

# Empathy and the Somatotopic Auditory Mirror System in Humans

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## Summary

How do we understand the actions of other individuals if we can only hear them? Auditory mirror neurons respond both while monkeys perform hand or mouth actions and while they listen to sounds of similar actions [1, 2]. This system might be critical for auditory action understanding and language evolution [1–6]. Preliminary evidence suggests that a similar system may exist in humans [7–10]. Using fMRI, we searched for brain areas that respond both during motor execution and when individuals listened to the sound of an action made by the same effector. We show that a left hemispheric temporo-parieto-premotor circuit is activated in both cases, providing evidence for a human auditory mirror system. In the left premotor cortex, a somatotopic pattern of activation was also observed: A dorsal cluster was more involved during listening and execution of hand actions, and a ventral cluster was more involved during listening and execution of mouth actions. Most of this system appears to be multimodal because it also responds to the sight of similar actions. Finally, individuals who scored higher on an empathy scale activated this system more strongly, adding evidence for a possible link between the motor mirror system and empathy.

## Results

We conducted an fMRI experiment with 16 subjects and tested auditory and motor properties in the same subjects on two separate days. During the auditory day, subjects listened to 4 s sounds from five categories (see Table S1 in the Supplemental Data available online). We presented sounds in a randomized sequential order by using a sparse sampling block design. Sounds were presented in the silent interval between the acquisition

of two consecutive brain volumes. We compared the sounds of bimanual hand actions (HandSnd) and mouth actions (MouthSnd) against environmental sounds not related to actions (EnvSnd) and phase-scrambled versions of the action sounds that had the same frequency composition but were not recognizable (ScrHandSnd and ScrMouthSnd). During the motor day, subjects were asked to execute actions similar to those used in the auditory stimuli within the constraints of the scanner. For hand actions, subjects were requested to use both their hands to reach out, grasp an object (a peanut or a sheet of paper), rip or break the object apart, and return to the resting position (HandExe). For mouth actions, subjects were requested to manipulate, by using their lips, a small object that was lowered onto their lips by the experimenter, who used a wooden “fishing rod” (MouthExe). In all motor trials, subjects had to watch a screen with instructions and were prevented from seeing and hearing their own actions. The auditory data were always collected on a day preceding that of motor scanning in order to avoid the possibility that the memory of executing the actions would bias perceptual brain activity toward premotor areas.

To investigate the presence of an auditory mirror system in humans, we combined the results of the auditory and motor testing for each effector separately (Figure 1A; Table S2). We required each voxel to be significantly activated by audition of actions of the specific effector (HandSnd-EnvSnd for the hand and MouthSnd-EnvSnd for the mouth,  $p < 0.005$ , see Figure S1A and Table S3) and by execution of similar actions with the same effector (HandExe-rest or MouthExe-rest,  $p < 0.005$ , see Figure S1B and Table S4). This analysis indicated that the left BA44, BA6, IPL and bilateral middle temporal gyrus (MTG) and superior temporal sulcus (STS) were active both when subjects listened to actions and when they executed them. Single-subject analysis with unsmoothed data confirm the consistency of this result (Figure S1C and Table S5). The mirror circuit was more strongly activated in the six subjects who ranked highest in perspective taking (PT [11, 12]) than in the six subjects who ranked lowest in this scale (Figures 1B and 1C). In the latter, although there was a trend for mirror activity, this activity failed to pass stringent statistical thresholding. Significant positive correlations between PT and visual activations ( $r > 0.5$ ,  $p < 0.03$ ) in mirror areas confirmed that this effect holds over the entire pool of subjects (Table S6). Because of the limited number of subjects in our experiment, this finding is tentative and will require replication in larger pools of subjects. Despite these differences in brain activations, there were no differences between the behavioral performance of the high PT subjects in the scanner and that of the low PT subjects. During scanning, subjects had to report by button press the rare occurrence of a sound from a different category within a block (e.g., a HandSnd in a block of MouthSnds). The number of “hits,” the number of “false alarms,” and the overall accuracy in the detection

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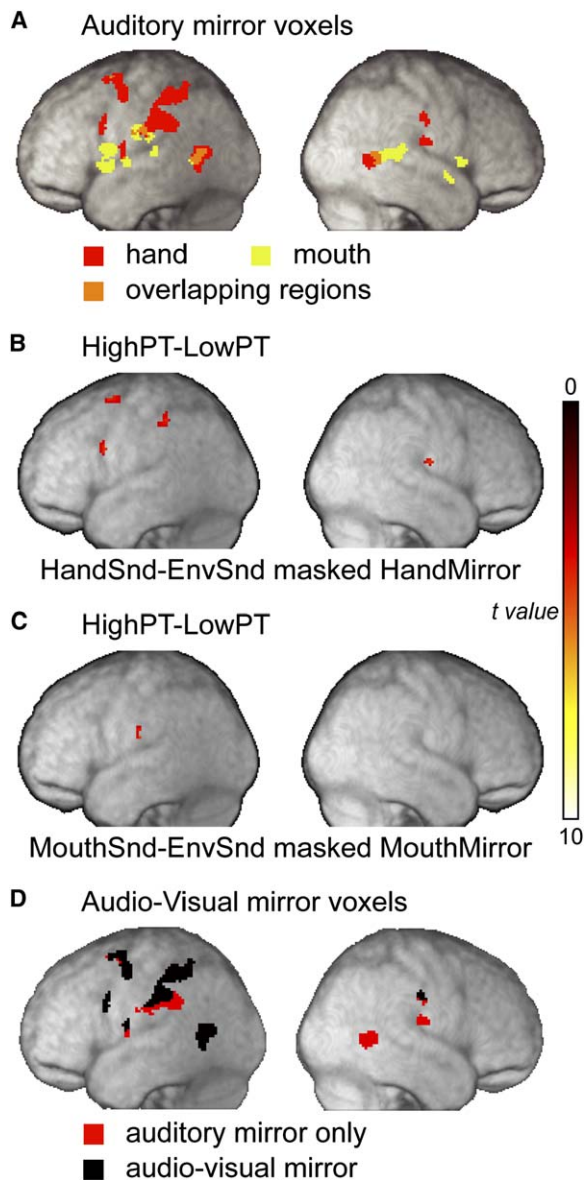


Figure 1. Voxels Significantly Activated by Audition of Actions of the Specific Effector and Execution of Similar Actions with the Same Effector

(A) Mirror activations rendered on the mean anatomical image of the 16 subjects with a transparency of 30 mm (random-effect analysis,  $p < 0.005$  separately for listening and execution,  $k = 20$ ). Red voxels were active during listening and execution of hand actions, yellow voxels were active during listening and execution of mouth actions, and orange voxels were active for both effectors. All these areas are significant even if a false discovery-rate correction for multiple comparisons is used at  $p < 0.05$ .

(B and C) The effect of PT on the activation of the mirror system. (B) Comparison of the contrast values of HandSnd-Env among the six subjects with highest PT (scores: 27, 24, 23, 23, 22, and 22) and the six subjects with the lowest PT score (scores: 18, 18, 16, 15, 13, 12, and 16) via a two-sample  $t$  test at  $p < 0.005$ . (C) Same for MouthSnd-Env. The tests were masked with results of (A) to be restricted to mirror areas. See Table S6 for coordinates.

(D) The audio-visual mirror system. The auditory mirror system for hand actions as defined in (A) is shown in red, and its sectors responding also to the sight-of-hand actions (HandVis – CtrlVis,  $p < 0.005$ , random-effect analysis) are shown in black.

task performed during scanning were high in all subjects (see Supplemental Data) but showed no significant differences between the groups (two-sample  $t$  test high versus low PT, all  $p > 0.2$ ). This lack of difference might, though, be due to a ceiling effect. Inter-individual differences were not observed along other dimensions of empathy (see Supplemental Data, including Figure S3).

To demonstrate the selectivity of this mirror system, we identified mirror regions that were activated more by the sounds and the execution of hand actions compared to mouth actions and vice versa (Figure 2D) within the mask of mirror areas defined above. The left hemisphere showed a somatotopical organization of the premotor mirror regions both during listening and during execution, with a dorsal region in BA6 responding more to the hand and a ventral region in BA44 responding more to the mouth. The IPL responded more to the hand than to the mouth (see also Table S8). A region of interest (ROI) analysis, in which we extracted the mean signal from the three main clusters identified in the previous analysis, revealed that in all three areas, the sound of the preferred action was the only sound contributing significant activations (Figures 2A–2C). The phase-scrambled versions of the preferred actions did not activate any of these areas, demonstrating that the effector preference is not based on the difference in frequency composition of hand and mouth actions. During motor execution, clusters also demonstrated significant activations during the use of the nonpreferred effector, but these activations were significantly smaller than those associated with the preferred action. Table S8 lists all clusters demonstrating preference for the same effector during execution and listening.

To examine the similarity between the auditory mirror system and the more classically described visual mirror system, we capitalized on the fact that the 16 subjects used in this experiment were also used in a separate experiment investigating the visual representation of hand actions (Gazzola et al., Cognitive Neuroscience Society Meeting Abstract, 2004; see Supplemental Data). We contrasted the brain activation during the sight of grasping actions (HandVis) against a control hand movement not involving an object (CtrlVis). In contrast with the left lateralized auditory activations, visual activations were bilateral (Figure S5B), but much of the auditory mirror system was also activated in the HandVis-CtrlVis contrast ( $p < 0.005$ , Figure 1D). Importantly, in a ROI analysis, only the hand-selective regions of Figure 2 responded significantly to the sight of hand actions while the mouth region was inhibited. Unfortunately, a similar analysis for mouth actions was not possible because only hand actions were tested in the visual experiment. It should be noted that the actions visually presented to the participants, e.g., grasping a wooden block, are not normally associated with salient sounds.

