Attention to Visual Speech Gestures Enhances Hemodynamic Activity in the Left Planum Temporale

Johanna Pekkola,^{1–3*} Ville Ojanen,^{1,3} Taina Autti,² Iiro P. Jääskeläinen,^{1,3,4}
 Riikka Möttönen,^{1,3} and Mikko Sams^{1,3}

¹Laboratory of Computational Engineering, Helsinki University of Technology, Espoo, Finland

²Helsinki Medical Imaging Center, Helsinki University Central Hospital, Helsinki, Finland

³Advanced Magnetic Imaging Centre, Helsinki University of Technology, Espoo, Finland

⁴Massachusetts General Hospital – Massachusetts Institute of Technology – Harvard Medical School, Athinoula A. Martinos Center for Biomedical Imaging, Charlestown, Massachusetts

Abstract: Observing a speaker's articulatory gestures can contribute considerably to auditory speech perception. At the level of neural events, seen articulatory gestures can modify auditory cortex responses to speech sounds and modulate auditory cortex activity also in the absence of heard speech. However, possible effects of attention on this modulation have remained unclear. To investigate the effect of attention on visual speech-induced auditory cortex activity, we scanned 10 healthy volunteers with functional magnetic resonance imaging (fMRI) at 3 T during simultaneous presentation of visual speech gestures and moving geometrical forms, with the instruction to either focus on or ignore the seen articulations. Secondary auditory cortex areas in the bilateral posterior superior temporal gyrus and planum temporale were active both when the articulatory gestures were ignored and when they were attended to. However, attention to visual speech gestures enhanced activity in the left planum temporale compared to the situation when the subjects saw identical stimuli but engaged in a nonspeech motion discrimination task. These findings suggest that attention to visually perceived speech gestures modulates auditory cortex function and that this modulation takes place at a hierarchically relatively early processing level. *Hum Brain Mapp* 27:471–477, 2006. © 2006 Wiley-Liss, Inc.

Key words: speech perception; attention; audiovisual; crossmodal; auditory cortex; planum temporale

INTRODUCTION

Speech is a unique stimulus with tightly linked auditory and visual components (heard speech sounds and seen articulatory gestures), the association between which strengthens during speech learning in early infancy. Possibly due to this overlearned association, seeing articulations can facilitate auditory speech perception in noisy conditions [Sumby and Pollack, 1954] and even change the auditory percept when the auditory and visual speech components are conflicting, as exemplified by the McGurk effect [McGurk and MacDonald, 1976]. Informing about possible neural events underlying these behavioral phenomena, seen articulations modify electric and magnetic auditory cortex evoked responses to speech sounds [Besle et al., 2004; Klucharev et al.,

Contract grant sponsor: Academy of Finland; Contract grant numbers: 206368; Contract grant sponsor: National Institutes of Health; Contract grant number: NIH-RO1 HD040712; Contract grant sponsor: Kordelin Foundation.

*Correspondence to: Dr. Johanna Pekkola, Helsinki University Central Hospital, Department of Radiology, POB 340, FIN-00029 HUS, Finland. E-mail: johanna.pekkola@finnet.fi

Received for publication 14 April 2005; Accepted 27 June 2005

DOI: 10.1002/hbm.20190

Published online 13 September 2005 in Wiley InterScience (www.interscience.wiley.com).

Figure 1.

Representative frames of four of the 16 different stimuli.

2003; Möttönen et al., 2002, 2004; Sams et al., 1991; Van Wassenhove et al., 2005]. Furthermore, seen articulations elicit hemodynamic responses in the auditory cortex also in the absence of heard speech [Bernstein et al., 2002; Calvert et al., 1997; Campbell et al., 2001; MacSweeney et al., 2000; Paulesu et al., 2003; Pekkola et al., 2005]. Recent evidence suggests that such modulation takes place even in the primary auditory cortex [Calvert et al., 1997; Pekkola et al., 2005] and is specific to the linguistic content of seen articulations [Calvert et al., 1997; Campbell et al., 2001; Pekkola et al., 2005].

