrected $p < 0.05$, n = 8). In contrast to infant calls, juvenile calls (Figure S3A) evoked activation of very limited

regions in the parents' brains of the PI group (Figure S3B, middle panel, FDR-corrected $p < 0.05$, n = 7) and no significant activation in the NI group (Figure S3B, bottom panel, FDR-corrected $p < 0.05$, n = 8). Thus, having young infants in the group increases the salience of infant-call stimuli in activating specific cortical areas in the parents' brains.

DISCUSSION

We have developed a novel paradigm for studying altruistic behaviors of marmosets, based on rescuing trapped group members. Marmoset parents showed a strong motivation to rescue a young infant but not juvenile marmosets beyond 2 months of age, when the marmoset has already acquired most of their motor skills [15, 16] and is likely to be capable of surviving independently. The older siblings also rescued infants in their family group. These specific young infant-directed altruistic behaviors may reflect a dedicated parenting activation pattern with the potential unique twist for marmosets that it is activated in mothers, fathers, and siblings rather than mother alone. Furthermore, the presence of infants could also induce mutual rescue behaviors between parents in the group. Kinship between group members is thought to play an important role in the evolution of cooperative breeding in non-human mammals [17, 18]. There is reproductive suppression in marmoset groups and thus levels of genetic relatedness within groups are quite high. Altruistic behaviors in marmoset family groups may be the production of kin selection.

The cooperative breeding and allomaternal care has also been thought as a predictor of interspecific variation in proactive prosociality [19]. Indeed, altruistic behavior of marmosets has been previously reported in an easy experimental setting that they spontaneously provide food to other non-related individuals [9], suggesting that marmosets can take advantage of low-cost opportunities to provide resources to others. In contrast to this low-cost situation, our experimental paradigm imposes a high-cost task that could be used to study the cost-benefit balance in the altruistic behaviors of marmosets. In our experimental settings, altruistic behaviors were also not restricted to kin or familiar group members, due to that parents' responses to "novel" infants from other family groups were similar to that to their own infants. This may suggest a generalized motivation of parental care to other young infants. However, an alternative explanation is that marmoset parents could not discriminate their own infants by the visual and auditory cues when they were trapped. In the natural environment, marmoset parents do not often find themselves in a position to provide care for unrelated infants; thus, they may not acquire the ability of such parental discrimination in evolution.

Our fMRI studies on awake marmosets further showed that infant calls significantly activated the auditory and insular cortices only in adult marmosets currently having young infants, a

(L–O) Parents showed higher percentage (L) and shorter latency (M) of jumping when playing calls from their own infant or a novel infant than that of calls from juvenile, but very low percentage (N) and long latency (O) of opening for all three conditions.

(P–R) The spectrogram of representative infant calls when they were trapped. The infant call signal contained more complex types of call types than that of juvenile calls. The spectrogram of Compound-Cry and Trill-Twitter were magnified in (Q) and (R), respectively.

(S) The spectrogram of representative juvenile calls when they were trapped.