The hand actions that subjects executed in the scanner (ripping paper, breaking peanuts) produced sounds. Even though these sounds were covered by the noise of the scanner, participants may have imagined the sound of these actions, and this may have rendered the finding of activations common to listening and executing hand actions trivial. We therefore performed alternative analyses in which motor areas were defined based on the execution of actions that do not produce salient sounds

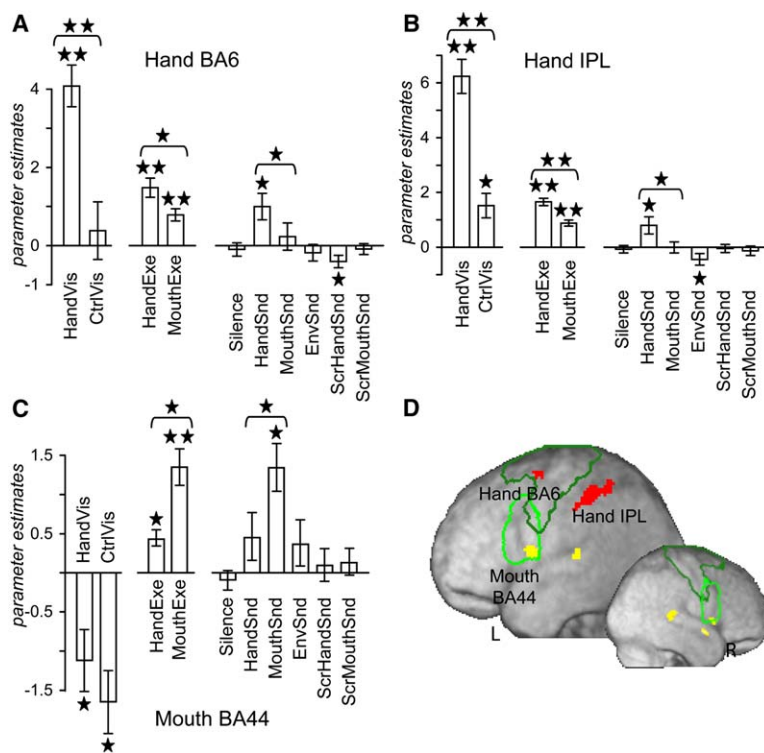


Figure 2. Somatotopy

(A–C) Signal extraction from the hand clusters in BA6, IPL, and mouth clusters in BA44 (as shown in [D]) of the left hemisphere during listening, execution, and observation of actions. An asterisk denotes significant differences at  $p < 0.05$ , and a double asterisk denotes those at  $p < 0.01$  according to a two-tailed  $t$  test against 0 or a matched-pair  $t$  test ( $n = 16$ ,  $df = 15$ ). Error bars represent the SEM.

(D) Brain activations of hand-selective (red) and mouth-selective (yellow) areas. The dark green lines represent the border of BA6 based on Amunts’s probabilistic maps (at least 3/10 subject threshold), and the light green lines represent the border of BA44. All these areas are significant even if a false-discovery-rate correction for multiple comparisons is used at  $p < 0.05$ .

(see Figure S6). These analyses revealed extremely similar results, indicating that auditory imagery during motor execution cannot explain our results.

## Discussion

After the discovery of auditory mirror neurons in monkeys [1, 2], the existence of a similar system in humans has been suggested by a number of studies [7–10]. Here we show that a left lateralized circuit composed of bilateral mid-temporal gyrus (MTG), left inferior parietal lobule, and left premotor cortex (BA44/6) responds for both action execution and action sounds in the same subject. Although the fMRI data alone cannot demonstrate that the same neurons within a voxel respond to the sound and the execution of actions, these data, in light of primate [1, 2, 13] and TMS [7, 9] experiments, suggests that our parietal and premotor findings represent the activity of auditory mirror neurons in these areas. Interestingly, the MTG was also found to be common to action listening and execution. This area does not appear to contain mirror neurons in the monkey [5] but is critical for the auditory and visual perception of biological actions [5, 14–19]. MTG activations to the sound of actions are thus likely to reflect the sensory elaboration of these sounds [15–18], and this sensory elaboration could then be sent through direct reciprocal connections [5] to the parietal and from there to the premotor cortex. During action execution, neurons in the temporal lobe have been shown to be inhibited in the monkey [20, 21], suggesting that MTG activity during motor execution could reflect the inhibition of expected sensory consequences [5, 20, 21], the metabolic cost of which could lead to BOLD (blood-oxygen-level-dependent) signal increase without an increase of neural firing

[22]. Alternatively, it could reflect the internal generation of the auditory and visual consequences of the executed actions [23]. In either case, the MTG would be a close functional “partner” of the auditory mirror system proper and could be composed of parietal and premotor areas. Although some studies find MTG activation during motor execution [23, 24], others do not [25, 26]. Careful investigations of the factors determining these differences will be required.

Much of the auditory mirror system also responds to the vision of actions, indicating that, except for differences in lateralization, the auditory and visual mirror systems are similar in humans. Further experiments will be necessary to allow examination of whether, as in primates [1, 2], single neurons in those areas may combine auditory and visual mirror properties.

A critical feature of the mirror system is the *selective* mapping of *specific* heard or seen actions onto the motor programs for executing the *same* actions [1, 2, 27]. Showing the existence of a mirror area that is more activated by hand sounds than by mouth sounds and that has the same preference during execution, as well as the existence of an area with a complementary preference for mouth actions, could help establish such specificity in humans. So far, some studies have shown that the vision [28–30] (or sound [31]) of hand actions activates different sectors of the premotor cortex than the vision (or sound) of mouth actions, and other studies have shown that the execution of hand actions activates different sectors of the premotor cortex than the execution of mouth actions [30, 32–34]. However, none of these studies has compared the execution and perception of the actions from these two effectors (hand versus mouth) in the same subjects [28, 29, 31–34]. Here, testing hand and mouth actions during listening and

execution, we demonstrate that a ventral premotor cluster preferred mouth actions and that a dorsal one preferred hand actions, in *both conditions*. These findings provide direct neuroimaging evidence for *selective* mapping in the human mirror system. This dorso-ventral organization is in agreement with the auditory, visual, and motor somatotopy derived in separate studies [29–35] and with observations in the monkey [1, 2, 27], where many mirror neurons respond to both hand and mouth actions but where the most dorsal ones respond more to hand actions and the most ventral ones respond more to mouth actions. This suggests that the sound of a particular action is mapped onto the motor program for executing that particular action. This finding is in accord with the selective nature of auditory facilitation in TMS studies [7, 9] and with the somatotopical representation of action words [36, 37]. Because the actions composing the HandSnd and MouthSnd conditions differed not only in the effector used (hand versus mouth) but also in the type of action performed (e.g., to open versus to crunch), it will therefore remain for future experiments to establish whether our dorso-ventral differentiation reflects the difference between hand and mouth in our stimuli or differences in the type of actions. Either way, the sound of particular actions was mapped onto premotor regions more involved in performing similar actions—a central pillar of the mirror matching theory [1–6, 27, 38].

It has been postulated that the mirror system is important for understanding others because it simulates their actions onto one's own sensory-motor representations [1–5, 27, 30, 38, 39]. If the mirror system is indeed involved in “slipping into another's shoes,” then we may predict that individuals who are better at taking the perspective of other people should show stronger activation in their mirror areas (see [Supplemental Data](#) for example items from the different subscales). Here we report that people scoring high on perspective taking (PT) [11, 12] show stronger auditory mirror activations. Interestingly, correlations with PT not only included premotor areas but also extended into SI and SII [39–45], areas that appear to mirror the tactile experiences of others [39, 40]. This suggests that with increasing PT, individuals start to share the tactile consequences of heard actions in addition to their motor programs. The fact that there were no significant differences in performance between the two groups suggests that the differences in the mirror activations observed here are not simply reflections of attention to the task during scanning but that the excellent performance of all subjects in the task may have led to a ceiling effect potentially masking such differences. Given the limited number of subjects in our analysis (6 versus 6), such findings should be considered tentative, and they require replication in larger groups of subjects. In addition, the mechanisms through which higher PT scores lead to differences in brain activity remain to be investigated; both differences in the efficacy of the connection linking sensory and premotor structures and top-down processes such as selective attention to other individuals' actions could play important roles. Other subscales measuring interpersonal reactivity (empathic concern [EC], fantasizing [FS], and personal distress [PD] [11, 12]) did not correlate with mirror activations in our experiment. EC has

been shown to correlate with insular activation while subjects were aware of other people's pain [46, 47]. Different aspects of empathy thus could depend on different neural substrates [3, 4]. Interestingly, unusually low mirror activity has been observed in autistic subjects in both the premotor [48, 49] areas, found to correlate with PT in our study, and the insula [49], found to correlate with EC in other experiments.

Most of the sounds we have used in the current experiment result from events that are evolutionarily novel (e.g., opening a zipper, a can of soft drink, etc.). The mirror activations we demonstrate are therefore likely to reflect *learned* associations between novel actions and their sounds. Studies on pianists yield corroborating evidence for the effect of learning [8, 50]: Compared to novices, expert pianists show significantly stronger activations to the sound/sight of piano playing in their premotor cortex. Together, these data indicate that the mirror system is not restricted to genetically preprogrammed actions; rather, it is plastic and also responds to learned actions, in agreement with the idea that mirror neurons could result from hebbian learning [5].

