Hearing Shapes Our Perception of Time: Temporal Discrimination of Tactile Stimuli in Deaf People

Nadia Bolognini[1], Carlo Cecchetto[1], Carlo Geraci[1], Angelo Maravita[1], Alvaro Pascual-Leone[2], and Costanza Papagno[1]

Abstract

■ Confronted with the loss of one type of sensory input, we compensate using information conveyed by other senses. However, losing one type of sensory information at specific developmental times may lead to deficits across all sensory modalities. We addressed the effect of auditory deprivation on the development of tactile abilities, taking into account changes occurring at the behavioral and cortical level. Congenitally deaf and hearing individuals performed two tactile tasks, the first requiring the discrimination of the temporal duration of touches and the second requiring the discrimination of their spatial length. Compared with hearing individuals, deaf individuals were impaired only in tactile temporal processing. To explore the neural sub-strate of this difference, we ran a TMS experiment. In deaf individuals, the auditory association cortex was involved in temporal and spatial tactile processing, with the same chronometry as the primary somatosensory cortex. In hearing participants, the involvement of auditory association cortex occurred at a later stage and selectively for temporal discrimination. The different chronometry in the recruitment of the auditory cortex in deaf individuals correlated with the tactile temporal impairment. Thus, early hearing experience seems to be crucial to develop an efficient temporal processing across modalities, suggesting that plasticity does not necessarily result in behavioral compensation. ■

INTRODUCTION

Humans are endowed with specialized receptors capable of capturing different types of electromagnetic waves, temperature, etc. Thus, we perceive the world by means of distinct modality-specific systems that feed into specialized brain networks. The selectivity of these sensory channels enables us to experience uniquely unimodal sensations. Pitch, for example, can only be experienced through audition. However, the acquisition of information through separate modalities allows us to process the different features of sensory experience in parallel, thus building a unitary multimodal percept (Neville & Bavelier, 2002).

The unified nature of multimodal sensory experiences is the product of dynamic neural interactions and connections, which in turn are influenced by our experiences and developmental constraints. Current evidence supports the notion that multisensory integration enhances overall perceptual accuracy and saliency through cooperative advantages and provides for a redundancy of cues necessary to characterize objects in our environment (Stein & Stanford, 2008; Calvert, 2001). Information gathered through one sense can effectively modulate information acquired via others as demonstrated, for example, by well-known perceptual phenomena, such as the McGurk effect (McGurk & MacDonald, 1976).

What are then the consequences of losing or growing up without one sense?

It would be reasonable to expect that the loss of one sense must lead to functional and, perhaps, structural changes in the brain, significantly affecting cognitive abilities, and the interaction with the environment. On one side, losing one type of sensory information at specific developmental times, may lead to deficits across all sensory perception with widespread cognitive and perceptual breakdown. On the other side, if the lack or loss of a sensory modality can lead to a compensatory enhancement of other senses, this may result in a minimal functional loss or even a functional gain through compensatory cross-modal plasticity (Merabet & Pascual-Leone, 2010). Some earlier studies have demonstrated that, at least for the visual modality, no enhanced sensory sensitivity is present in deaf individuals to compensate for the loss of hearing; this evidence has questioned the traditional assumption that sensory compensation results in greater sensory sensitivity (Bross & Sauerwein, 1980; Bross, 1979).

With respect to time perception, studies in profoundly deaf individuals have focused on visual temporal abilities in the range of seconds, showing poorer performance in deaf individuals than hearing controls (Kowalska & Szelag, 2006). More specifically, congenitally deaf adolescents were asked to produce or reproduce the duration of visually presented stimuli: In the production task, participants

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[1]University of Milano Bicocca, [2]Harvard Medical School

had to judge when a visual stimulus lasted for 3 sec by interrupting the presentation. In the reproduction task, they were asked to reproduce the same 3-sec visual stimulus by interrupting the stimulus delivered on the screen. Other studies have examined temporal processing in profoundly deaf individuals in the range of milliseconds, rather than seconds. In this case, no differences were found in the processing of rapidly changing visual stimuli between congenitally deaf and normal hearing adults (Poizner & Tallal, 1987; Bross & Sauerwein, 1980). However, a recent study with adults who suffered early hearing loss (Heming & Brown, 2005), investigating tactile and visual temporal processing by means of a simultaneity judgment task, showed that perceptual thresholds were significantly higher for the deaf group than for the controls, suggesting an impairment of temporal processing following early deafness. Opposite results were obtained when a different task, namely a visual temporal order judgment task instead of a simultaneity one, was used in 10 profoundly deaf individuals and two groups of hearing controls, either experimentally auditory-deprived or not (Nava, Bottari, Zampini, & Pavani, 2008). Temporal order thresholds and points of subjective simultaneity for the two visual stimuli did not differ between groups, in accordance with other results obtained with a temporal order judgment task (Poizner & Tallal, 1987). However, discrimination responses were faster in deaf individuals than in hearing controls, especially when the two stimuli appeared at peripheral locations. Together, the available evidence indicates that the type of task and stimuli are crucial in determining the results.