(T) The number of each call type in infants calls (n = 10) and juveniles calls (n = 10). Trapped infants made much more calls than that of juvenile. Mean ± SEM, n = 5; ns: no significance, *$P < 0.05$, **$P < 0.01$; Friedman test. See also Figure S2.
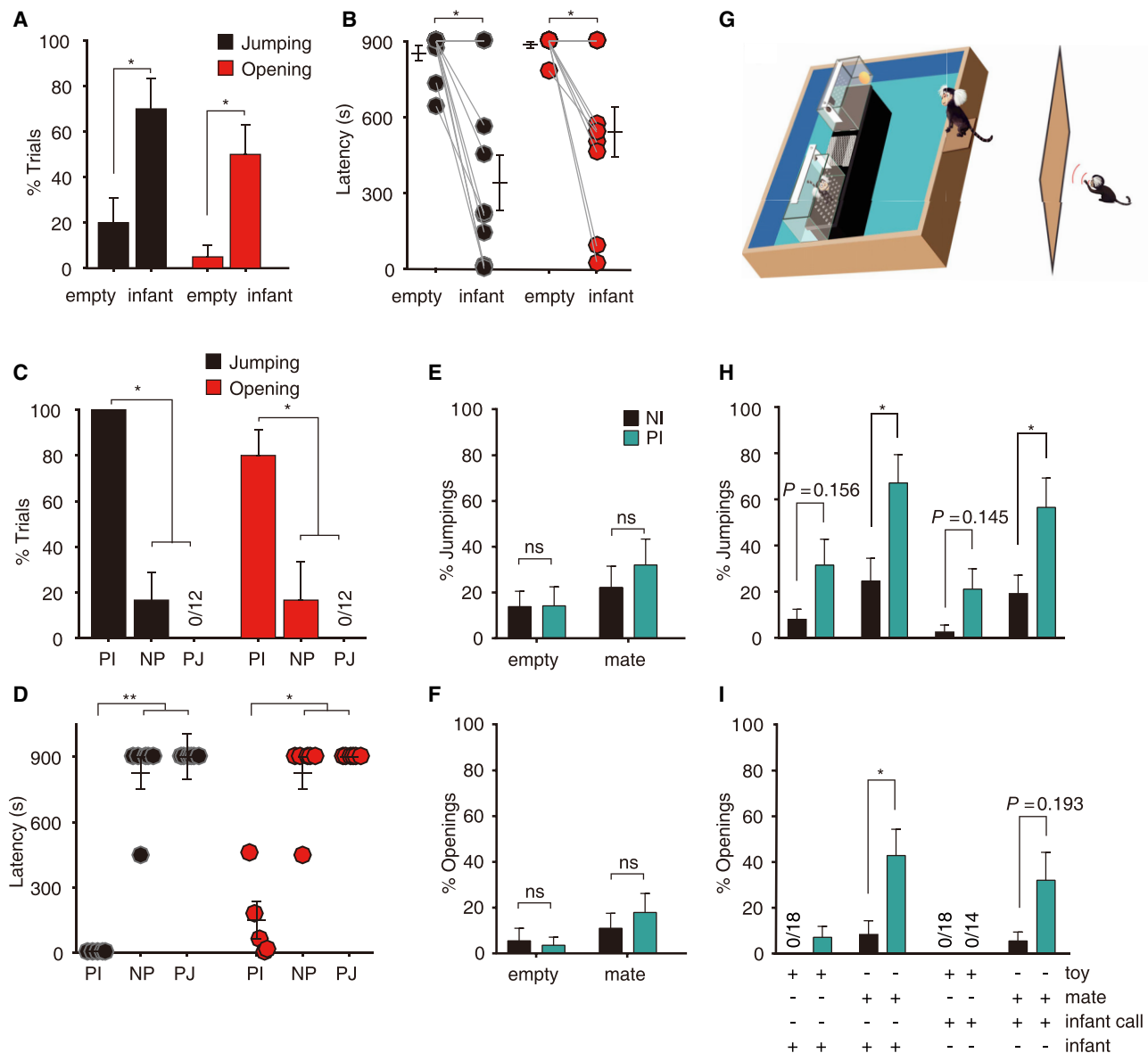
Figure 3. Rescue Behavior Depended on Currently Having Young Infants in the Family Group

(A and B) Older siblings showed higher percentage (A) and shorter latency (B) of both jumping and opening to rescue young infants than that of empty restraining box. Mean ± SEM, n = 10; *p < 0.05, Wilcoxon signed ranks test.

(C and D) Parous couples with infant (PI, n = 5, data from Figure 2) showed higher percentage (C) and shorter latency (D) of both jumping and opening to rescue a novel infant than that of nulliparous couples (NP, n = 6) or parous couples having only juveniles (PJ, n = 6). Mean ± SEM; *p < 0.05, **p < 0.01, Kruskal-Wallis test.

(E and F) Few mate rescue revealed by low percentage of both jumping (E) and opening (F) in both PI group (n = 7) and groups with no infant (NI group, n = 9). Mean ± SEM; ns: no significance, Mann-Whitney U test.