Here we have considered areas to be truly mirror only if they respond more to action sounds than to environmental sounds that are equally recognizable (as determined by stimulus pretesting) and similarly complex. Furthermore, because our environmental sounds were also chosen by pretesting to be as easy to verbalize as our action sounds, subtracting the latter from the former should minimize the possibility that our results are due to verbalization. However, unlike our bilateral visual and motor activations, our auditory activations in BA44 were left lateralized. The finding that an auditory mirror system in humans is specialized to the left hemisphere is in agreement with previous TMS findings [7]. One might speculate that the left-lateralized spoken language may be linked to a left-lateralized multimodal mirror system that associates the sounds, in addition to the sight of actions with the motor programs required to produce these actions [1, 2, 6, 9, 36, 37, 51–53]. Indeed, evolutionarily, vocalization, which dates back to amphibians, is the oldest lateralized brain system [54]. It is possible that this initial lateralization for vocalization may have influenced the lateralization for the representations of the sounds of actions as well.

## Experimental Procedures

### Subjects and General Procedures

Sixteen healthy volunteers (14 right and two left handed; nine female and seven male; mean age = 31 years, range = 25–45 years) with normal or corrected-to-normal vision and normal hearing were tested. All subjects were informed about the content of the study, and all signed an informed-consent agreement. All experiments were approved by the Medical Ethical Commission (METc) of the University Medical Center Groningen (NL).

### Auditory Stimuli

Five categories of auditory stimuli were used, as shown in [Table S1](#). ActionSnds (referring to HandSnds and MouthSnds jointly) were recorded with an omnidirectional microphone (Earthworks TC30 K) placed at 1 m from the human executing the actions and digitized with an A/D preamplifier with phantom power supply (MindPrint AN/DI PRO) and a digital I/O sound card (RME Digi 96/8 PST). The ActionSnds were then processed with CoolEdit Pro. Because this study focuses on higher-order cortical areas, sounds were not



equated for loudness so that their ecological validity would be preserved. Unlike the action sounds that were recorded in house, EnvironmentalSounds were downloaded from the internet ([www.audiosparx.com](http://www.audiosparx.com)). The phase-scrambled sounds were obtained by application of a Fourier transform to each action sound, the phase spectrum was permuted for frequencies above 125 Hz, and the sounds were reconstructed with an inverse Fourier transform. These sounds were equal to the original action sounds in terms of their global frequency composition. All sounds are included as supplemental sounds 1–25 and were psychophysically tested on ten subjects not participating in the main study (see [Supplemental Data](#) for further details). They were presented with the program Presentation ([www.neuro-bs.com](http://www.neuro-bs.com)) and pneumatic headsets. Subjects wore earplugs to avoid potential hearing damage due to the loudness of the EPI sequences. Although the combination of pneumatic headphones and earplugs resulted in substantial drop off in the high frequency range (>5 kHz), pilot testing showed that subjects were able to recognize the sounds perfectly (well over 90%) during scanning and that the brain activity could be adequately triggered even with these frequency-attenuated stimuli.

#### Auditory Experimental Design and Scanning Sequences

We used a sparse block design [55]. A scan cycle (TR) was composed of twenty-five axial slices (4.5 mm thickness, 3.5 × 3.5 mm in plane resolution, 0.1 mm slice gap) collected in 1.5 s followed by silence lasting 4.1 s. We presented our 4 s stimuli during this period of silence. Stimuli were arranged in blocks of three consecutive sounds of the same category, with two TR without sounds between blocks. The silence condition was a block of three TRs without sound presentation. The experiment was split in four runs, with a total of 12 blocks for each category in pseudorandomized order. Subjects performed an odd-ball detection task throughout the scanning and performed at 98% on average (see [Supplemental Experimental Procedures](#)).

#### Motor Task

Subjects performed two runs of motor testing. In the hand motor run, participants watched a back-projected screen, which contained either a green or a red cross. During the red cross, subject were requested to stay immobile. When the cross turned to green, subjects had to extend their arms forward and grasp an object given to them by the experimenter. If the object was a peanut, they had to break it in two; if it was a sheet of paper, they had to rip it in two. Because the actions had to be done out of sight, the object was handed over to the subject in a predetermined position. Subjects then had to return to the resting position. The end of the action was recorded by the experimenter, who used a button box. The action lasted approximately 5 s, with eight repetitions of peanut breaking and eight repetitions of paper ripping in pseudorandomized order. Two actions were separated by  $10 \pm 2$  s of rest condition.

In the mouth motor run, the onsets of the green cross coincided with the lowering of a small object onto subjects' lips and signaled that they should start to manipulate it with their lips while keeping their jaws closed. Four seconds after the onset of the green cross, the red cross appeared and ordered them to stop the movement. A 4-s-on,  $10 \pm 2$ -s-off design was used with 16 repetitions. Again, subjects were unable to see the object being lowered onto their lips. The small object was a little red plastic dwarf, approximately 1 cm high, that was found in a Kinder-Surprise Egg and had no magnetic properties. Inspection of the EPI images during the mouth motor runs compared to the other runs, in which no object was present close to the subject's head, revealed that the presence of the object caused no measurable magnetic artifact.

Subjects were unable to hear the sound of their own actions (<80 dB) because of the approximately 120 dB of scanning noise, earplugs, and protective headphones.

#### Data Analysis, Preprocessing, and Visual Task

Data were preprocessed and analyzed with standard SPM2 ([www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)) random-effect procedures and the general linear model (GLM). See [Supplemental Experimental Procedures](#) for details.

#### Supplemental Data

Supplemental data include additional experimental procedures, eight tables, and six figures and are available online at <http://www.current-biology.com/cgi/content/full/16/18/1824/DC1/>.

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# Supplemental Data

S1

## Empathy and the Somatotopic Auditory Mirror System in Humans

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### Supplemental Experimental Procedures

#### Cytoarchitectonic Maps

The cytoarchitectonic maps of Amunts et al. ([http://www.fz-juelich.de/ime/ime\\_brain\\_mapping\\_eng](http://www.fz-juelich.de/ime/ime_brain_mapping_eng)), in their implementation as a toolbox for SPM2 by Eickhoff ([http://www.fz-juelich.de/ime/spm\\_anatomy\\_toolbox](http://www.fz-juelich.de/ime/spm_anatomy_toolbox)), have been used throughout the manuscript whenever we make reference to particular Brodmann areas (BA). A voxel was considered to belong to a particular area if its likelihood of belonging to that area was higher than that of belonging to any other area.

#### Selection of Auditory Stimuli

Five stimuli of each category were chosen based on results from psychophysical pretesting. Ten subjects not included in the fMRI study participated in the pretesting. These subjects were presented with 20 action sounds and were asked to describe and name the sounds verbally and to mime the sounds out if possible. Based on the outcome of that testing, the five best mouth and hand action sounds of each category were chosen based on the following criteria: ease of recognition/verbalization, bimanual involvement for hand actions (judged from whether subjects mimed the sounds with both hands; this ensured that lateralized brain activity could not be due to handedness alone), predominance of mouth for the mouth actions (i.e., we looked at how much people used their hands while they mimed the action), perceived transitivity (i.e., interaction with an object). Once these hand/mouth actions were selected, environmental sounds were chosen to match the actions based on pretesting of measures of ease of recognition/verbalization and the absence of perceived direct human actions. All sounds were also approximately matched on the shape of their envelopes by two independent observers. Note that the action sounds were selected to be object-directed because object-directed actions were found to be most effective in our primate studies. This resulted in many of the sounds including evolutionary novel actions (e.g., drinking with a straw). The fact that activations in the mirror system were found for these cultural actions illustrates the flexibility of the mirror system. All 16 subjects of the final study listened to all sounds before scanning, and this ensured that sounds were unambiguously attributed to the right category. All subjects were able to recognize all sounds with 100% accuracy before scanning. This score refers to recognizing individual sounds.

#### Phase-Scrambled Stimuli

The best control sounds would be identical in all physical aspects to the original action sounds but not recognized as action sounds. Because this is impossible, we resorted to phase scrambling to produce sounds that had the same frequency composition as the original sounds but that were unrecognizable as action sounds. In pretesting, we established that frequencies in the range of 0–125 Hz could be left unpermuted without rendering the sounds recognizable as action sounds. Preserving the original phase of higher frequencies, on the other hand, resulted in sounds being recognized as action sounds. All phase-scrambled sounds are thus the result of a reverse fourier transform in which frequencies up to 125 Hz preserve their original phase and all frequencies above 125 Hz had their phase exchanged with that of another frequency.

#### Auditory Task

Auditory stimuli were presented in blocks of three sounds of the same category. Occasionally (1–3 times per experiment) a sound of a different category “snuck” into a block, e.g., an EnvSnd in a block of MouthSnd. Subjects had to report such an intruder by pressing a button. The probability of intrusion was equal for all categories of sounds, except that a sound was never introduced in a block of silence and a scrambled mouth (hand) sound was never

introduced into a block of scrambled hand (mouth) sounds because subjects were not aware of the distinction between these scrambled categories or the fact that the noises were obtained by scrambling action sounds. Accuracy during scanning was calculated as (hits + correct rejections)/total number of blocks and was averaged at 98% ( $\pm 0.4\%$  SEM). Subjects were also asked not to verbalize sounds during the study, but the contrast of interest in the experiment (ActionSounds – EnvironmentalSounds) is unaffected by whether subjects verbalized or not because both ActionSounds and EnvironmentalSounds were equally able to be verbalized. Blocks containing intruders and blocks during which a button press occurred were excluded from the analysis so that motor contamination would be avoided.