Whether attention affects the auditory cortex activation by visual speech gestures has remained unexplored, since in all previous neuroimaging studies on seeing articulatory gestures the subjects have been closely attending to the visual speech stimuli. However, facilitation of the McGurk effect by attending to the visual component of audiovisual speech [Tiippana et al., 2004] suggests that voluntary attention plays a role in modulating auditory cortex function during visual speech perception.

The effects of attention on auditory cortex activity have been more widely studied in the auditory modality. Several functional studies have shown that selective attention to acoustic stimuli enhances activity within the sensory-specific auditory cortex [Alho et al., 1999; Grady et al., 1997; Hashimoto et al., 2000; Jäncke et al., 1999; Lipschutz et al., 2002; O'Leary et al., 1996; Pugh et al., 1996]. These effects have mostly emerged within the secondary auditory cortex (BA 42/22) [Grady et al., 1997; Hashimoto et al., 2000; Lipschutz et al., 2002; O'Leary et al., 1996; Pugh et al., 1996; Rinne et al., 2005], although evidence suggesting attention-driven modulation even at the level of the primary auditory cortex (BA 41, auditory koniocortex) also exists [Alho et al., 1999; Jäncke et al., 1999; Woldorff et al., 1993]. However, to our knowledge, no previous studies specifically address the effect of attention on auditory cortex activity during visual speech perception.

The current functional magnetic resonance imaging (fMRI) study asks whether selective attention to visual speech can modulate human auditory cortex activity and aims to probe the hierarchical level at which such modulation would emerge. We used identical visual stimuli (videos of a face that silently articulates vowels, with moving circles superimposed on the mouth of that face) during two active

conditions (attend to vowels and attend to circles) and studied possible between-conditions activation differences at both the group- and individual-subject level. We specifically hypothesized that selective attention to visual speech gestures would enhance activity within the auditory cortex areas that process visual speech information, compared to the situation during which the same gestures were seen but ignored.

SUBJECTS AND METHODS

The subjects were the same 10 healthy, right-handed, Finnish-speaking volunteers (5 women; mean age 26 years; age range 22–31) as in our earlier experiment examining primary auditory cortex activation separately by lip-reading and by viewing geometrical visual stimuli in motion [Pekkola et al., 2005]. Prior to participation, each gave informed consent to the study protocol approved by the local ethics committee in accordance with the Helsinki declaration.

Figure 2.

Cortical activations ($Z > 2.3$, $P < 0.05$, corrected) during ATT_VOWELS and ATT_CIRCLES conditions relative to baseline and the differential between-conditions activation (ATT_VOWELS > ATT_CIRCLES) within the auditory cortex. Activation maps are overlaid on an averaged high-resolution image of the 10 participants' brains. L, left sagittal view; R, right sagittal view.

We prepared the stimuli from video clips of a female face silently articulating four Finnish vowels (/a/, /o/, /e/, and /y/) by adding a blue, semitransparent moving circle upon the mouth region of the articulating face. The subjects thus saw the articulatory movements and the moving circles on top of each other. The circle expanded and constricted in four alternative directions (horizontal, vertical, left oblique, and right oblique) following a time-scale and movement range similar to that of the articulatory movements. The movement of the circles was simultaneous with the articulatory movements. We combined the four vowels with the four circles to produce 16 different stimuli (e.g., /a/ + horizontal circle; /e/ + vertical circle, see Fig. 1) that we presented in random order during the active blocks of the experiment (stimulus duration 520 ms, interstimulus interval 420 ms), except that the occurrence of target sequences (see below) was set at 10/run. A gaze fixation dot was continuously visible in the mouth region of the face.