(G) A hidden novel infant or a hidden speaker to play back infant calls was put behind an opaque shield when testing mate rescue.

(H and I) In the presence of a hidden infant or a speaker playing infant calls, adult marmosets in PI group showed higher percentage of both jumping (H) and opening (I) to rescue their mates than that of NI group. In both group, adult marmosets rarely opened the box containing the toy in the presence of an infant or a speaker (I). Mean ± SEM; *p < 0.05, Mann-Whitney U test.

phenomenon that further corroborates the observed behavioral differences between the groups with and without infants. This is in line with the findings that the insular cortex is an important brain area critical for social interactions in rodents [20] and empathy in humans [21]. Due to the limited amount of imaging data and therefore relatively low statistical power, we have not

observed activation of other behavior-related brain regions, and there is no direct evidence of how the activation of auditory and insular cortices could trigger altruistic behaviors in marmosets. However, the significant activation of the auditory cortex by infant calls in the brain of marmoset parents was consistent with a previous finding that infant calls activated the auditory
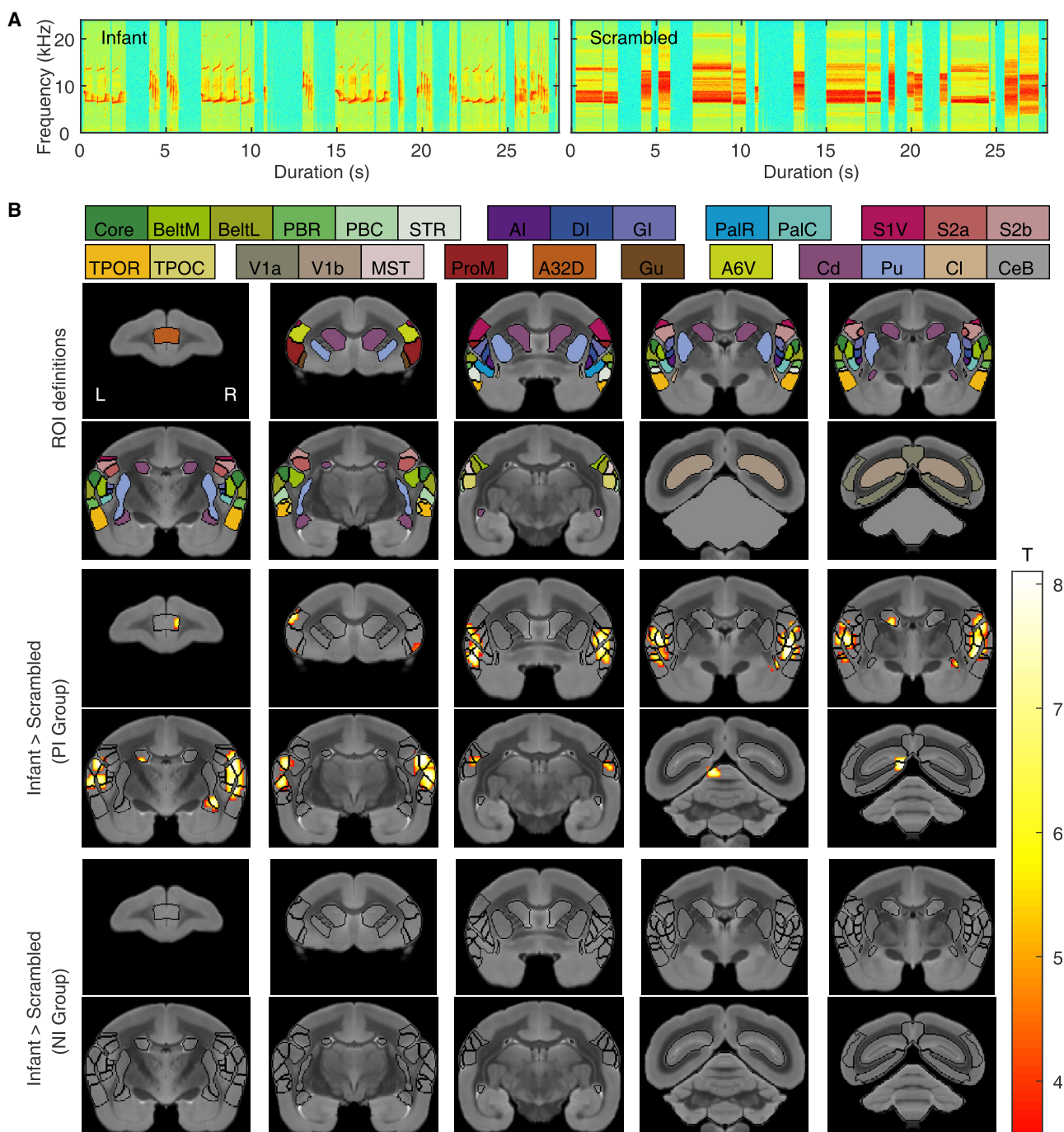
Figure 4. Infant Calls Activated Specific Cortical Areas in Marmosets Having Young Infants