#### Data Preprocessing

Data from the visual and motor, but not the auditory, sessions were slice-time corrected. Slice-time correction was not applied to the auditory data because in a sparse sampling design temporal resolution is less critical. EPI images from all sessions were aligned to the first volume of the auditory experiment. High-quality T1 images were coregistered to the mean EPI image and segmented. The coregistered gray-matter segment was normalized onto the MNI gray-matter template, and the resulting normalization parameters were applied to all EPI images. Smoothing with  $6 \times 6 \times 6$  mm FWHM was applied to all normalized EPI images (except for the subject-by-subject analyses in Figure S1C, where unsmoothed data were used). Data were then analyzed by application of a general linear model.

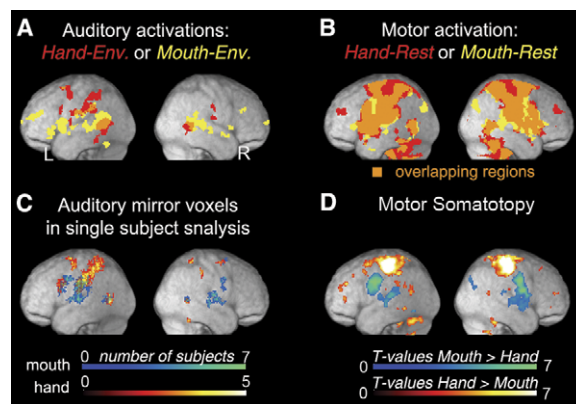


Figure S1. Core Results of the Auditory and Motor Sessions

Activations are rendered on the mean anatomical image of the 16 subjects with a transparency of 30 mm.

(A) Auditory activations in the indicated, color-coded contrasts (random-effect analysis,  $p < 0.005$  and  $k = 20$ ), with red showing hand-related voxels and yellow showing mouth-related voxels; orange voxels (and not simply the transparency between red and yellow, which could occur at a different depth in the brain) are common to both.

(B) Motor activations in the indicated contrasts conventions as in (A).

(C) HandMirrorVoxels and MouthMirrorVoxels as defined in the text. All these areas are significant even if a false-discovery-rate correction for multiple comparisons is used at  $p < 0.05$ .

(D) Single-subject data. The number of subjects showing mirror voxels in any given voxel is color coded, with warm colors standing for MouthMirrorVoxels and cold colors for HandMirrorVoxels. Green represents transparency between MouthMirrorVoxels and HandMirrorVoxels.

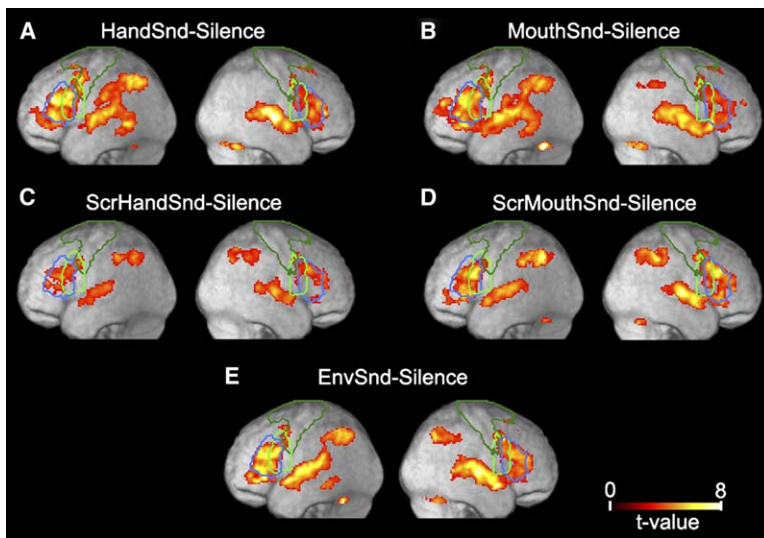


Figure S2. Results of the Auditory Experiment Contrasted against the Silence Conditions as Rendered on the Average Brain for the Five Experimental Conditions

The contours of BA6, BA44, and BA45 are shown in dark green, light green, and blue, respectively (30% limit in the cytoarchitectonic maps).

### General Linear Model

The EPI time series were then modeled via the general linear model with a box-car predictor for each condition convoluted with the hemodynamic response function via standard SPM2 procedures. This analysis resulted in a single parameter estimate (“ $\beta$ -weight”) for each condition and subject. These  $\beta$ -weights could then be

subtracted against each other to form contrast values. The EPI time series could be either voxel-by-voxel data via SPM2 or the mean signal of a set of voxels defined as region of interest (ROI) via the MarsBar tool for SPM (<http://marsbar.sourceforge.net>). The  $\beta$ /contrast values obtained for each subject were then analyzed at the second level with t tests to implement a random-effect analysis.

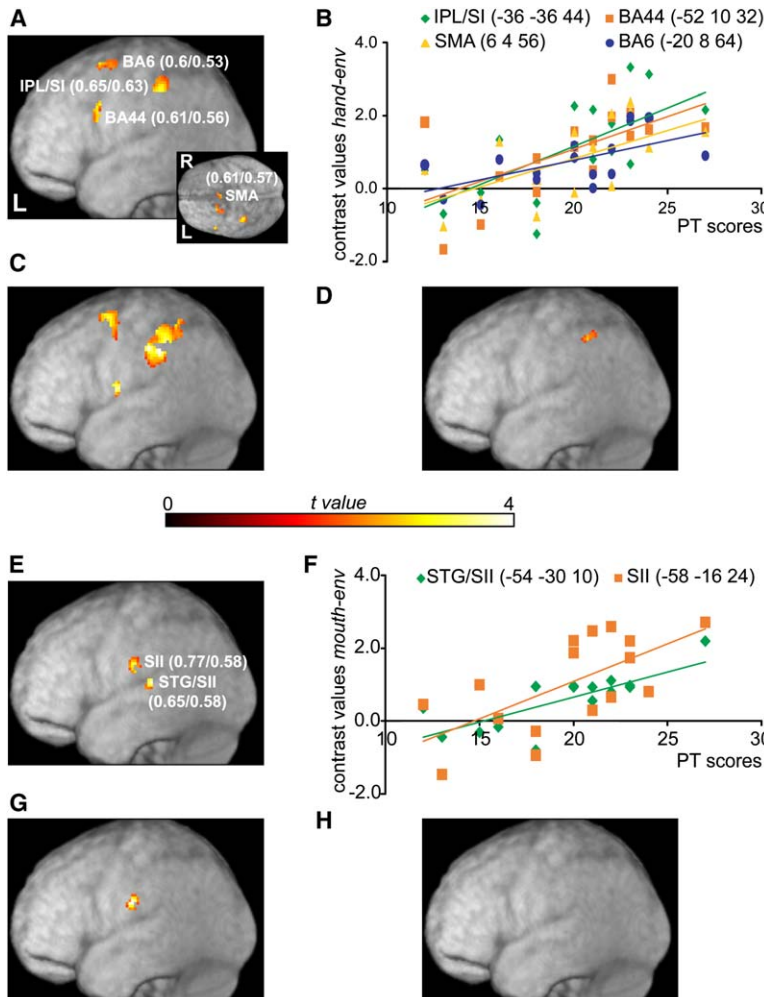


Figure S3. Correlation between Mirror Activity and Empathy

Only the left hemisphere is shown because the right hemisphere did not correlate with empathy in this data set.

(A) Correlation between PT and the contrast HandSnd – EnvSnd (masked with the HandMirrorVoxels of Figure 1A). Four clusters correlated significantly with PT, and for each of them in parenthesis, the r value is given for the peak/the whole cluster.

(B) Correlation plot of the contrast values as a function of PT for the four peak voxels.

(C–G) Same analysis for (C) HandSnd and (D) EnvSnd, both versus baseline. All correlations are thresholded at  $p < 0.05$  (uncorrected) and  $k = 20$  and masked with the HandMirrorVoxels. The same analysis is shown for MouthSnd – EnvSnd (E and F), MouthSnd (G), and EnvSnd (H), all masked with the MouthMirrorVoxels of Figure 1A.