We scanned the subjects with a 3 T GE (Milwaukee, WI) Signa system and a quadrature birdcage head coil during two 5-min runs using a block-design with intermittent 30-s active and baseline blocks. The order of runs was randomized across subjects. The two runs shared an identical BASELINE condition (a still face image without any movement). During the active blocks of both runs, the subjects saw an identical set of stimuli (articulatory movements and moving circles on top of each other) but were to direct their attention differentially. During ATT_VOWELS run they were instructed to “see what vowel the person is saying,” to ignore the circles, and to press a button with the right index finger if any vowel occurred twice in succession. During ATT_CIRCLES run the instruction was to concentrate on watching the circles, ignore the articulations, and perform an analogous 1-back task based on the occurrence of two circles moving successively in the same direction. Throughout the experiment, the subjects were told to fixate their gaze on the fixation mark visible in the mouth region of the face.

Thus, the runs shared an identical baseline, 1-back task, and motor response. The physical stimuli were identical in both runs, but the instruction required selectively directed attention either to identify the phonetic content of the visually perceived articulations or the direction of movement of simple, nonverbal visual stimuli.

During each run we acquired 120 functional gradient-echo-planar T_2^* -weighted volumes depicting BOLD contrast [Ogawa et al., 1990] in 28 axial-oblique, contiguous 3.4 mm thick planes (TE 30 ms, TR 2,500 ms, flip angle 90°, FOV 22x22cm, matrix size 64 × 64). For anatomic co-alignment, we obtained a T_1 -weighted inversion recovery echo-planar volume with a slice prescription identical to the functional volume but denser (0.9 × 0.9 mm) in-plane resolution. The functional data and the anatomical volume were acquired during the same session and the subjects were instructed to stay as immobile as possible throughout the experiment, with their head secured with foam cushions.

Preprocessing of the functional data included discarding the first two volumes of each run, nonbrain tissue extraction,

motion correction [Jenkinson et al., 2002], Gaussian spatial smoothing (full-width-half-maximum, FWHM, 5 mm), intensity normalization, and high-pass temporal filtering. The temporal de-trending was done separately for each run. At the single-subject level, we analyzed the time-series data for each run with fMRI Expert Analysis Tool software (FEAT, v. 3.1) that uses a general linear model with local autocorrelation correction [Woolrich et al., 2001] and thresholded the resulting statistical maps at $Z > 2.3$, $P < 0.05$ (corrected for multiple comparisons across the acquisition volume). The functional data were aligned to the anatomical T_1 -weighted volume and to a standard-space template using linear registration [Jenkinson et al., 2002].

At the group level, we contrasted ATT_VOWELS and ATT_CIRCLES conditions with the baseline in a mixed-effects (often referred to as “random-effects”) analysis [Woolrich et al., 2004], where the significance level was set at $Z > 2.3$, $P < 0.05$ (corrected). We then probed the differential activation within the auditory cortex between ATT_VOWELS and ATT_CIRCLES conditions by contrasting the runs to each other in a mixed-effects group analysis using a two-sample paired *t*-test. According to our hypothesis, we limited this search to the auditory cortex (BA 41/42/22) areas that survived thresholding in ATT_VOWELS > BASELINE comparison, and thresholded the resulting statistical maps at $Z > 2.3$, $P < 0.05$ (corrected). An analogous reverse contrast (ATT_CIRCLES > ATT_VOWELS) was run in a region of interest defined by the auditory cortex areas that survived thresholding in ATT_CIRCLES > BASELINE contrast. To seek for differential activation in brain areas other than the auditory cortex, the two runs were also contrasted in a group analysis including the whole acquisition volume ($Z > 2.3$, $P < 0.05$, corrected). The baselines of the runs were also contrasted to each other in a mixed-effects group analysis ($Z > 2.3$, $P < 0.05$).