(A) Representative infant-call stimuli and its phase scrambled version used for fMRI sessions.

(B) Top panel: anatomical ROI definitions. Black lines and various colors indicated areas of different ROIs, overlaid on the structural marmoset template [14]. Group analysis map showing brain regions significantly more activated by infant calls than by the scrambled stimuli (FDR-corrected p < 0.05) in the PI group (middle panel) and NI group (bottom panel) is shown. Color bar is in t-values. Core, auditory core area; BeltM, auditory belt area medial; BeltL, auditory belt area lateral; PBR, auditory parabelt area rostral; PBC, auditory parabelt area caudal; STR, superior temporal rostral area; AI, argranular insular cortex; DI, dysgranular insular cortex; GI, granular insular cortex; PalR, parainsular cortex rostral; PalC, parainsular cortex caudal; S1V, primary somatosensory ventral; S2a, secondary somatosensory area a; S2b, secondary somatosensory area b; TPOR, temporo-parito-occipital association area rostral; TPOC, temporo-parito-occipital association area caudal; V1a, visual area V1 a; V1b, visual area V1 b; MST, medial superior temporal area; ProM, proisocortical motor region; A32D, area 32 dorsal; Gu, gustatory cortex; A6V, area 6 ventral; Cd, caudate; Pu, putamen; CI, claustrum and endopirform claustrum; CeB, cerebellum. See also Figure S3.

cortex in maternal but not pup-naive female mice, a phenomenon mediated by the increased expression of oxytocin receptors in the auditory cortex of mouse brain [22]. Thus, our results may provide an important clue for further investigation on how having infants alters the activity of the auditory cortex in marmosets, thus revealing an evolutionarily conserved mechanism of parental responses to infant calls.

Parental behaviors in marmosets are intimately related to the level of hormones [2]. For example, parenting experience elevated the neurocrine hypothalamic release of reproductive hormones, such as oxytocin and prolactin, in male marmosets [23], as that found in maternal females. Intracerebroventricular infusion of oxytocin increased the tolerance of adult male marmosets toward its offspring in food transfer [24]. Oxytocin also enhanced the responsiveness to infant stimuli in adult marmosets [25] and facilitated fidelity in well-established marmoset pairs by reducing prosocial behavior toward strangers [26, 27]. Marmoset prolactin levels could be elevated by infant carrying in both father and older siblings in the group [28], also in parentally inexperienced marmosets outside of the group [29]. Thus, it would be of interest to further explore the potential involvement of hormones in infant-induced altruistic behaviors of marmosets and underlying neural mechanisms.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2020.07.045.