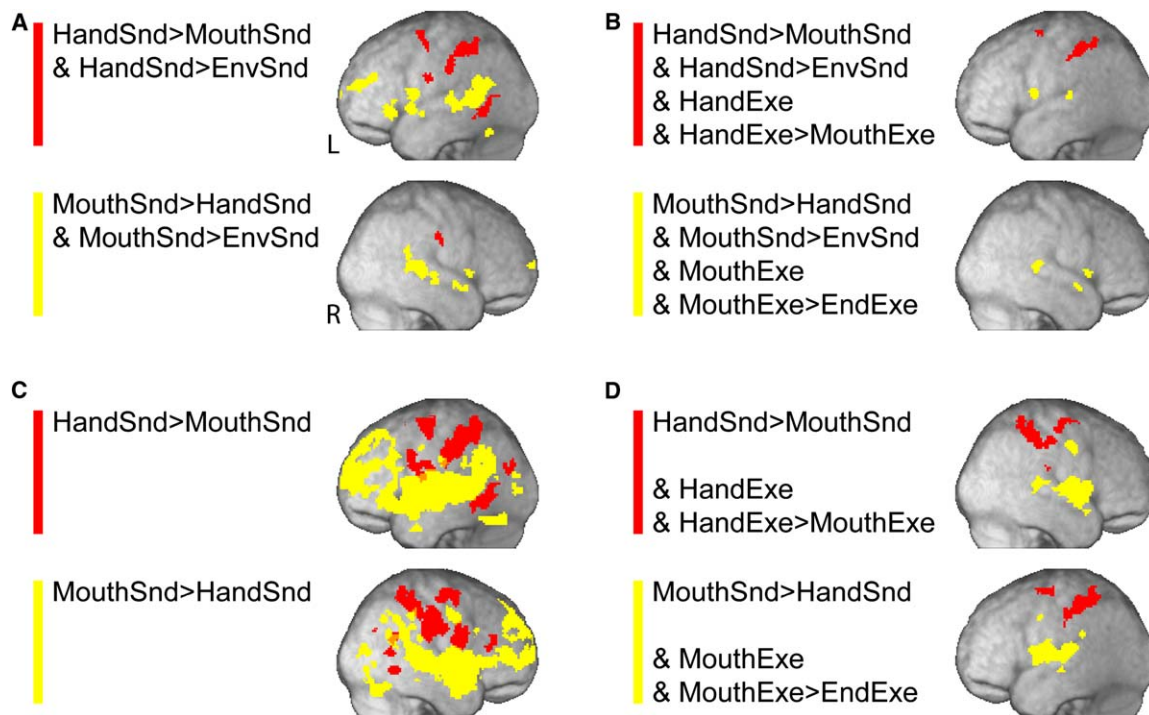


Figure S4. HandSelectiveVoxels and MouthSelectiveVoxels According to a Variety of Criteria as Indicated on the Left of Each Panel  
HandSelectiveVoxels are in red, and MouthSelectiveVoxels are in yellow. Contrasts are always indicated in the same order, with blank spaces for contrasts that are not included in a particular analysis.  
(A) Auditory somatotomy; the results of the motor execution day are ignored, but it is required that ActionSnd > EnvSnd.  
(B) Analysis as in Figure 2D for comparison.  
(C) Auditory somatotomy; both the motor execution and the EnvSnd are ignored.  
(D) Somatotomy including the motor data but not requiring ActionSnd > EnvSnd. The basic contrasts (HandSnd > EnvSnd and MouthExe > Rest) are at  $p < 0.005$ , the direct comparisons (HandSnd > MouthSnd, MouthSnd > HandSnd, HandExe > MouthExe, and MouthExe > HandExe) at  $p < 0.05$ , all uncorrected.

#### Analyses of Motor Data Alone

Data were analyzed with a general linear model considering a single predictor per run. Results were thresholded at  $p < 0.005$  at the second level. The relatively lenient threshold of  $p < 0.005$  was chosen at

this point because the masking used in later analysis results in a multiplication of the false positive rate of the contrasts involved and leads to an overall very conservative false positive. To compare hand and mouth movements for the analysis of somatotomy, we

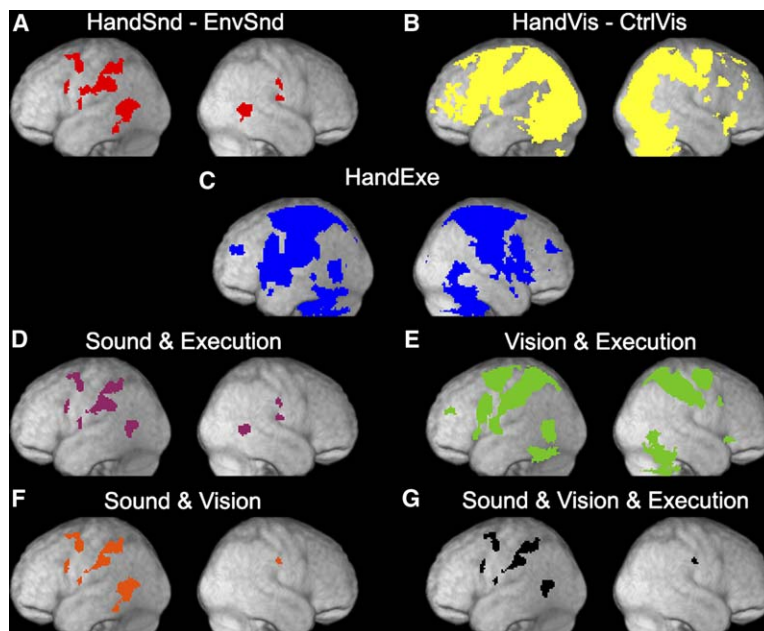


Figure S5. Multimodality of the Hand Mirror System

Results of the auditory (A), visual (B), and motor (C) experiments alone. All are at  $p < 0.005$  and  $k = 20$ . (D–F) pairwise conjunction of the data (with inclusive masking) and (G) conjunction of all three. In (D)–(F) the threshold of each individual contrast entering into the conjunction was kept at  $p < 0.005$ . The visual and motor systems are more bilateral than the auditory system. Note the similarity between the auditory mirror system (D) and the visual one (E) in the left hemisphere.

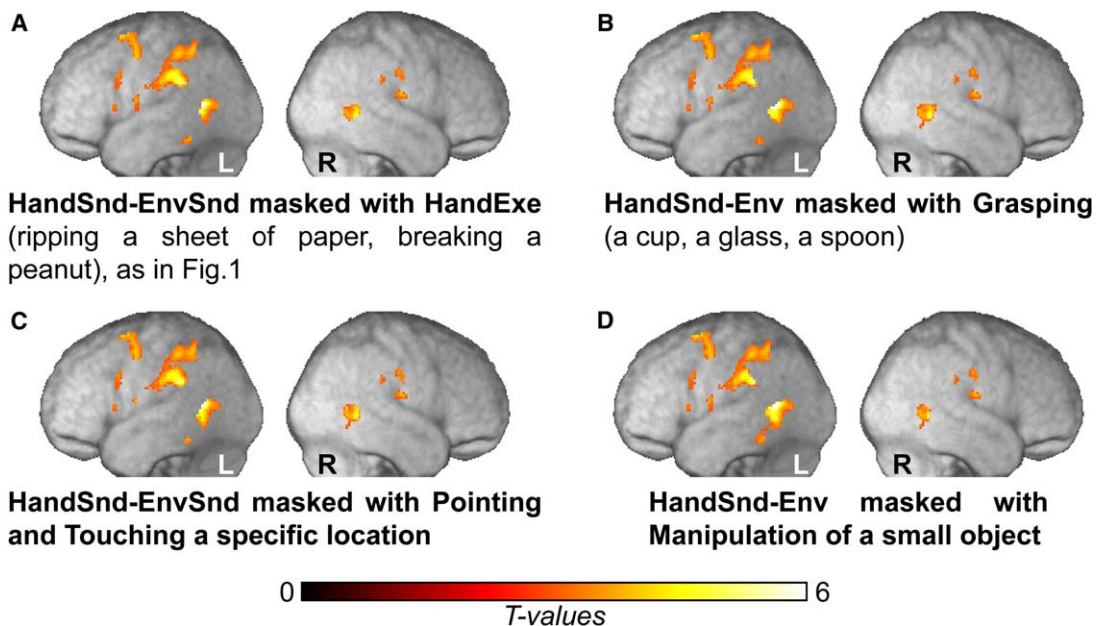


Figure S6. The Effect of the Motor Task on the Definition of the Auditory Mirror System

In all cases, the auditory contrast is the same, as described in the main text. What changes between the panels is the motor task used to define the HandExe – Rest contrast. The auditory contrast is then masked with the different motor tasks via a threshold of  $p < 0.005$ .

(A) Motor task as in Figure 1A.

(B) One of three objects had to be grasped from a plate, lifted, and replaced on the plate.

(C) Subjects had to extend their arm, touch a pre-specified location on a table, and return to the resting position.

(D) Subjects had to turn a little plastic object around and around between their fingers.

In (B–D), half the trials were performed with the right and half with the left hand. The parameter estimates from the two hands were then added together to form the contrast. The extent of the auditory mirror system is extremely similar in all four cases.

directly compared the contrast values of Hand-Rest and Mouth-Rest by using a two-sample, matched-pair *t* test at the second level.

#### Head Motion and Motor Execution

Inspection of the realignment parameters revealed that 13/16 subjects moved their heads by less than 1.5 mm along *x*, *y*, and *z* and

rotated by less than  $2^\circ$ . Of the remaining three subjects, only one had movements of more than a voxel, and these movements exceeded a voxel only in the *z*-direction. To exclude confounding effects of head motion on our data, we performed a full random-effect analysis of the motor runs both with and without head-motion parameters as covariates in the general linear model. Using a matched-pair *t* test, we compared the parameter estimates in each voxel for MouthExe (or HandExe) according to the GLM with and without motion parameters as covariates. We then masked the results of this test with the MouthMirrorVoxels (or HandMirrorVoxels) to check whether differences exist within the areas we report in this manuscript. Neither test revealed significant differences at our standard threshold ( $p < 0.005$ ,  $k = 20$ ) between these two alternative analyses, suggesting that head motion did not significantly influence our motor results. As a result, we only report motor results obtained without including head motion as covariates. Visual inspection revealed no consistent motion artifacts even at the single-subject level. The advantage of using random-effect analysis for motor mapping is the fact that motion artifacts that are inconsistent in location increase the residual error at the level of the single subject, but this residual error has no impact on the second level of analysis.

Table S1. Stimuli Used in the Auditory Experiment

Sound Category	Examples Used
Mouth action sounds (MouthSnd)	Crunching a candy with the teeth Kissing Gurgling Crunching potato chips Finishing a can of soft-drink with a straw
Hand action sounds (HandSnd)	Ripping a sheet of paper Unrolling an adhesive tape Opening a zipper Opening a soft-drink can Crushing a soft-drink can
Environmental sounds (EnvSnd)	Train passing by Howling wind Braking waves on the beach Electric discharge Water slowly dripping in a cave
Scrambled mouth action sounds (ScrMouthSnd)	Phase scrambled versions of all the MouthActionSounds
Scrambled hand action sounds (ScrHandSnd)	Phase scrambled versions of all the HandActionSounds
Silence	
All sounds can be found in the supplemental online sounds.	