The primary auditory cortex (BA 41, auditory koniocortex) resides in the medial part of Heschl’s gyrus (HG), the lateral part of which is covered by less granular secondary auditory cortex (BA 42) analogous to primate’s belt area [Rademacher et al., 1993]. Due to substantial interindividual anatomical variation within this region [Penhune et al., 1996; Rademacher et al., 1993], effects within the primary auditory cortex or HG can be overlooked if several individuals’ brains are normalized to a standard-space template in order to perform group-level analyses. To avoid this, we studied activity within HGs at a participant level by utilizing the fact that we had determined HGs according to MR-visible anatomical landmarks in this subject population for our earlier experiment [Pekkola et al., 2005]. We assessed the extension of significant activation to the anatomical area of HGs and to their medial parts for each subject during both runs and compared the differential activity between runs by entering maximum percentage signal changes within each HG into a 2 × 2 analysis of variance (ANOVA) with stimulus type and hemisphere as the factors.

TABLE I. Cortical regions active during ATT_VOWELS and ATT_CIRCLES conditions relative to the baseline

Condition/Cortical region	Brodmann area	Side	Voxels	Max. Z	x, y, z*
ATT_VOWELS					
Calcarine, superior and middle occipital and fusiform gyri	37/19/18/17	Bilateral	10,574	5.46	-14, -90, -9
Inferior and middle frontal gyri, precentral gyri, insula	6/44/45/46/47/48	Right	4,346	4.16	34, 25, 4
Inferior frontal, pre- and postcentral gyri, insula	4/6/44/45/47/48	Left	3,816	5.15	-36, 18, 8
Superior and inferior parietal lobuli	7/40	Left	2,002	4.16	-34, -46, 48
Superior and inferior parietal lobuli, precuneus	7/40	Right	2,444	4.31	46, -44, 48
Supplementary motor area, anterior and middle cingulate	6/32	Bilateral	1,597	4.20	-10, 6, 48
Superior and middle temporal gyri	41/42/22/21	Right	668	4.88	62, -34, 20
Superior and middle temporal gyri	41/42/22/21	Left	500	4.00	-57, -36, 21
ATT_CIRCLES					
Calcarine, superior and middle occipital and fusiform gyri	37/19/18/17	Bilateral	11,857	5.35	-40, -80, 2
Inferior and middle frontal and precentral gyri, insula	6/44/45/46/47/48	Right	6,128	5.05	42, 6, 40
Inferior and middle frontal, pre- and postcentral gyri, insula	4/6/44/45/46/47/48	Left	5,674	5.19	-50, -11, 56
Superior and inferior parietal lobuli	7/40	Left	2,144	4.18	-24, -57, 67
Superior and inferior parietal lobuli, precuneus	7/40	Right	3,297	4.24	46, -46, 48
Supplementary motor area, middle and anterior cingulate	6/32	Bilateral	1,722	4.45	-2, 9, 56
Superior and middle temporal gyri	41/42/22/21	Right	1,325	4.34	59, -36, 20
Superior and middle temporal gyri	41/42/22/21	Left	493	3.62	60, -38, 20

*Peak voxel's Talairach coordinates.

RESULTS

The subjects correctly identified more than 80% of the target sequences during both runs (ATT_VOWELS $81.0 \pm 4.8\%$ and ATT_CIRCLES $84.0 \pm 5.2\%$, mean $\pm$ SEM). Identification accuracy showed no significant difference between runs. The maximum head movement during the runs was less than 0.2 mm, as estimated by the motion correction algorithm [Jenkinson et al., 2002].

At the group level, both ATT_VOWELS and ATT_CIRCLES conditions activated auditory and visual cortices. The bilateral temporal-lobe activation during both conditions extended to the planum temporale, the posterior parts of the superior temporal gyri (STG), and the superior temporal sulci (STS). In addition, both conditions activated an extensive, overlapping cortical network including Broca's area and its right-hemisphere homolog, the left motor cortex, bilateral premotor cortex, superior and inferior parietal lobules, supplementary motor areas, anterior and middle cingulate cortex, and frontal eye field areas in the caudal parts of the middle frontal gyri (Fig. 2, Table I).