An intriguing question is whether the actual experience of temporal processing of somatosensory (e.g., *vibrotactile*) stimuli can also change as a function of auditory experience. Indeed, in the particular case of vibratory patterns, the senses of hearing and touch are not only sensitive to the very same class of physical events, "but within a certain range of frequencies, the very same vibratory stimulus can be experienced simultaneously by the peripheral receptor organs of both sensory modalities" (Soto-Faraco & Deco, 2009, p. 146).

With this aim, we investigated the effects of early deafness on the causal role and timing of the recruitment of somatosensory and auditory areas during the temporal and spatial discrimination of tactile stimuli. Congenitally deaf, right-handed individuals and an equivalent number of hearing individuals performed two tactile discrimination tasks. Subjects were required to discriminate the *duration* of two tactile stimuli (25 msec vs. 15 msec) in the temporal task and the *length* of two linearly arranged tactile stimuli (2 vs. 3 tactile pulses) in the spatial task. In both cases, the tactile stimuli were delivered to the right or left index finger. We explored the neural substrate of their behavior by means of TMS by targeting the primary somatosensory area (SI) or the auditory association cortex (superior temporal gyrus, STG) at different time intervals.

METHODS

Main Experiments

Participants

In the temporal task, we tested nine hearing right-handed (Oldfield, 1971) healthy individuals (mean age = 38 years, range = 27–60 years, six women; four of them participated also in the spatial task) and nine right-handed congenitally deaf individuals (mean age = 41 years, range = 25–52 years, four women; six of the deaf subjects participated also in the spatial task, see below). Seven deaf people used Italian Sign Language (LIS) as their primary language and were exposed to LIS before the age of 3, either because they had one or two deaf signing parents or because they attended a school where LIS was used. The remaining two deaf subjects had no experience of LIS. All deaf participants had a binaural hearing loss of >90 dB and had normal nonverbal intelligence as assessed by means of the Raven Colored Progressive Matrices.

Seven right-handed hearing individuals (mean age = 32 years, range = 24–49 years, four women) and seven congenitally deaf right-handed individuals (mean age = 44, range = 25–53, three women) took part in the spatial discrimination task. Five deaf participants made use of LIS as their primary language and were exposed to it before the age of 3, whereas the remaining two had no experience of LIS. All deaf individuals had a binaural hearing loss of >90 dB. Their nonverbal intelligence was in the normal range as assessed by means of the Raven Colored Progressive Matrices.

The two groups were comparable for their educational level (three hearing and three deaf individuals had an academic background in each experiment).

Hearing participants had no knowledge of LIS, and Italian was their primary language. All participants had normal or corrected-to-normal vision.

Deaf participants were recruited through the Italian Association of Deaf People (i.e., Ente Nazionale Sordi) and personal acquaintance; they were paid for their participation. Hearing participants were recruited from the panel of the University of Milano-Bicocca.

Participants gave written informed consent before participating in the experiments. They were naive to the experimental procedure and to the purpose of the study. All the accepted recommendations for the use and safety of TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009) were applied. None of the participants had neurological, psychiatric, or medical disorders or any contraindication to TMS. The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki (BMJ 1991; 302: 1194) and was approved by the ethical committee of the University of Milano-Bicocca.

Tactile Temporal Discrimination Task

Custom-made electromagnetic solenoids (diameter = 0.8 cm, Heijo Research Electronics, Beckenham, UK;

www.heijo.com), attached to the participants' index fingers, were used to deliver the tactile stimulations. Two types of stimuli were randomly delivered to the distant phalanx of either index finger and differed with respect to their temporal duration: The target stimulus consisted of a long vibration of 25-msec (three 5-msec on phases, with two 5-msec off intervals, 100 Hz of frequency); the control stimuli consisted of a short vibration of 15-msec (two 5-msec on phases, with one 5-msec off interval, 100 Hz of frequency). White noise delivered from two external loudspeakers was used throughout to mask any auditory cues from the tactile stimulators in hearing subjects. Target and control stimuli were randomly presented (see below for randomization details). The intertrial interval varied between 6 and 8 sec to prevent carryover effects of TMS on cortical excitability (Walsh & Pascual-Leone, 2003).

During the temporal discrimination task, subjects attempted to discriminate the target stimulus from the control stimulus. More specifically, on each trial the participant was requested to report the long vibration (target) by saying "Yes" when the target was presented and refrain from responding to the short vibration (control stimulus). Verbal "Yes" responses were recorded and analyzed off-line. Sequence and timing of both the tactile and TMS stimuli were under computer control (E-prime software, Psychology Software Tools, Inc., Pittsburgh, PA; www.psychotoolbox. org; see Figure 1A).

Tactile Spatial Discrimination Task

Stimuli and procedure were identical to those used in the temporal task. The only difference was in the stimulus type: Now subjects were asked to discriminate the spatial length of tactile stimuli.[1] Three vibrotactile stimulators (diameter = 0.8 cm) were strapped to the participant's index finger of each hand: one stimulator on the distal phalanx and two stimulators on the middle phalanx (this arrangement was used throughout the task). The target stimulus consisted of a vibration produced by the simultaneous switch on of the three stimulators. The control stimuli consisted of a vibration produced by switching on only two of the three stimulators (the first plus the second stimulators or the second plus the third stimulators). Given the arrangement of the vibrators along the finger, the target stimulus consisted of a spatially "long" stimulus, whereas the control stimulus was proportionally "shorter." Both the target and the control stimuli had the same duration of 5 msec (one 5-msec on phases, with one 5-msec off interval, 100 Hz of frequency; see Figure 1B).