#### Analyses of Auditory Data Alone

Data were analyzed with a general linear model with six predictors (HandSnd, MouthSnd, EnvSnd, ScrHandSnd, ScrMouthSnd, and Sil). All results were thresholded at  $p < 0.005$ .

#### Group Analyses of Mirror Activities

In the monkey, a mirror neuron is a neuron responding during the sound and the execution of a particular action. We thus defined HandMirrorVoxels as voxels at which HandSnd-EnvSnd was significant at  $p < 0.005$  and at which HandExe-Rest was significant at  $p < 0.005$ , resulting in a false-positive rate of  $0.005^2 = 0.000025$  (uncorrected for multiple comparison based on the global null hypothesis); we defined MouthMirrorVoxels as those for which MouthSnd-Env and MouthExe-Rest were both significant at  $p < 0.005$ , resulting

Table S2. Mirror Activity, Group Analysis

Hemisphere	Anatomical Description	K	p(unc.)	T	MNI (x,y,z)
<b>HandSnd – EnvSnd and HandExe – Rest<sup>a</sup></b>					
L	BA44	31	0.002	3.47	-52 10 32
L+R	BA6 (SMA)	341	0	6.11	0 -2 64
L	IPL/supramarginal/SII	326	0	5.28	-58 -40 26
L	SI/IPL	231	0	4.09	-38 -38 50
L	STS/MTG	190	0	6.29	-46 -58 8
L	insula/SII	29	0.001	3.8	-36 -4 12
R	STS/MTG	113	0	5.3	50 -50 0
R	SII	30	0.001	3.86	62 -12 16
R	SI	37	0.001	3.64	60 -16 34
<b>MouthSnd – EnvSnd and MouthExe – Rest<sup>a</sup></b>					
L	BA44	61	0	4.89	-54 8 6
L	BA6/SMA	24	0	4.3	-8 0 64
L	MTG/STS	61	0	4.89	-48 -60 8
L	SII	85	0.001	3.89	-54 -14 24
L	insula	59	0.001	3.8	-44 8 -4
L	STG	22	0.001	3.68	-56 -28 6
L	insula	20	0.002	3.48	-40 -8 2
R	STG/STS/MTG	155	0	4.8	60 -32 10
R	putamen	117	0	5.2	26 -6 14
R	ACC	59	0.001	3.91	0 28 22
R	insula	45	0	4.22	32 8 8

Mirror activity (group analysis), i.e., results of the auditory contrast HandSnd – EnvSnd masked with HandExe and MouthSnd – EnvSnd masked with MouthExe (all at  $p < 0.005$  and  $k = 20$ ) as shown by a random-effect analysis of  $n = 16$  subjects. For each cluster, from left to right, we describe: the hemisphere containing the cluster; the anatomical/cytoarchitectonic description of the cluster; the number ( $k$ ) of  $2 \times 2 \times 2$  mm voxels contained in the cluster; information regarding the peak voxel in the cluster, namely its uncorrected  $p$  and  $T$  value and its coordinates in the MNI space. Activations are first shown for the regions of interest for this paper (BA44/6, IPL, STS/MTG), then for the remaining brain.  $T$  refers to  $t$  value in the auditory condition.

<sup>a</sup> Both at  $p < 0.005$  and  $k = 20$ .

again in a false-positive rate of 0.000025. We used ImageCalc to perform the logical “AND” function between the two contrasts. Results are shown at a minimum cluster size of 20 to further avoid false positives. EnvSnd were always subtracted to eliminate voxels whose activity is not specific for action sounds and voxels whose activity could be due to verbalization of the sounds. The calculation of the overall false-positive rate of 0.005<sup>2</sup> is based on a global null hypothesis (i.e., the likelihood of finding a voxel if both the contrasts entering in the logical “AND” are non-significant) and is thus smaller than that of a conjunction searching for voxels where both are significant. On the other hand, if one assumes that the overall  $p = 0.005$  is overly conservative (see [S1] for a discussion of that issue). The true conjunction false positive is thus  $0.005^2 < p < 0.005$ . A logical “AND” was used instead of a traditional global null hypothesis as implemented in SPM to ensure that both contrasts involved were

Table S3. Results of the Contrasts HandSnd – EnvSnd and MouthSnd – EnvSnd

Hemisphere	Anatomical Description	k	p	T	MNI (x,y,z)
<b>HandSnd – EnvSnd</b>					
L	BA44	33	0.002	3.47	-52 10 32
L	BA6 SMA	387	0	6.11	0 -2 64
L	IPL/SI	264	0	4.09	-38 -38 50
L	supramarginal gyrus	423	0	5.28	-58 -40 26
L	MTG	610	0	7.64	-46 -56 8
R	SII	30	0.001	3.86	62 -12 16
R	SI	46	0.001	3.84	52 -12 28
R	MTG/STS	189	0	5.3	50 -50 0
<b>MouthSnd – EnvSnd</b>					
L	BA44	118	0	4.89	-54 8 6
L	BA44/45	110	0.001	3.9	-40 30 -4
L	BA6	43	0	5.45	-12 6 64
L	IPL	93	0.001	3.89	-54 -14 24
L	supramarginal	56	0.002	3.4	-54 -32 28
L	MTG/STS	1171	0	5.91	-60 -54 4
L	MFG	161	0.001	4.05	-24 48 20
L	insula	101	0.001	3.8	-44 8 -4
L	cerebellum	69	0	5.56	-36 -64 -26
L	thalamus	48	0	5.33	-10 -8 -4
L	insula/heschl	27	0.002	3.48	-40 -8 2
L	IFG p orbitalis	20	0	4.22	-32 26 -16
R	IFG p triang	26	0	4.83	30 30 28
R	MTG/STS	618	0	4.96	60 -32 8
R	ACC	342	0	5.26	0 28 18
R	putamen/pallidum	152	0	5.2	26 -6 14
R	insula	51	0.002	3.53	40 10 -12
R	insula	47	0	4.22	32 8 8
R	SMG	43	0	4.14	8 70 10
R	MCG	42	0.001	3.99	8 -14 36

$p < 0.005$ ,  $k = 20$ ; conventions are as in Table S2.

significant in their own right. Results were extremely similar, although somewhat more restrictive than had a global null conjunction been used [S1] as in the original distribution of SPM2 at 0.005<sup>2</sup>. All the mirror clusters obtained from the contrasts HandSnd-Env and HandExe as well as those of MouthSnd-Env and MouthExe survived an FDR correction at 0.05. This correction was applied via a technique resembling that suggested by Friston et al. [S1]: The motor contrast was corrected for multiple comparison via FDR within that inclusive mask of those voxels passing the auditory contrast at 0.005 uncorrected.

**Analyses of Mirror Somatotopy**

In the above analysis, a voxel could be both Mouth- and Hand-Mirror. To identify voxels that selectively responded more to a particular effector, we performed an additional analysis of somatotopy. To be a HandSelectiveMirror Voxel, a voxel had to be HandMirror

Table S4. Results of Motor Testing

Hemisphere	Anatomical Description	K	p(unc.)	T	MNI (x,y,z)
<b>HandExe – Rest</b>					
L+R	BA44/BA6/SMA/M1/S1/IPL/Cerebellum/Basal Ganglia	40433	0	23.7	-44 -30 52
L+R	MTG/STS	370	0	8.04	-56 -62 6
L	MFG	112	0	4.59	-30 52 26
R	BA44	606	0	7.43	54 14 -6
R	MFG	85	0	5.15	36 46 28
<b>MouthExe – Rest</b>					
L+R	BA44/6, SMA, M1, SI, IPL, Cerebellum, Basal Ganglia	35924	0	17.13	-54 2 30
L	MTG/STS	302	0	6.9	-54 -62 4

Conventions as in Table S2.  $p < 0.005$ ,  $k = 20$ .

Table S5. Mirror Activity in the Subject-by-Subject Analysis

Hemisphere	Anatomical Description	k	N	MNI (x,y,z)
<b>HandSnd – EnvSnd and HandExe – Rest<sup>a</sup></b>				
L	IPL/SI/SII	896	6	-54 -32 42
L	BA6	157	6	-22 -12 54
L	BA44	107	4	-50 14 34
L	MTG	85	6	-52 -66 6
L	parietal operculum/SII	41	4	-54 -22 20
R	SI	30	5	42 -32 46
R	SI	26	5	34 -46 66
R	SFG	26	4	28 0 64
R	MTG	22	7	54 -54 2
R	cerebellum (VI)	22	5	34 -52 -28
<b>MouthSnd – EnvSnd and MouthExe – Rest<sup>a</sup></b>				
L	parietal operculum/SII	458	5	-58 -24 24
R	parietal operculum/SII	232	4	56 -14 12
R	BA6	168	5	6 4 58
L	BA6	95	4	-52 0 38
L	supramarginal	81	3	-48 -32 26
R	BA6	69	3	56 0 36
L	MTG	61	3	-50 -58 10
L	BA44	45	4	-60 6 22

For each single subject, we determined voxels where HandSnd – EnvSnd masked with HandExe or where MouthSnd – EnvSnd masked with MouthExe was significant. We then analyzed for each voxel of the brain how many of the individual subjects satisfied the criteria. Clusters of at least 20 voxels where at least two subjects satisfied the criteria are shown below. For each cluster we indicate the anatomical location and size (k) in voxels. In addition, we determined a peak overlap as the voxel showing most individuals satisfying the criteria. For this peak, we indicate the number (N) of subjects and the MNI location. Given that N is an integer numbers, many voxels within a cluster often have the same peak value, and coordinates of the peak closest to the center of mass of the cluster are indicated.