In the region-of-interest (ROI) analysis of the auditory cortex, attending to visual articulations enhanced activity within the left planum temporale (BA 42/22, cluster size 72 voxels, peak Z-value 3.2), compared to when the articulations were visible but ignored (Fig. 2). No such effect emerged within the right auditory cortex. The left auditory cortex area more strongly activated during ATT_VOWELS than ATT_CIRCLES was active ($Z > 2.3$, $P < 0.05$) during both conditions when compared to baseline. Thus, its

greater activation during ATT_VOWELS condition could not be due to deactivation during ATT_CIRCLES condition. The reverse contrast (ATT_CIRCLES $>$ ATT_VOWELS) did not show significant activity differences within auditory cortex in either hemisphere. However, stronger activation during the ATT_CIRCLES than the ATT_VOWELS condition emerged in the between-condition analysis of the whole brain within the right superior parietal lobule and precuneus (BA 7), the right prefrontal cortex (BA 9/10), the caudal part of the right middle frontal gyrus (BA 46), and the right premotor cortex (BA 6); see Table II for cluster extents and peak Z values. The contrast between the two baselines did not produce significant activation.

At the single-subject level, the activation extended to the area of the left HG in seven subjects during the ATT_VOWELS condition and in five of these also during the

TABLE II. Regions activated more strongly during ATT_CIRCLES than ATT_VOWELS condition in the whole-brain analysis

Cerebral region (BA)	Side	Voxels	Max Z	x, y, z*
Superior parietal lobule, precuneus (BA 7)	Right	952	4.01	12, -69, 57
Middle and superior frontal gyri (BA 9/10/46)	Right	518	3.42	22, 54, 29
Middle and superior frontal gyri (BA 6)	Right	424	3.48	28, -3, 55

*Peak voxel's Talairach coordinates.

TABLE III. Number of subjects showing activation within HG and its medial part during ATT_VOWELS and ATT_CIRCLES runs

	Left		Right	
	HG	medial half	HG	medial half
ATT_VOWELS	7	6	3	2
ATT_CIRCLES	5	3	3	3

ATT_CIRCLES condition. Three of these subjects showed bilateral HG activation during both conditions. Six subjects showed activation within the medial half of HG (the anatomical area of the primary auditory cortex) during the ATT_VOWELS condition and three during the ATT_CIRCLES condition (Table III).

We detected no significant main effect for stimulation type or hemisphere or a significant interaction between the factors when comparing BOLD signal strength within HGs. Although activation levels were slightly higher in the left than in the right HG, this difference did not reach statistical significance (Fig. 3).

DISCUSSION

Together with earlier work showing access of visual speech information to the classical auditory cortex [Bernstein et al., 2002; Besle et al., 2004; Calvert et al., 1997, 1999; Campbell et al., 2001; Klucharev et al., 2003; MacSweeney et al., 2000; Möttönen et al., 2002, 2004; Paulesu et al., 2003; Pekkola et al., 2005; Sams et al., 1991; Van Wassenhove et al., 2005], our findings suggest an active role for the auditory cortex in processing visual speech information. As a novel finding, we detected enhancement of left planum temporale activity during selective attention to visual speech, showing that attention to visually received speech input can modulate activity of the secondary auditory cortex.

Identification of the shape changes in circles was relatively simple. Even when engaged in this task the subjects probably had quite enough resources also to analyze the visual speech stimuli. This could have led to activation of speech processing circuits, regardless of the lack of voluntary attention to speech stimuli, and explain why the bilateral auditory cortices and the adjacent multisensory STS areas were active both during attention to articulations and when they were ignored. Another explanation for auditory cortex and STS activity during the ATT_CIRCLES condition could be their activation by the moving circles themselves. When similar circle and vowel stimuli were presented separately in a recent study, the circles activated the auditory cortex within Heschl's gyri in several subjects, but the vowel stimuli activated it more strongly [Pekkola et al., 2005]. Although the issue cannot be clearly resolved, we consider it possible that visual speech activated the auditory cortex in the current experiment, in part without voluntary attention.