Figure 1. Experimental procedure. (A) In the temporal discrimination task, participants were asked to discriminate the *temporal* duration of the target stimulus delivered to the index finger by reporting the temporally long stimulus (target, i.e., a 25-msec vibration from one electromagnetic solenoid) and refraining from responding to the temporally short stimulus (control, i.e., a 15-msec vibration from one electromagnetic solenoid). (B) In the spatial discrimination task, three vibrotactile stimulators (i.e., electromagnetic solenoids) were attached to the index finger. Participants were asked to report the spatially long stimulus (target, i.e., simultaneous switch on of all the three vibrotactile stimulators) and refraining from responding to the spatially short stimulus (control, i.e., switching on two stimulators only, namely the first plus the second stimulator or the second plus the third stimulator). Both the target and the control stimuli lasted 5 msec. In both tasks, stimuli were randomly delivered to the left or right index finger. (C) In the TMS sessions, single TMS pulses were delivered to the targeted areas (left SI or left STG) at different ISIs (i.e., 60, 120, and 180 msec) after the tactile stimulus onset. The stimulation sites were chosen according to the coordinates reported by a previous fMRI study (Schurmann et al., 2006): SI (BA 1): $x = -45$, $y = -23$, $z = 53$; STG (BA 22): $x = -44$, $y = -31$, $z = 12$.
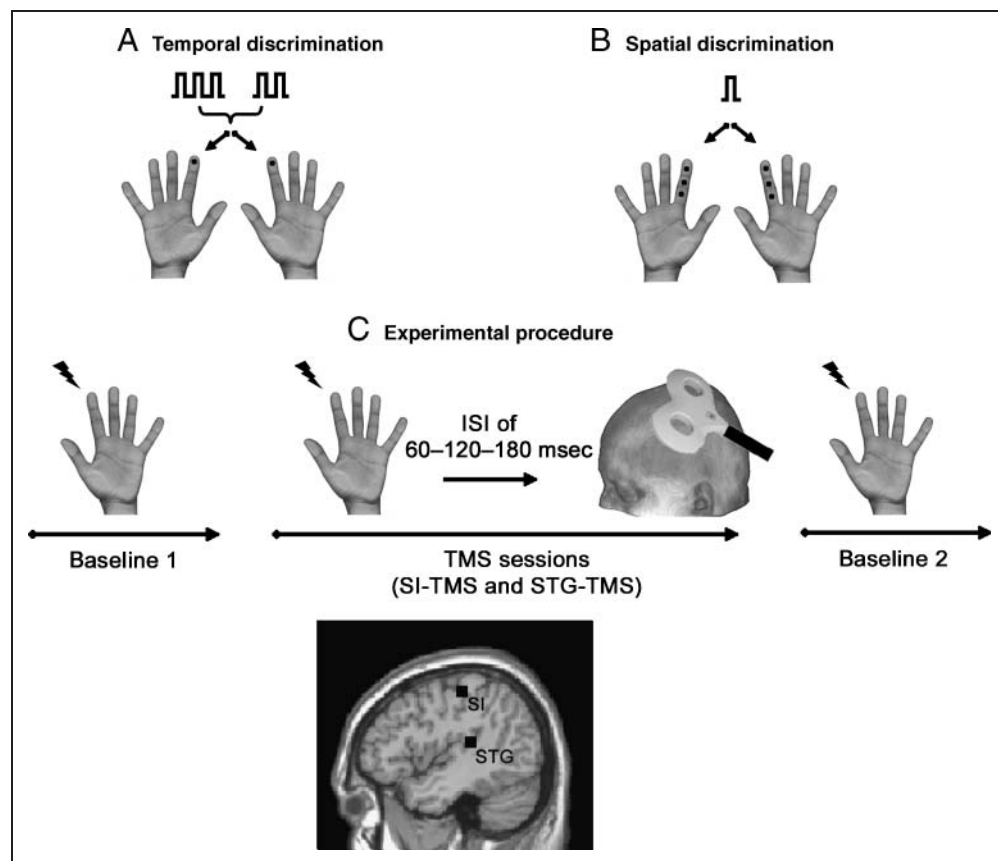
Although the tactile stimuli in the spatial and temporal tasks differed with respect to additional features, for instance, their overall intensity, we named the first task "temporal," as it required to discriminate the tactile stimulus with respect to the temporal dimension (i.e., temporal duration), whereas the second task was spatial, as it required to discriminate the tactile stimulus with respect to its spatial dimension (i.e., spatial length).

TMS Protocol

To explore the neural substrate of such behavioral findings and assess the possible cross-modal recruitment of auditory areas for tactile processing in deaf individuals, we ran two TMS experiments, one with the temporal and one with the spatial task. During tactile temporal and spatial discrimination, single-pulse TMS was delivered over either the left SI or the left STG at different interstimulus intervals (ISIs; i.e., 60, 120, and 180 msec) after the tactile stimulus onset. The choice of these sites and specific timing of stimulation was based on previous brain imaging (Hegner, Lee, Grodd, & Braun, 2010; Schurmann, Caetano, Hlushchuk, Jousmaki, & Hari, 2006) and magnetoencephalography (Caetano & Jousmaki, 2006; Levänen, Jousmaki, & Hari, 1998) studies. The comparison between the SI and STG activity in hearing and deaf individuals would allow exploring possible functional differences in their recruitment during tactile processing as a consequence of auditory deprivation.