AUTHOR CONTRIBUTIONS

N.G. conceived and designed the study. J.H., S.Z., L.C., and X.L. performed the behavioral experiments. X.C. and Z.L. performed the fMRI study. J.H. and X.C. analyzed data and prepared the figures. N.G., Z.L., J.H., and X.C. wrote the manuscript. All authors have read and approved the manuscript submission.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
Common marmoset (*Callithrix jacchus*)	Non-human Primate Facility, Institute of Neuroscience, CAS	N/A
Software and Algorithms		
MATLAB 2018b	Mathworks	https://www.mathworks.com/products/matlab.html
SPSS Version 20.0	IBM Corp.	https://www.ibm.com/analytics/spss-statistics-software
SPM12	UCL Queen Square Institute of Neurology	https://www.fil.ion.ucl.ac.uk/spm/
ITK-SNAP	Paul Yushkevich & Guido Gerig	http://www.itksnap.org/
Audition 3.0	Adobe Corp.	https://www.adobe.com/products/audition.html
Other		
9.4T Bruker BioSpec	Bruker	BioSpec94/30USR
8-channel marmoset receiver array	Fine Instrument Technology	Custom made
Canon XA10	Canon Inc.	http://www.canon.com.cn/overview/dv.html
Canon Legria HFR406	Canon Inc.	http://www.canon.com.cn/overview/dv.html
360 Wireless Cam	Qihoo 360 Technology Co., Ltd	http://jia.360.cn/
Audio-Technica AT2031	Audio-Technica Inc.	http://www.audio-technica.com.cn/
Roland UA-1010	Roland Corp	https://www.roland.com/global/
Kuwo S7	Kuwo Co., Ltd	https://kuwo.cn/
HCJYET HT-8351 sound meter	HCJYET Co., Ltd	http://www.hcjyet.com/

RESOURCE AVAILABILITY

Lead Contact
Further information and requests for data or analysis code used in this study should be directed to and will be fulfilled by the Lead Contact, Neng Gong (ngong@ion.ac.cn).

Materials Availability
This study did not generate new reagents.

Data and Code Availability
All raw data and analyses supporting the current study are available from the corresponding author on request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

In this study, we used 68 groups of common marmosets (with group sizes ranging from 1 to 10) in behavior test in behavior test, and 11 marmosets (6 males and 5 females, aged 2 - 5 years and weighted 300 - 500 g) were further used in fMRI study. Marmoset less

than 2 months was defined as "infant" and marmoset from 2 - 18 months was defined as "juvenile." All marmosets were housed in metal wire-meshed cages [90 cm (L) × 80 cm (W) × 85 cm (H)], equipped with a sleeping box and other enrichment materials. Marmosets had *ad libitum* access to food and water, and colony rooms were maintained at a temperature range from 27°C to 30°C and a 12-h: 12-h light-dark cycle. All procedures complied with the guideline of the Animal Advisory Committee at the Institute of Neuroscience, Key Laboratory of Primate Neurobiology, CAS Center for Excellence in Brain Science and Intelligence Technology, Chinese Academy of Sciences.

METHOD DETAILS

Experimental procedure of behavioral tests

The experiments were carried out at home cage and its adjacent test cage. Both cages were 90 cm (L) × 80 cm (W) × 85 cm (H) and were blocked by an opaque shield which would be pulled out to connect the cages during testing. The inside facets of adjacent cage were covered by smooth plates to prevent marmosets to climb the mesh. The apparatus was composed of three parts: a water pool, a takeoff platform and a restraining platform (Figure 1A; Video S1). The water pool was 84 cm (L) × 74 cm (W) × 20 cm (H), which was made of acrylic resin and filled with water to the depth of 12 cm. The takeoff platform was a black box with metal mesh measuring 17 cm (L) × 13 cm (W) × 10 cm (H), and could be attached to the water pool so that marmosets could jump from it to the restraining platform. The restraining platform had a landing platform with two restraining boxes. The landing platform was a black box [50 cm (L) × 10 cm (W) × 20 cm (H)] with a mesh [17 cm (L) × 17 cm (W) × 1 cm (H)] centering on the upper surface and two transparent, Plexiglas restraining boxes at each end of the platform. The restraining box was 20 cm (L) × 10 cm (W) × 10 cm (H), with perforated surfaces and a door which could be opened by pressing the lever on the box. In some sessions (Figures 2F–2O), black tape was pasted on five surfaces of restraining box to block visual information of the trapped marmoset, and the surface on the back side remained transparent for ventilation and illumination. In the experiment to test whether marmoset would rescue a "novel" infant from other groups (Figure 2), the door of the restraining box was buckled loosely by cable ties so that the potential rescuer could only open the door partly, a design that may prevent possible hurt of the "novel" infant.