Activity within the secondary auditory cortex was enhanced when the subjects directed their attention to the

visual speech stimuli. Taking into account the dominant role of the left hemisphere in right-handed individuals' speech processing, this left-lateralization of the attention-driven activity enhancement is compatible with greater activation of left-hemisphere neural networks specialized in speech processing. It could thus be specifically due to enhanced processing of the visual articulations' phonetic content in the ATT_VOWELS condition compared to that in the ATT_CIRCLES condition, in which the task did not include explicit processing of the seen articulations. This is in agreement with earlier findings of left-lateralization of attention effects on auditory cortex activity during auditory speech stimulation [Jäncke et al., 1999; Pugh et al., 1996].

Planum temporale, where the differential activation between the attention conditions emerged, resides within the superior temporal plane immediately posterior to Heschl's gyrus and is considered to represent sensory-specific secondary auditory cortex. Its role is likely to involve processing of complex acoustic information (both speech and non-speech) and possibly matching that information to learned spectrotemporal representations (for a recent review of functional studies of planum temporale activation by speech and nonspeech sounds, see Griffiths and Warren [2002]). Thus, the top-down modulation of the left planum temporale activity observed during voluntary attention to visual speech supports the view that phonetic information carried by visual articulations can affect relatively early hierarchical stages of speech processing. This view also gains support from electrophysiological studies with fine-grained temporal resolution showing audiovisual interactions in the auditory cortex within 200 ms after speech sound onset [Besle et al., 2004; Klucharev et al., 2003; Möttönen et al., 2002, 2004; Van Wassenhove et al., 2005] and modulation of the responsiveness of auditory-cortex neurons by seen articulatory gestures [Jääskeläinen et al., 2004].

Although fewer subjects showed significant HG activation during ATT_CIRCLES than during ATT_VOWELS condi-

Figure 3.

Maximum percentage signal changes (mean ± SEM) within Heschl's gyri (HG) during ATT_VOWELS and ATT_CIRCLES conditions. Ns = nonsignificant.

tion, the lack of difference in maximum BOLD signals within HGs between the conditions suggests that the attentional modulation of auditory cortex activity during visual speech perception may be limited to the secondary auditory cortex. This might also indirectly imply that our earlier finding of activation within Heschl's gyri during visual speech perception [Pekkola et al., 2005] is unlikely to represent top-down modulation of auditory cortex activity by attention but rather a direct pre-attentive effect. However, with fMRI it is impossible to distinguish the temporal order of cortical activations, and therefore conclusions concerning such issues must be cautious.

In addition to the sensory-specific cortices, both active conditions activated the parietal lobules, frontal eye field areas, supplementary motor areas, and anterior cingulate cortex (Fig. 2, Table I). This activation covered the network engaging in visual spatial attention [Nobre, 2001]. Consistent with a central process that could modulate processing in the sensory-specific cortices, activations within these areas during the two conditions were mostly similar. Part of this network (the right superior parietal lobule and the right frontal eye field area) and the right prefrontal cortex were more strongly activated during ATT_CIRCLES than during the ATT_VOWELS condition. This could reflect greater demands for attention when the task required focusing on stimuli that, unlike the visual speech stimuli, lack any specific meaning in communication.

The left motor cortex activation during the active conditions appeared in the location of right hand motor representation and is thus attributable to the motor task not present in the baseline condition. The activation observed within Broca's area (BA 44/45, trigonal and opercular parts of the left inferior frontal gyrus), its right-hemisphere homolog, and the bilateral premotor cortex during both active conditions may in turn be related to engagement of motor-articulatory strategies in visual speech perception, as suggested earlier [Ojanen et al., 2005; Paulesu et al., 2003]. Interestingly, we detected no effect of attention on activity within these regions.

CONCLUSION

These results demonstrate enhancement of left planum temporale activity during attention to lip-reading, showing that attention to visually perceived speech stimuli can modulate auditory cortex activity and suggesting that voluntary attention does play a role in modulating auditory cortex activity during visual speech perception.