Single-pulse TMS was delivered using a Magstim Super Rapid Transcranial Magnetic Stimulator (Magstim, Whitland, UK) connected with a figure-of-eight coil (70-mm diameter), allowing focal cortical stimulation (Pascual-Leone, Walsh, & Rothwell, 2000). Before each experiment, the motor threshold (MT) at rest was determined for each participant. MT was defined as the minimum intensity that induced a visible contraction in the contralateral first interosseus dorsalis muscle on at least three of six consecutive single TMS pulses. In the temporal task, the mean $\pm$ *SD* of MT was 65% $\pm$ 5% of the maximal output of the stimulator for the hearing group and 60% $\pm$ 7% for the deaf group. In the spatial task, the mean $\pm$ *SD* of MT was 63% $\pm$ 6% for the hearing group and 62% $\pm$ 8% for the deaf group. In both experiments, no difference in the MT was found between the two groups, as assessed by *t* tests ($p > .09$).

The stimulus intensity used during the experiment was set at 120% of the individual MT. Participants tolerated TMS well and did not report any adverse effects.

In both experiments, TMS was applied over the left SI and STG; these sites were chosen following the coordinates reported in a previous fMRI study (Schurmann et al., 2006): SI (BA 1), $x = -45$, $y = -23$, $z = 53$; STG (BA 22), $x = -44$, $y = -31$, $z = 12$.

To appropriately localize these sites on the subject's scalp, Talairach coordinates underlying coil locations were estimated for each participant by using the SofTaxic Navigator system (EMS Electro Medical Systems, Bologna,

Italy, www.emsmedical.net). This is a frameless stereotaxic image guidance system that allows reconstructing the cerebral cortex in Talairach coordinates on the basis of an MRI-constructed stereotaxic template (accuracy of ± 1 cm, Talairach space; Talairach & Tournoux, 1988). The SofTaxic Navigator system therefore permits the computation of an estimated MRI of each participant to guide the TMS coil positioning. This system allows reconstructing the cerebral cortex in Talairach coordinates on the basis of digitized skull landmarks (nasion, inion, and two pre-auricular points) as well as 50 additional, uniformly distributed points that are mapped on the scalp via a graphic user interface and a 3-D optical digitizer (NDI Polaris Vicra, Northern Digital, Inc., Waterloo, Canada). An estimation of the single subject's cerebral volume is automatically calculated by means of a warping procedure, through the use of a generic MRI volume (template) on the basis of a set of points digitized from the subject's scalp. With respect to using the individual subject's MRIs for the coil localization, the mean $\pm$ *SD* accuracy of the estimated MRI images obtained with the above procedure is 4.06 ± 1.54 mm, as computed by the EMS (Electro Medical Systems, Bologna, Italy) on 28 healthy adults having their own MRIs used as gold standard (see www.softaxic.com). This error is comparable to the spatial accuracy of TMS at MT intensity using the individual subject's MRIs (Herwig et al., 2001; Bastings et al., 1998). This localization system has been successfully used in several previous TMS studies (e.g., Bolognini, Rossetti, Maravita, & Miniussi, 2011; Bolognini, Papagno, Moroni, & Maravita, 2010; Bolognini & Maravita, 2007; Harris, Miniussi, Harris, & Diamond, 2002).

The coil was positioned over SI (i.e., SI-TMS) or STG (i.e., STG-TMS) in separate sessions. In both experiments, on each TMS session trial, a tactile vibration was followed by a TMS pulse after an ISI of 60, 120, or 180 msec, randomly selected.

Experimental Procedure

Throughout the two TMS experiments, subjects were comfortably seated in an armchair, in a quiet, dimly illuminated room. Each experiment consisted of five sessions: a training session and four experimental sessions. Between the sessions, subjects were allowed to rest and have refreshments. The whole procedure lasted about 2 hr.

The training session preceded the experimental ones, so that participants familiarized with the discrimination task. Verbal feedback was given concerning the subject's performance after each trial during the training phase only.

The experimental sessions consisted of two baseline sessions, one preceding (Baseline 1) and one following (Baseline 2) the two TMS sessions. In each baseline session, 16 target stimuli and 16 distractors to either the left or right index finger were delivered, for a total of 64 trials. During each TMS session (SI-TMS and STG-TMS), the same number of targets as in the baseline was delivered

for each different ISI (i.e., the interval between the onset of the stimuli and the onset of the TMS pulse could be of 60, 120, or 180 msec). This yielded a total number of 192 trials for each TMS session, given in four different blocks (i.e., 48 trials in each block), separated by short pauses. The order of the TMS sessions was counterbalanced across participants (see Figure 1).