Subjects had a habituation process to get familiar with the environment and apparatus. For details, the marmoset group would be marked for identity and would be removed into the test cage to live for at least 1 day before being tested. The restraining platform was put into the test cage so that marmoset could explore the apparatus. In addition, the restraining platform was put into the water pool at 0 cm distance and marmoset could explore it for 2 hours. After the subject marmoset had acclimated, 2 trials at home cage would be performed to help marmoset explore how to open the door of restraining box (data not shown). During the habituation, the trapped animal (infant, juvenile or mate) was same to that used in the following test. Because the open mechanism was very easy, all marmosets could easily open the door in 15 min during habituation regardless who was trapped. After habituation, behavior test would be performed. The experimenter gently removed one marmoset into the restraining box, with an inert object (a ball) in the other restraining box, and put the restraining platform in the water pool at 50 cm distance. Then the shield between the water pool and the potential rescuer marmoset was pulled out and the rescuer had 15 min to rescue the trapped. If the door of restraining box did not be opened in 15 min, the trapped marmoset would be liberated by experimenter. In general, a subject was tested only twice to ensure that rescue behavior was spontaneous instead of over-training. In the experiment to test rescue behavior between mates, the male or female was assigned as the trapped or rescuer in a counter-balanced sequence. All behavior tests were performed during 9:00 - 19:00.

Experimental procedure of fMRI study

The fMRI study included 5 female and 6 male adult marmosets, which were assigned into 2 groups: parous marmosets having infants (< 2 months) in the groups ("PI," n = 7, 3 males and 4 females) and marmosets without infants ("NI," n = 8, 5 males and 3 females, 4 marmosets in NI group was also included in PI group when they had infants). We used a 4-week habituation protocol adapted from AC Silva et al. [30] for the awake marmoset fMRI study. In this procedure, the restraint apparatus included an animal bed, clothes for body restraining and individually customized helmets for head fixation. Briefly, in the first week, only body restraining was applied with an increasing period from 15 to 60 min. In the second week, recorded MRI noise was added and habituation periods gradually increased to 120 min. In the third week, head fixation using the customized helmet was added. In the fourth week, sound-delivering soft tubes were inserted in animal's ear canal, to mimic the actual auditory fMRI experiment. For marmoset couples in PI group, we only trained one parent per day, and the other remained with their infants in the home cage.

After habituation, marmosets were briefly anesthetized with 4% isoflurane for setting up, and animals were fully awake during imaging. Four types of auditory stimuli (85 - 110 dB SPL) were used in the fMRI study: the natural calls recorded from the infant marmoset (age = 5 days) and juvenile marmoset (age = 158 days), and corresponding phase scrambled infant calls and juvenile calls (Figures 4A and S3A). These phase scrambled calls were obtained by first performing a Fourier transform (FFT) of natural calls, then randomizing the phases of each vocalization, and performing an inverse Fourier transform (iFFT). During each EPI run, all 4 types of auditory stimuli were delivered twice in a random order, with a variable interval of 15 s - 25 s. The duration of each stimulus was 28 s. All fMRI experiments were conducted in a 9.4T Bruker scanner, with a 154 mm diameter volume coil (Bruker) for transmission and an 8-channel marmoset receiver array (Fine Instrument Technology, Brazil) for receiving. Anatomical images were acquired using a T2 RARE sequence (matrix size: 256 × 256, field of view: 50 × 50 mm^2, repetition time: 5100 ms, echo time: 33 ms, slice thickness: 0.8 mm, slices: 42, voxel size: 0.195 × 0.195 × 0.8 mm^3). Functional images were acquired with a gradient-echo EPI (echo planar

imaging) sequence [110 volumes, matrix size: 80 × 70,field of view: 40 × 35mm^2,repetition time: 3500 ms, inter-volume delay (silent period): 2 s, echo time: 15 ms, slice thickness: 1 mm, slices: 33, voxel size: 0.5 × 0.5 × 1 mm^3). In total, 220 EPI runs were acquired in 19 sessions from 7 animals in PI group (Female: 124 runs; Male: 96 runs), 224 EPI runs were acquired in 19 sessions from 8 animals in NI group (Female: 90 runs; Male: 134 runs).