<sup>a</sup> Two or more subjects, k = 20.

(see above, false-positive rate = 0.005<sup>2</sup>) and additionally had to respond more to the hand during execution and sound, as ensured by the requirement that HandSnd-MouthSnd be significant at  $p < 0.05$  and HandExe-MouthExe at  $p < 0.05$  (both uncorrected for multiple comparison). In other words, we searched for congruent auditory and motor somatotopy within a mask of mirror areas as defined above. The total false-positive rate is difficult to estimate for this analysis because HandSnd and HandExe (for the hand) were taken into account more than once in this procedure, leading to tests that were not fully, but it remains less than 0.005<sup>2</sup> according to a global null hypothesis. We further analyzed all clusters of Hand- and

Mouth-SelectiveMirror Voxels by performing a ROI GLM for these regions in all conditions (auditory, visual, and motor). This analysis is only illustrative for the contrasts involved in the definition of the ROI itself (because they are significant by definition) but is informative for the other conditions. Results for only three of the ROIs are shown in Figure 2 for lack of space.

#### Analysis of Correlation with Empathy

Empathy scores were collected with the questionnaire of Davis [S2, S3]. At enrolment, subjects received the questionnaire as a Microsoft Excel sheet to be filled out on their own computer at home. Subjects then sent the sheet back to the experimenters, who analyzed it to provide scores for the subscales PT, EC, FS, PD. The 16 contrast images of the contrast HandSnd-EnvSnd (one per subject) were then analyzed with a simple regression model in which the four subscales were used separately. Results were masked with the HandMirror-Voxels to identify HandMirrorVoxels correlating with the empathy subscales and were examined at  $p < 0.05$  and  $k = 20$ . For each cluster, the data from the peak voxel were then analyzed and displayed in Figure S3, and the correlation value was calculated at the peak. Correlation was also calculated after the parameters for each subject were estimated from the mean BOLD signal within the entire cluster via MarsBar. The analysis was then repeated with the Hand-ActionSounds and EnvironmentalSounds parameter estimates that had entered into the contrast. The same logic was applied to Mouth-MirrorVoxels, where MouthSnd-EnvSnd was correlated against the four subscales.

#### fMRI Parameters

Scanning was performed with a Philips Intera 3T Quaser and a synergy SENSE head coil and 30 mT/m gradients. The scanning parameters for the auditory experiment differed from those used in the motor and visual experiments. The former are detailed above. For the motor and visual experiments, standard single-shot EPI with echo time = 30 ms, acquisition time (TA) = repetition time (TR) = 2 s, 39 axial slices of 3 mm thickness, with no slice gap and a 3 × 3 mm in plane resolution, were acquired to cover the entire brain and cerebellum; a SENSE factor of 2.1 was used.

#### Basic Activations

##### Auditory Activations

Figure S1A illustrates the results of the contrasts HandSnd – EnvSnd and MouthSnd – EnvSnd via random-effect analyses ( $p < 0.005$ ,  $n = 16$  subjects). These contrasts revealed that the ActionSnd (i.e., HandSnd or MouthSnd) selectively activate a circuit composed of bilateral mid-temporal gyri (MTG), left inferior parietal lobule (IPL), and left premotor cortices (BA44 and BA6). In addition, the contrasts revealed activation in a number of smaller clusters, which can be found in Table S3.

As in monkeys (C.K., unpublished data), the parietal and premotor areas were also activated (albeit less) by sounds not relating to actions (ScrHandSnd, ScrMouthSnd, and EnvSnd, see Figures S2C–S2E).

Table S6. ■ ■ ■

Hemisphere	Description	k	t	$p_{unc.}$	$p_{fdr}$	r	$P_r$	MNI (x,y,z)
<b>(HandSnd-EnvSnd)<sub>highPT</sub> – (HandSnd-EnvSnd)<sub>lowPT</sub> Masked with Hand Mirror System from Figure 1A<sup>a</sup></b>								
L	BA6	14	4.37	0.001	0.049	0.58	0.009	-50 8 26
L	BA44	29	4.17	0.001	0.049	0.51	0.021	-18 6 64
L	SII	38	4.15	0.001	0.049	0.61	0.006	-36 -36 48
R	SI	11	4.38	0.001	0.049	0.56	0.013	62 -12 16
<b>(MouthSnd-EnvSnd)<sub>highPT</sub> – (MouthSnd-EnvSnd)<sub>lowPT</sub> masked with mouth mirror system from Fig.1A<sup>a</sup></b>								
L	SII	14	4.44	0.001	0.109	0.59	0.008	-56 -18 18

Clusters showing larger contrast values in the high-PT ( $n = 6$ ) compared to the low-PT ( $n = 6$ ) group, during examination of the HandSnd – EnvSnd (top) and MouthSnd – Env (bottom) contrasts via a two-sample t test ( $p < 0.005$ ,  $df = 10$ ). The results were masked with the mirror areas as defined in Figure 1A. Uncorrected and FDR-corrected p values are given for the peak voxel. In addition, the correlation (r) and associated p value ( $p_r$ ) between PT scores and the parameter estimate of the contrast HandSnd – EnvSnd (top) and MouthSnd – Env (bottom) are indicated, with all 16 subjects at the peak voxel coordinates of the group difference coordinates taken into consideration.

<sup>a</sup>  $p < 0.005$ ,  $k = 10$ .



Table S7. Results of the Correlation of the Individual Contrast Values for Hand, or Mouth, Snd – EnvSnd with the PT scores, masked with the Hand, or Mouth, MirrorVoxels

Hemisphere	Anatomical Description	K	p(unc.)	T	MNI (x,y,z)
HandSnd – Env Correlated with PT <sup>a</sup> in HandMirrorVoxels, i.e., HandSnd – EnvSnd and HandExe – Rest <sup>b</sup>					
L	IPL/SI	108	0.003	3.2	-36 -36 44
L	BA44	29	0.005	2.9	-52 10 32
L	BA6	61	0.007	2.8	-20 8 64
R	BA6 (SMA)	31	0.006	2.87	6 4 56
MouthSnd – Env Correlated with PT <sup>a</sup> in MouthMirrorVoxels, i.e., MouthSnd – EnvSnd and MouthExe – Rest <sup>b</sup>					
L	STG/SII	21	0	4.49	-54 -30 10
L	STG/Parietal Operculum/SII	40	0.003	3.24	-58 -16 24

Conventions as in Table S2.

<sup>a</sup>p < 0.05.

<sup>b</sup>p < 0.005, k = 20.

### Motor Activations

Figure S1B and Table S4 illustrate the findings from the motor day. Both the execution of hand actions and that of mouth actions caused strong activations in bilateral premotor (BA44/BA6), primary motor, somatosensory (primary and secondary), and posterior parietal areas. The motor results indicated a somatotopic organization of the premotor, motor, and somatosensory areas, with stronger activations for HandExe in dorsal and for MouthExe in ventral regions (Figure S1D).

Also the MTG/STS was bilaterally activated during the execution of actions. This activation occurred although subjects were prevented from seeing and hearing their own actions. Activation of structures classically considered to be sensory during motor execution is a finding encountered by a growing number of studies, including activations in V5/MT during toe and finger movements [S4], activations of the extrastriate body area during motor acts [S5], and activations of the MTG during finger movements [S6].

### Single-Subject Analysis of Mirror Property

To ensure that this finding is not a result of smoothing data and using group analyses, a similar analysis was performed in each single subject. For each subject separately, a traditional fixed-effect SPM2 analysis was performed with the GLM but without the data being smoothed. Based on this single-subject analysis, the same definitions were applied as for the group (i.e., HandMirrorVoxels = HandActionSounds – Environment, significant at p < 0.005; HandExecution-Rest significant at p < 0.005; idem for Mouth). When a logical “AND” was used in ImageCalc, this resulted in a separate three-dimensional maps for HandMirror and MouthMirror, where voxels contained the value 1 if mirror and 0 if not. Arithmetic addition of the 16 maps (one per subject) for Hand and Mouth separately led

to maps in which values could range from 0 (none of the subjects showed mirror activity) to 16 (all subjects did so). The maps were thresholded by the requirements that at least two subjects needed to show mirror activity (leading to an overall false-positive rate of p < 10<sup>-7</sup> according to the binomial distribution and a global null hypothesis) and that clusters needed to contain at least 20 voxels (Figure S1C and Table S5). As one can see by comparing these results with Figure 1A and Table S2, this analysis revealed a circuit very similar to that of the group analysis; this circuit was again composed of bilateral MTG, left IPL, and left premotor cortex. Differences between Figure 1A and Figure S1D reflect the fact that the group analysis emphasizes regions that are consistent between subjects, even if they are only weakly activated, whereas the subject-by-subject analysis emphasizes strong activations, even if they are present only in two subjects.