Control Experiments

Participants

In the first control experiment, six right-handed hearing subjects (mean age = 32 years, range = 24–49 years, five women) and three right-handed congenitally deaf individuals (binaural hearing loss > 90 dB), exposed to LIS before the age of 3 and using LIS as their primary language (mean age: 41, range 26-45, 1 woman), participated in a control experiment, in which the parietal operculum (i.e., the OP4 area) was stimulated during the temporal discrimination task. This area was chosen as a general control site to rule out a nonspecific effect of TMS.

A second control experiment was run on six additional right-handed hearing subjects (mean age = 28 years, range = 24–34 years, four women). Now, the OP1 area was stimulated during the temporal discrimination task. This area is more posterior, thus closer to STG, as compared with OP4 (Burton, Sinclair, & McLaren, 2008; Eickhoff, Amunts, Mohlberg, & Zilles, 2006). Thus, the stimulation of this site represented a specific control relative to the STG effects in the temporal task. Indeed, TMS effects over STG could be actually because of an interference spreading to the OP1 hand representation area.

In both control experiments, stimuli and procedure were the same as in the main experiments (see above). The only difference was that the control experiments comprised four sessions: the training session, the two baseline sessions, and only one TMS session, which was carried out between the two baseline sessions. The whole procedure lasted about 90 min. OP4 ($x = -57$, $y = -12$, $z = 14$) and OP1 ($x = -54$, $y = -27$, $z = 19$) were localized following the coordinates reported in previous fMRI studies (Burton et al., 2008; Eickhoff et al., 2006).

In the OP4 experiment, the mean $\pm$ *SEM* of MT was 61% $\pm$ 7% of the maximal output of the stimulator for the hearing group and 64% $\pm$ 5% for the deaf group. In the OP1 experiment (hearing group only), the mean $\pm$ *SEM* of MT was 57% $\pm$ 11% of the maximum output of the stimulator.

Statistical Analyses

Statistical analyses were performed using Statistica for Windows (StatSoft). In both experiments, we assessed the effect of TMS following the Signal Detection Theory (Green & Swets, 1966), which allows determining the contribution of stimulus-related (i.e., perceptual sensitivity, d') and subject-related (i.e., response bias, c) influences on tactile processing.

Because there was no difference between the two baseline conditions in each experiment (as assessed by t tests in both the temporal and the spatial task, $p > .1$ for all comparisons), data from the two baseline sessions were collapsed.

In the main experiments, a first analysis (behavioral performance) was run considering only the behavioral performance at the baseline (i.e., no-TMS), to highlight the difference between the temporal and the spatial discrimination in the two groups. Changes in sensitivity (d') and in response criterion (c) were quantified for each task and then analyzed via a repeated measures ANOVA, with two between-group factors, that is, Group (hearing vs. deaf) and Task (temporal vs. spatial), and one within-group factor, that is, Side (right-sided vs. left-sided touches).

In the second analysis, the TMS effects on sensitivity and response criterion were assessed separately for each task, via a repeated measures ANOVA with a between-group factor, that is, Group (hearing vs. deaf), and three within-subject factors, namely, Side (right-sided vs. left-sided touches), Area (SI, STG), and Time (ISI: 60, 120, 180 msec).

Finally in the control experiments, with respect to OP4 stimulation, sensitivity and response criterion were analyzed via a repeated measures ANOVA with a between-group factor, that is, Group (hearing vs. deaf), and two within-subject factors, that is, Side (right-sided vs. left-sided touches) and Time (ISI: 60, 120, 180 msec). The data of the OP1 experiment were analyzed via a repeated measures ANOVA with two within-subject factors, that is, Side (right-sided vs. left-sided touches) and Time (ISI: 60, 120, 180 msec).

When appropriate, post hoc comparisons were run using the Newman–Keuls test.

Finally, we measured the effect size in the ANOVAs by calculating the $p\eta^2$, which measures the degree of association between an effect and the dependent variable, namely, the proportion of the total variance that is attributable to a main factor or to an interaction (Cohen, 1973).

RESULTS

Behavioral Performance

With respect to perceptual sensitivity (d' values), we found a significant main effect of Group ($F_{1, 28} = 13.22$, $p < .01$, $p\eta^2 = 0.3$), with a lower sensitivity in deaf individuals than in hearing individuals. The main effect of Task ($F_{1, 28} = 6.77$, $p < .01$, $p\eta^2 = 0.19$) showed lower d' values for the temporal than for the spatial task. In addition, the significant interaction Group × Task ($F_{1, 28} = 5.1$, $p < .03$, $p\eta^2 = 0.3$) showed that perceptual sensitivity in the temporal task was significantly lower in deaf individuals than in hearing individuals ($p < .01$), although the two groups

did not differ in the spatial task ($p = .8$; see Figure 2). The performance in the two tasks did not differ in hearing subjects ($p = .8$), suggesting that the two tasks had a comparable level of difficulty. Other effects (Side, Side × Task, Group × Side, Group × Side × Task) did not reach significance ($p > .5$).

No significant effect emerged in the analysis of the response criterion (c values, Group, Task, Side, Side × Task, Group × Task, Group × Side, Group × Side × Task, $p > .2$), confirming the perceptual basis of the temporal impairment in deaf individuals.