QUANTIFICATION AND STATISTICAL ANALYSIS

Data analysis of behavioral tests

Marmoset's behaviors were recorded by a digital camera (Canon XA10 or Canon Legria HFR406) in front of the cage and were monitored by a web camera (360 Wireless Cam). All behavior videos were analyzed offline by 2 - 3 experimenters to record the percentage and latency of both jumping and opening. If the subject did not jump into the platform or open the restraining box, the latency was regarded as 900 s (15 min). Since a subject marmoset was test only twice, the percentage of jumping or opening for the marmoset could be 0%, 50% or 100%, and the latency of the marmoset was the average latency between the 2 trials. All statistical tests were two-tailed and non-parametric, with $\alpha < 0.05$ as criterion for significance. A Spearman's rank correlation was used to test the correlation of rescue performance (percentage or latency) and infant's age (Figures 1G–1J). To compare between two samples, Mann-Whitney U test (for un-paired samples) or Wilcoxon signed rank test (for paired samples) was conducted. For hypothesis testing among more than two samples, Kruskal-Wallis test (for un-paired samples) or Friedman test (for paired samples) were conducted with Dunn-Bonferroni test for post hoc analysis. All statistical analysis was accomplished with SPSS Version 20.0 and MATLAB 2018b.

Marmoset's calls were recorded in a soundproof room when marmoset was trapped in the restraining box in the pool, with a condenser microphone (Audio-Technica AT2031) and digitized through an audio interface (Roland UA-1010) at 32 - bits and 48 kHz sample rate. For playback in the behavioral tests, the calls were delivered by a wireless speaker (Kuwo S7) at 90~100 dB SPL (measured by HCJYET HT-8351 sound meter). The entire sound signal was first high-pass filtered at 3 kHz and then short-time energies of the signal was calculated for detecting the onset and offset of calls by double-threshold algorithm. After determining the onset and offset of calls, the entire signal was segmented and each vocal segment was checked and categorized manually by an experienced researcher based on its spectrogram [31]. We processed the call signal by a 2048-point fast Fourier transform (FFT) with an 87.5% overlapping Hanning window. The duration of call was the time between onset to offset. The dominant frequency of call was the average frequency which had maximum power. Mann-Whitney U test was conducted to compare the difference between infant and juvenile vocalizations. Hedges' g value was used to calculate the effect size of such difference, with g = 0.2, 0.5 or 0.8 means a small, moderate or larger effect size respectively [31]. All statistical analysis was accomplished with SPSS Version 20.0 and MATLAB 2018b.

Data analysis of fMRI study

Data analysis was performed using custom scripts written in MATLAB 2018b (MathWorks, Natick, MA) and SPM12 (https://www.fil.ion.ucl.ac.uk/spm/). After data format conversion, the brain was extracted using ITK-SNAP (http://www.itksnap.org/). All volumes in each run were realigned to the first volume, registered to a marmoset brain template [14], and spatially smoothed with a Gaussian Kernel (FWHM = 1 × 1 × 1 mm^3).The preprocessed functional data was analyzed using a conventional general linear model (GLM) in SPM, with motion parameters (6 realignment parameters and their 1st order derivatives) used as nuisance regressors in 1st level analysis. In 2nd level group analysis, paired t test was conducted to generate two contrast maps (infant calls versus scrambled infant calls; juvenile calls versus scrambled juvenile calls) in PI group and NI group, respectively, with FDR corrected p < 0.05 and cluster size > 5.