Report

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

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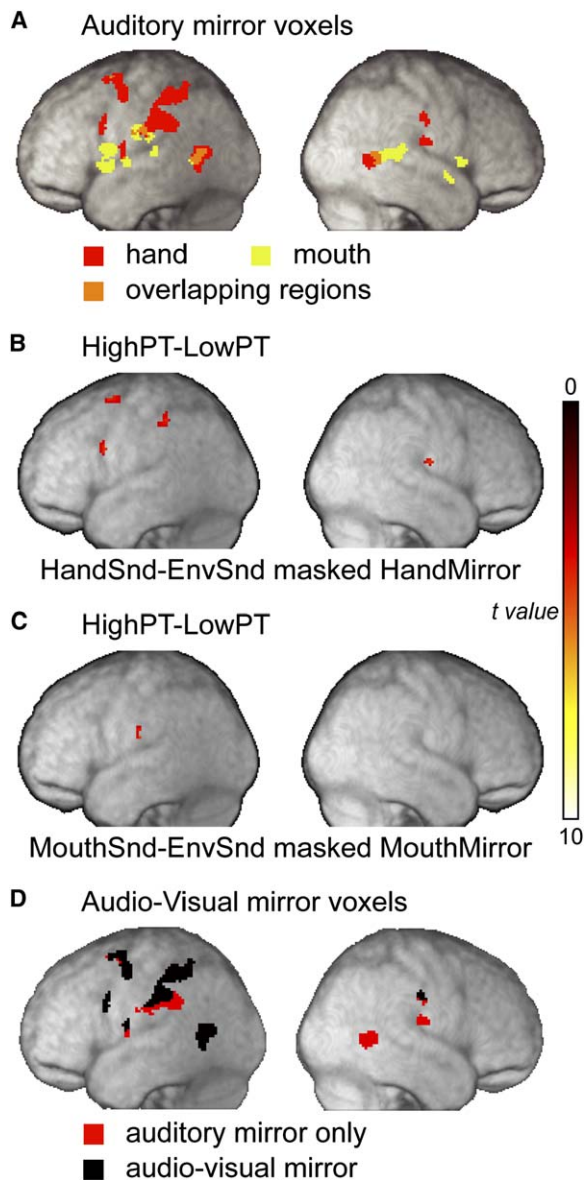
Figure 1. Voxels Significantly Activated by Audition of Actions of the Specific Effector and Execution of Similar Actions with the Same Effector

(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
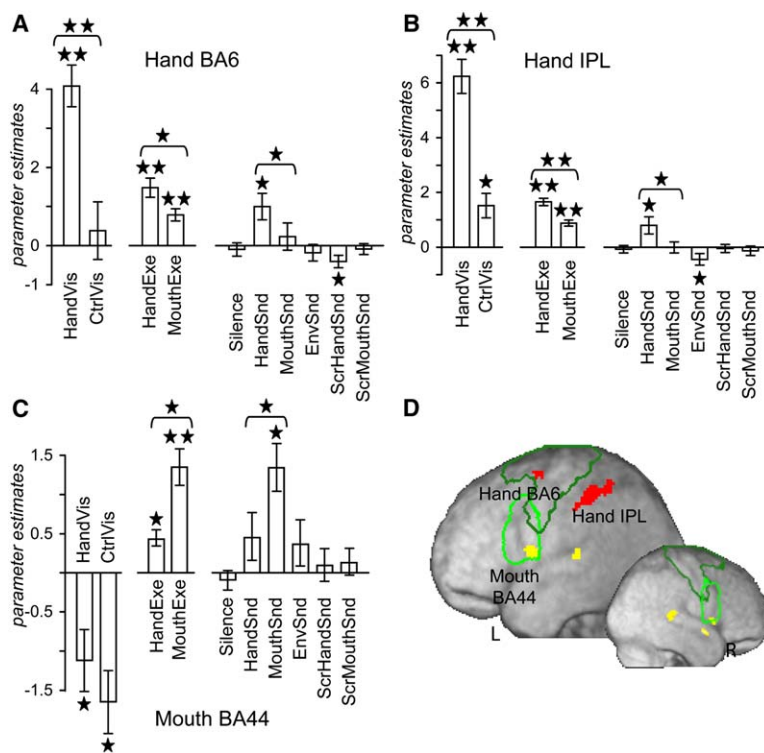
Figure 2. Somatotopy

(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 probalistic 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). The phase-scrambled sounds were obtained by application of a Fourier transform to each action sound, the phase spectrum was permutated 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) 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 ± 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 ± 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) random-effect procedures and the general linear model (GLM). See Supplemental Experimental Procedures for details.

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