TMS Effects

When TMS was applied during the tactile temporal task, we found a significant effect of group ($F_{1, 16} = 10.35, p < .01, p\eta^2 = 0.4$), with a lower sensitivity in the deaf individuals than in the hearing participants. The effect of side ($F_{1, 16} = 32.11, p < .001, p\eta^2 = 0.7$) showed lower sensitivity in response to contralateral right-sided touches as compared with ipsilateral left-sided touches. The significant Side × Time interaction ($F_{2, 32} = 5.13, p < .01, p\eta^2 = 0.2$) showed a decrement in sensitivity for contralateral touches when TMS was delivered at 60 msec poststimulus onset ($p < .01$ for all comparisons). Moreover, there was a significant Area × Time interaction ($F_{2, 32} = 7.06, p < .01, p\eta^2 = 0.3$), because sensitivity decreased during SI-TMS at 60 msec ($p < .05$ for all comparisons). The Group × Area × Time ($F_{2, 32} = 8.79, p < .001, p\eta^2 = 0.3$) showed that only in hearing individuals sensitivity significantly decreased, specifically for SI stimulation at 60 msec ($p < .01$ for all comparisons). In deaf individuals, the sensitivity was overall lower, without any differences across conditions ($p > .09$). The significant Group × Side × Time interaction ($F_{2, 32} = 6.2, p < .01$,

Figure 2. Behavioral performance. Perceptual sensitivity (d') in tactile temporal (gray bars) and spatial (black bars) discrimination tasks in hearing and deaf individuals. The asterisk indicates a significant lower sensitivity in temporal tactile discrimination for deaf as compared with hearing subjects. Error bars denote *SEM*.

$p\eta^2 = 0.3$) showed that in hearing participants sensitivity for contralateral touches decreased in each Time condition ($p \leq .01$) as compared with ipsilateral touches, whereas in deaf individuals there was a decrease in sensitivity specifically at 60 msec ($p < .01$ for all comparisons). Finally, the interaction Group × Side × Area × Time was also significant ($F_{2, 32} = 3.38, p < .05, p\eta^2 = 0.3$): Multiple comparisons showed that, in the hearing group, contralateral sensitivity in temporal discrimination was significantly lower during SI-TMS at ISI of 60 msec and during STG-TMS at 180 msec, as compared with all other conditions ($p < .01$), without differences between SI-TMS at 60 msec and STG-TMS at 180 msec ($p = .3$). These results are in line with previous findings (Bolognini et al., 2010). Instead, in deaf subjects contralateral tactile processing deteriorated only with TMS delivered over both SI and STG ($p < .01$) at the same ISI of 60 msec poststimulus onset, without any difference between these two conditions ($p = .4$). No effect was found when TMS was delivered over STG at 180 msec. TMS over SI at 60 msec induced a comparable decrease in sensitivity for hearing and deaf individuals ($p = .7$), in spite of their difference at the baseline. A comparable decrease in sensitivity in hearing and deaf individuals was also found when TMS was delivered over STG ($p = .2$).

Other effects (Area, Time, Side × Area, Side × Area × Time, Group × Side, Group × Area, Group × Time, Group × Side × Area) did not reach significance ($p > .4$; see Figure 3).

With respect to the response criterion, only a significant effect of Time emerged ($F_{2, 32} = 13.24, p < .001, p\eta^2 = 0.5$), with a decrease in c values when TMS was delivered at 60 msec ($p < .01$) versus 120 and 180 msec, suggesting a nonspecific alertness effect induced by the early onset of the TMS pulse, in line with previous findings (Bolognini et al., 2010). Other effects (Group, Side, Area, Side × Area, Side × Time, Area × Time, Side × Area × Time, Group × Side, Group × Area, Group × Time, Group × Side × Area, Group × Side × Time, Group × Area × Time, Group × Side × Area × Time) did not reach significance (all $p > .5$).