ACKNOWLEDGMENT

We thank Carol Norris for help in preparing the manuscript.

REFERENCES

Alho K, Medvedev SV, Pakhomov SV, Roudas MS, Tervaniemi M, Reinikainen K, Zeffiro T, Näätänen R (1999): Selective tuning of

- the left and right auditory cortices during spatially directed attention. *Brain Res Cogn Brain Res* 7:335–341.
- Bernstein LE, Auer ET Jr, Moore JK, Ponton CW, Don M, Singh M (2002): Visual speech perception without primary auditory cortex activation. *Neuroreport* 13:311–315.
- Besle J, Fort A, Delpuech C, Giard MH (2004): Bimodal speech: early suppressive visual effects in human auditory cortex. *Eur J Neurosci* 20:2225–2234.
- Calvert GA, Bullmore ET, Brammer MJ, Campbell R, Williams SC, McGuire PK, Woodruff PW, Iversen SD, David AS (1997): Activation of auditory cortex during silent lipreading. *Science* 276:593–596.
- Calvert GA, Brammer MJ, Bullmore ET, Campbell R, Iversen SD, David AS (1999): Response amplification in sensory-specific cortices during crossmodal binding. *Neuroreport* 10:2619–2623.
- Campbell R, MacSweeney M, Surguladze S, Calvert G, McGuire P, Suckling J, Brammer MJ, David AS (2001): Cortical substrates for the perception of face actions: an fMRI study of the specificity of activation for seen speech and for meaningless lower-face acts (gurning). *Brain Res Cogn Brain Res* 12:233–243.
- Grady CL, Van Meter JW, Maisog JM, Pietrini P, Krasuski J, Rauschecker JP (1997): Attention-related modulation of activity in primary and secondary auditory cortex. *Neuroreport* 8:2511–2516.
- Griffiths TD, Warren JD (2002): The planum temporale as a computational hub. *Trends Neurosci* 25:348–353.
- Hashimoto R, Homae F, Nakajima K, Miyashita Y, Sakai KL (2000): Functional differentiation in the human auditory and language areas revealed by a dichotic listening task. *Neuroimage* 12:147–158.
- Jääskeläinen IP, Ojanen V, Ahveninen J, Auranen T, Levänen S, Möttönen R, Tarnanen I, Sams M (2004): Adaptation of neuro-magnetic N1 responses to phonetic stimuli by visual speech in humans. *Neuroreport* 15:2741–2744.
- Jäncke L, Mirzazade S, Shah NJ (1999): Attention modulates activity in the primary and the secondary auditory cortex: a functional magnetic resonance imaging study in human subjects. *Neurosci Lett* 266:125–128.
- Jenkinson M, Bannister P, Brady M, Smith S (2002): Improved optimization for the robust and accurate linear registration and motion correction of brain images. *Neuroimage* 17:825–841.
- Klucharev V, Möttönen R, Sams M (2003): Electrophysiological indicators of phonetic and non-phonetic multisensory interactions during audiovisual speech perception. *Brain Res Cogn Brain Res* 18:65–75.
- Lipschutz B, Kolinsky R, Damhaut P, Wikler D, Goldman S (2002): Attention-dependent changes of activation and connectivity in dichotic listening. *Neuroimage* 17:643–656.
- MacSweeney M, Amaro E, Calvert GA, Campbell R, David AS, McGuire P, Williams SC, Woll B, Brammer MJ (2000): Silent speechreading in the absence of scanner noise: an event-related fMRI study. *Neuroreport* 11:1729–1733.
- McGurk H, MacDonald J (1976): Hearing lips and seeing voices. *Nature* 264:746–748.
- Möttönen R, Krause CM, Tiippana K, Sams M (2002): Processing of changes in visual speech in the human auditory cortex. *Brain Res Cogn Brain Res* 13:417–425.
- Möttönen R, Schurmann M, Sams M (2004): Time course of multisensory interactions during audiovisual speech perception in humans: a magnetoencephalographic study. *Neurosci Lett* 363: 112–115.
- Nobre AC (2001): The attentive homunculus: now you see it, now you don't. *Neurosci Biobehav Rev* 25:477–496.