### The Mirror System in High- and Low-PT individuals

In addition to the perspective-taking scale (e.g., “I sometimes try to understand my friends better by imagining how things look from their perspective”; “I believe that there are two sides to every question and try to look at them both”; “When I’m upset at someone, I usually try to ‘put myself in his shoes’ for a while”), the IRI is composed of three other scales. Empathic concern (EC) measures the degree to which one’s feelings are affected by seeing the distress of others (“I often have tender, concerned feelings for people less fortunate than me”) (italics were not in the original questionnaire but are used here to underline the emotional/feeling aspect of this scale). The emphasis on feelings in the questions is in accord with the observation that this subscale relates more to a shared circuit in the domain of pain [S7, S8], one of the most intense feelings. Fantasy (FS) measures the degree to which a reader gets involved with characters in novels

Table S8. Congruent Somatotopic Organization of the Mirror System

Hemisphere	Anatomical Description	K	p(unc.)	T	MNI (x,y,z)
HandSnd > MouthSnd <sup>a</sup> , HandExe > MouthExe <sup>a</sup> , HandSnd – EnvSnd <sup>b</sup> , and HandExe – Rest <sup>c</sup>					
L	BA6	18	0.005	2.99	-22 -4 66
L	IPL/SI	156	0.001	3.56	-36 -38 48
L	IPL/SI	16	0.005	2.9	-46 -28 40
MouthSnd > HandSnd <sup>a</sup> , MouthExe > HandExe <sup>a</sup> , MouthSnd – EnvSnd <sup>b</sup> , and MouthExe – Rest <sup>c</sup>					
L	BA44	26	0.003	3.25	-56 6 8
L	STG/parietal operculum/SII	21	0.001	3.68	-58 -28 10
R	STG/MTG	45	0.002	3.53	58 -32 10
R	Insula	22	0	4.46	34 2 -10
R	Pallidum	64	0.001	4	22 -4 8
R	Insula	34	0.005	2.94	34 10 8

Conventions are as in Table S2. T refers to t value in the HandSnd – MouthSnd or the MouthSnd – HandSnd contrast.

<sup>a</sup>p < 0.05.

<sup>b</sup>p < 0.005.

<sup>c</sup>p < 0.005, k = 5.

("I really get involved with the feelings of the characters in a novel"). Personal distress (PD) measures the emotional tumult of subjects in situations where they witness the distress of others. ("In emergency situations, I feel apprehensive and ill-at-ease").

Using a simple regression model, we correlated the individual contrast values for HandSnd – EnvSnd with PT scores and masked the results with the HandMirrorVoxels (i.e., HandSnd – EnvSnd and HandExe – Rest, significant at  $p < 0.005$  as in Figure 1A). Figure S3A and Table S7 show the result of this analysis with  $p < 0.05$  (uncorrected) and  $k = 20$ . Four clusters of mirror voxels demonstrate significant correlations with PT, most of them in the left hemisphere. They were located in the left BA44, BA6, and the IPL extending rostrally into SI and in the right SMA. Subjects showing stronger activity in these mirror areas thus also report engaging in more perspective taking (Figure S3B). This correlation could be due either to the brain activity during HandSnd being positively correlated with PT or to the EnvSnd being negatively correlated with PT. Repeating the correlation analysis with HandSnd and EnvSnd separately demonstrates that the correlation was due to HandSnd (Figure S3C) not EnvSnd (Figure S3D). Significant negative correlations with PT were not observed in the mirror system. Correlating of HandActionSounds with the scales FS, EC, and PD did not reveal any significant correlation at the same threshold (not shown).

A similar analysis was applied for the MouthMirrorVoxels (Figures S3E and S3F and Table S7). The correlation between MouthSnds – Env and PT revealed two significant clusters: one localized in the parietal operculum (functional area SII) and a second, smaller cluster located within the sylvian fissure and encompassing both the STG and the parietal operculum. Again, this correlation was not due to the subtraction of EnvSnd because a similar pattern was observed in the correlation with MouthSnd alone (Figure S3G). None of the other subscales demonstrated any significant correlations with MouthSnd – Env.

With 16 subjects, the power of a correlation analysis is relatively low and would not survive corrections for multiple comparisons. To explore this problem, we used alternative methods in the main text. The group was split into low- and high-PT subgroups, a paired  $t$  test identified regions of peak difference among the 12 subjects showing high and low PT (excluding the intermediate 4), and the correlation over all 16 subjects was then calculated at the voxels of peak difference. Results are reported in Table S6.

Overall, the relationship between PT and mirror activity will require replication and investigation with larger groups of subjects, and the current results should be considered tentative.

Our correlations and high-low differences are found in the left hemisphere. Given that the results of the correlation analysis and high-low comparison were masked with the results of the basic mirror activations, which in turn were confined to the left hemisphere, this result is not surprising. Interestingly, Dapretto et al. [S9] found correlations between the ADOS and ADI scores and activations in the right hemisphere in a task where subjects viewed and imitated facial expressions. This difference in lateralization could reflect a difference in lateralization between viewing and hearing actions, as demonstrated in the present data, and/or between hand actions and facial expressions. Indeed, the processing of emotional facial expressions has been associated in particular with the right hemisphere [S10].

#### Additional Analysis of Somatotopy

Criteria for demonstrating somatotopy vary in the literature. For the main paper, we used a very stringent definition that requires effector selectivity both during listening (e.g., HandSnd > MouthSnd) and execution (HandExe > MouthExe), and we also required the auditory responses to be action selective (HandSnd > EnvSnd) and the voxels to be involved in the execution of the preferred action (HandExe > Rest). Here we explored alternative criteria.

Up until now, none of the experiments had used an action execution condition to define somatotopy. Without taking action execution into consideration, Figure S4A illustrates the results of requiring HandSnd > MouthSnd ( $p < 0.05$ ) and HandSnd > EnvSnd ( $p < 0.005$ ) only. This definition resulted in much more extensive somatotopy compared to our more stringent analysis (shown in Figure S4B and Table S8).

Somatotopy may also be defined without requiring ActionSnd > EnvSnd. Figure S4C shows the results of this analysis without consideration of the motor data, and Figure S4D shows the results with consideration of these data. Both analyses reveal somatotopical arrangements to be more bilateral and extensive than our original definition (Figure S4B).

What is common to all analyses though is that regardless of the definition used, some areas of the mirror circuit demonstrate the capacity to differentiate between hand and mouth action sounds. Two of the analyses (Fig. S4B,D) also demonstrate that regions exist that have the same preference during action listening and execution. This common message is essential, as it demonstrates that the auditory mirror system could provide information in the brain of the listener about what type of actions (Hand vs. Mouth) the other individual is performing. Although using the most stringent of the analysis (Fig. S4B) may underestimate the spatial extent of congruent selectivity, we believe it to provide the most convincing proof of congruent selectivity in the human auditory mirror system.

#### The Visual Experiment

##### Visual Stimuli

Twelve movies (six with the hand entering from the left and six with it entering from the right) of six different manipulations of colored wooden blocks (Visual Hand Action – HandVis) were contrasted against control movies of the same durations in which the same hand moved to rest on the table (Visual Control Movement – CtrlVis). These control stimuli contain movements, but these movements are not directed at an object. The visual experiment included other control conditions, such as a fixation cross and clips of a stationary hand behind objects, but these additional controls led to results resembling those obtained with the CtrlVis, and will thus not be reported here.

##### Visual Experimental Design

All conditions were presented in a block design, with four examples of each condition picked out at random to form 13 s blocks containing four different actions or four different movements. Consecutive blocks were separated by a 10 s pause of blank screen with a fixation cross. The experiment was split into four runs with a total of 12 repetitions per condition. Half of the blocks depicted only hands entering from the right of the screen, and half depicted only hands entering from the left of the screen. Subjects were instructed to watch the movies carefully and to pay particular attention to "what the hands were doing." These data were acquired prior to the auditory experiment and the action execution to ensure that the other experiments would not bias the results of the visual experiment. Note that the actions used in this experiment are not directly equivalent to those used in the auditory main experiment because they involved only the hand, and not the hand and mouth, and because the grasping actions involved here are not characterized by salient sounds, whereas those in the auditory experiment are. These differences make it unlikely that visual responses in the ROI's of Figure 2 and overlaps with visual responses in Figure 1D are due to auditory associations with the movies. Movies were recorded with a digital video camera, elaborated with AdobePremiere ([www.adobe.com](http://www.adobe.com)), presented with Presentation ([www.neuro-bs.com](http://www.neuro-bs.com)), projected with an LCD projector on a semi-opaque screen placed at the head end of the bore, and seen through a mirror placed on the head coil. The visual experiment contained additional conditions that are irrelevant to the present paper.

##### Overlap between Visual, Auditory, and Motor Activations for Hand Actions

Figures S5D–S5G illustrate the overlaps between the different combinations of visual, auditory, and motor activations and hand actions.

##### Overlaps with Other Motor Tasks

For HandExe, we used actions that matched as closely as possible the actions subjects had to listen to during the auditory day. This may have led to the automatic generation of the sounds normally associated with these actions in the mind of the subjects. To avoid this confound, we also tested subjects in three additional motor tasks that involved hand actions but were not associated with strong sounds. In the "manipulation" run, subjects had to manipulate a little object unknown to them with their fingers out of their line of sight. Periods of manipulation (4 s) were alternated with periods of rest

( $10 \pm 2$  s). In the “point” task, subjects had a T-shaped plate on their lap and were instructed by a visual stimulus to go and touch with their hand the corresponding location of the T-shaped table, then return to the resting position (5 s on,  $10 \pm 2$  s off design). In the “grasp” task, subjects had to grasp an object located on that T-shaped plate, lift it up, and replace it on the plate (5 s on,  $10 \pm 2$  s off design). All three tasks had slightly different cognitive requirements, but none had strong sound associations. Figure S6 illustrates the results of masking the HandSnd – EnvSnd with our original task (Figure S6A) and with these three alternative tasks (Figures S6C and S6D). As can be seen, results are extremely similar; the same basic circuitry of BA6/44, parietal, and MTG activations is seen. This indicates that imagination of sounds associated with the HandExe were not critical for determining overlaps between motor execution and action listening.

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