In the spatial task, when considering sensitivity, there was a significant effect of Side ($F_{1, 12} = 8.99, p < .01, p\eta^2 = 0.4$). The effect of Time ($F_{2, 24} = 5.53, p < .01, p\eta^2 = 0.3$) showed that sensitivity was reduced when TMS was delivered at 60 and 120 msec, as compared with 180 msec. The interaction Group × Area ($F_{1, 12} = 13.88, p < .01, p\eta^2 = 0.5$) showed that in hearing individuals SI stimulation reduced sensitivity, as compared with STG stimulation ($p < .01$), whereas in deaf individuals, the difference between these two areas was not significant ($p = .4$); the SI effect was similar in the two groups ($p = .8$). The interaction Side × Area ($F_{1, 12} = 12.7, p < .01, p\eta^2 = 0.5$) showed a significant reduction of d' scores for contralateral touches during SI-TMS ($p < .01$ for all comparisons), whereas the Side × Time interaction ($F_{1, 12} = 5.7, p < .01, p\eta^2 = 0.3$) showed an effect of TMS at
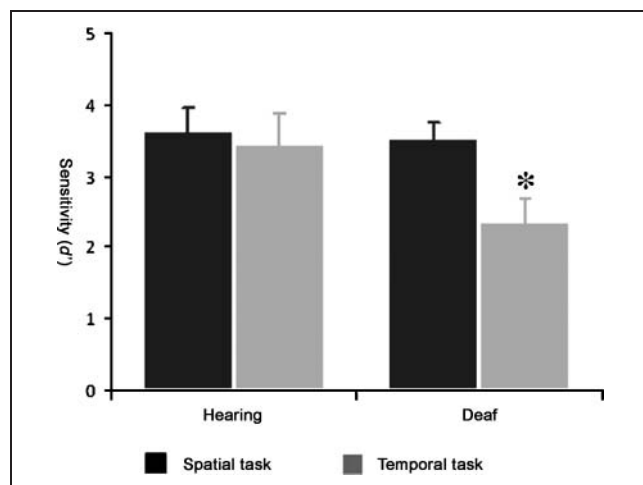
Figure 3. TMS effects. Perceptual sensitivity (d') and response criterion (c) in deaf and hearing participants at baseline and during TMS: (A) temporal tactile discrimination and (B) spatial tactile discrimination tasks. Columns refer to sensitivity for contralateral (dark gray) and ipsilateral (light gray) touches. Lines refer to response bias for contralateral (black line) and ipsilateral (gray line) touches. Asterisks indicate a significant decrease of sensitivity for the contralateral touches induced by TMS. Error bars denote *SEM*.
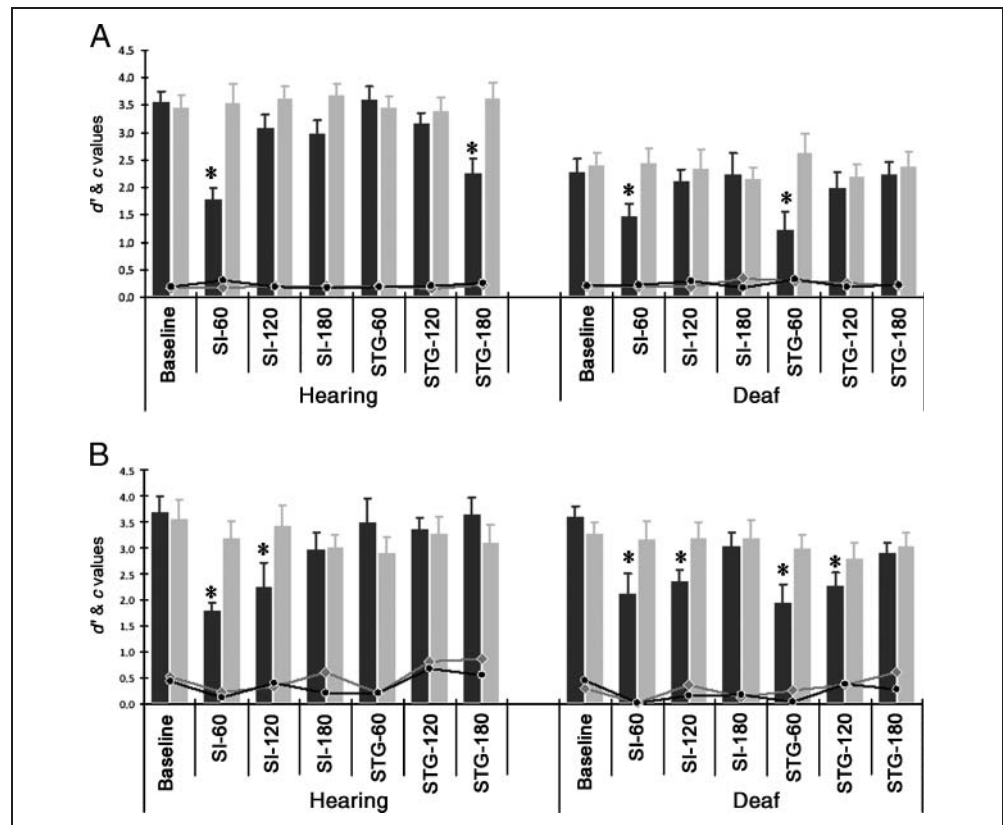
60 and 120 msec, which was specific for contralateral touches ($p < .01$), without difference between these two ISIs. The crucial result was the significant interaction Group × Side × Area ($F_{1,\ 12} = 9.14, p < .01, p\eta^2 = 0.5$): Multiple comparisons showed that in hearing participants the sensitivity for contralateral touches significantly decreased during SI-TMS, as compared with the other conditions ($p < .01$), in agreement with previous evidence (Bolognini et al., 2010). In deaf participants, sensitivity for contralateral touches decreased during both SI-TMS ($p < .01$) and STG-TMS ($p < .04$), without differences between these two conditions ($p = .4$). Other effects (Group, Area, Area × Time, Side × Area × Time, Group × Side, Group × Time, Group × Side × Time, Group × Area × Time, Group × Side × Area × Time) did not reach significance ($p > .3$).

As for response bias, again we found a significant main effect of Time ($F_{2,\ 24} = 7.8, p < .01, p\eta^2 = 0.4$), with lower *c* values when TMS was delivered at 60 msec ($p < .01$) versus 120 and 180 msec. The significant effect of Area ($F_{1,\ 12} = 9.85, p < .01, p\eta^2 = 0.3$) showed a difference between SI-TMS and STG-TMS.[2]

Control Experiments

With OP4 stimulation, the analysis of the perceptual sensitivity showed only a significant main effect of Group ($F_{1,\ 7} = 5.07, p < .05, p\eta^2 = 0.4$), confirming that perceptual sensitivity for touches differing in temporal duration

was significantly lower in deaf than in hearing participants. Other effects (Side, Time, Side × Time, Group × Side, Group × Time, Group × Side × Time) did not reach significance ($p > .4$). With respect to the response criterion, no significant effects emerged ($p > .6$).