- Ogawa S, Lee TM, Kay AR, Tank DW (1990): Brain magnetic resonance imaging with contrast dependent on blood oxygenation. *Proc Natl Acad Sci U S A* 87:9868–9872.
- Ojanen V, Möttönen R, Pekkola J, Jääskeläinen IP, Joensuu R, Autti T, Sams M (2005): Processing of audiovisual speech in Broca's area. *Neuroimage* 25:333–338.
- O'Leary DS, Andreason NC, Hurtig RR, Hichwa RD, Watkins GL, Ponto LL, Rogers M, Kirchner PT (1996): A positron emission tomography study of binaurally and dichotically presented stimuli: effects of level of language and directed attention. *Brain Lang* 53:20–39.
- Paulesu E, Perani D, Blasi V, Silani G, Borghese NA, De Giovanni U, Sensolo S, Fazio F (2003): A functional-anatomical model for lipreading. *J Neurophysiol* 90:2005–2013.
- Pekkola J, Ojanen V, Autti T, Jääskeläinen IP, Möttönen R, Tarkiainen A, Sams M (2005): Primary auditory cortex activation by visual speech: an fMRI study at 3T. *Neuroreport* 16:125–128.
- Penhune VB, Zatorre RJ, MacDonald JD, Evans AC (1996): Inter-hemispheric anatomical differences in human primary auditory cortex: probabilistic mapping and volume measurement from magnetic resonance scans. *Cereb Cortex* 6:661–672.
- Pugh KR, Shaywitz BA, Shaywitz SE, Fulbright RK, Byrd D, Skudlarski P, Shankweiler DP, Katz L, Constable RT, Fletcher J, Lacadie C, Marchione K, Gore JC (1996): Auditory selective attention: an fMRI investigation. *Neuroimage* 4:159–173.
- Rademacher J, Caviness VS Jr, Steinmetz H, Galaburda AM (1993): Topographical variation of the human primary cortices: implications for neuroimaging, brain mapping and neurobiology. *Cereb Cortex* 3:313–329.
- Rinne T, Pekkola J, Degerman A, Autti T, Jääskeläinen IP, Sams M, Alho K (2005): Modulation of auditory cortex activation by sound presentation rate and attention. *Hum Brain Mapp* 26:94–99.
- Sams M, Aulanko R, Hämäläinen M, Hari R, Lounasmaa OV, Lu ST, Simola J (1991): Seeing speech: visual information from lip movements modifies activity in the human auditory cortex. *Neurosci Lett* 127:141–145.
- Sumby WH, Pollack I (1954): Visual contribution to speech intelligibility in noise. *J Acoustic Soc Am* 26:212–215.
- Tiippana K, Andersen TS, Sams M (2004): Visual attention modulates audiovisual speech perception. *Eur J Cogn Psychol* 16:457–472.
- Van Wassenhove V, Grant KW, Poeppel D (2005): Visual speech speeds up the neural processing of auditory speech. *Proc Natl Acad Sci U S A* 102:1181–1186.
- Woldorff MG, Gallen CC, Hampson SA, Hillyard SA, Pantev C, Sobel D, Bloom FE (1993): Modulation of early sensory processing in human auditory cortex during auditory selective attention. *Proc Natl Acad Sci U S A* 90:8722–8726.
- Woolrich MW, Ripley BD, Brady M, Smith SM (2001): Temporal autocorrelation in univariate linear modeling of FMRI data. *Neuroimage* 14:1370–1386.
- Woolrich MW, Behrens TE, Beckmann CF, Jenkinson M, Smith SM (2004): Multilevel linear modelling for FMRI group analysis using Bayesian inference. *Neuroimage* 21:1732–1747.