When TMS was delivered over OP1 hand representation area during the temporal task in a group of hearing participants, neither sensitivity nor response criterion analysis showed significant effects (Side, Time, Side × Time; $p > .3$).

DISCUSSION

To sum up, in both deaf and hearing subjects, SI seems to contribute to contralateral tactile processing (Hegner et al., 2010) over an early time window (60–120 msec), in agreement with the time course found in previous TMS (Bolognini et al., 2010; Porro et al., 2007; Seyal, Siddiqui, & Hundal, 1997; Cohen, Bandinelli, Sato, Kufta, & Hallett, 1991) and electrophysiological studies (Iguchi, Hoshi, Nemoto, Taira, & Hashimoto, 2007; Caetano & Jousmaki, 2006; Levänen et al., 1998; Hamalainen, Kekoni, Sams, Reinikainen, & Näätänen, 1990; Hari et al., 1990). However, the recruitment of STG differed across subjects, depending on the task. In hearing subjects, STG was recruited at 180 msec in tactile processing, but specifically for discrimination of temporal information. The relatively long latency suggests that somatosensory

input to auditory association areas might be accomplished via afferent feedback connections from the parietal cortex (Musacchia & Schroeder, 2009). Overall, these results in hearing individuals suggest that cortical processing of spatial and temporal features of tactile stimuli are different. Their differences could be ascribed to the intrinsic physical structure of the two stimuli, to the specific way of internally representing spatial versus temporal tactile information and thus to different strategies undertaken in the temporal and spatial tactile discrimination. Spatial versus temporal tactile processing seems, indeed, to involve different neuronal populations (see also Bolognini et al., 2010; Hegner et al., 2010).

Crucially, in deaf subjects, both temporal and spatial tactile processing was disrupted by STG stimulation at an early stage (60–120 msec), showing the same time course as SI. This similarity between SI and STG recruitment in deaf subjects might reflect a comparable functional role played by these areas in the temporal and spatial analysis of touches, as opposed to the findings in hearing individuals. This result is consistent with a cross-modal functional reorganization of the auditory cortex following auditory deprivation (Auer, Bernstein, Sungkarat, & Singh, 2007; Levänen et al., 1998). Future studies in deaf individuals would be relevant to understand whether such additional involvement of STG implies that SI participates at a lesser extent in somatosensory processing in deaf than in hearing individuals, with the recruitment of STG acting as a compensatory mechanism.

It is worth mentioning that volumetric analyses based on MRI data from 25 congenitally deaf subjects and 25 hearing subjects (Emmorey, Allen, Bruss, Schenker, & Damasio, 2003) showed that deaf individuals did not differ from hearing individuals in the total volume of the gray matter in the Heschl's gyrus and STG, although deaf subjects exhibited significantly less white matter. Indeed, increased gray matter volume observed in hearing impaired infants seems to normalize by adulthood (Smith et al., 2011).

Therefore, in deaf individuals, two main results are evident with respect to the performance of hearing individuals: The tactile discrimination of time-related information was impaired, and TMS interfered with STG activity at an early stage of somatosensory processing. To verify whether the impaired tactile temporal sensitivity in deaf individuals was associated with the differential chronometry of STG, a Pearson correlation analysis was run between accuracy (percentage of errors) in the temporal discrimination task at baseline and magnitude of TMS disruption induced over STG at the critical ISIs of 60 and 180 msec. A significant negative correlation was found in the temporal task between the effects of STG-TMS at ISI of 180 msec and baseline accuracy ($r = -0.69$, $p < .01$; see Figure 4). This suggests that the better (low percentage of errors) the accuracy in tactile temporal discrimination, the greater the disruption induced by STG-TMS at 180 msec. Therefore, the somatosensory processing occurring at 180 msec in STG, which is lacking in deaf individuals, seems crucial for the integration of tactile and temporal features. It is noteworthy that in the spatial task we found no correlation between baseline performance and TMS effects over STG ($p > .5$). These findings suggest that the response of the human auditory cortex to somatosensory inputs is specialized for the temporal domain, in agreement with previous evidence, obtained with a different task, showing that enhanced activity in the left auditory association cortex (~150–200 msec of latency), but not in somatosensory areas, is related to an improvement in the ability to discriminate vibrotactile frequencies (Iguchi et al., 2007).

Our results also illustrate the differential consequences in losing a sense early in life. Indeed, the lack of auditory experience in congenitally deaf subjects appears to lead to decreased temporal processing capacity in the somatosensory modality. Early hearing seems, therefore, critical to develop an efficient temporal processing, in agreement with Heming and Brown (2005), who used simultaneity judgments. Very few tactile studies have been performed

Figure 4. Correlation between the level of the behavioral performance on the temporal discrimination task and the TMS effects induced by STG stimulation at 180 msec.
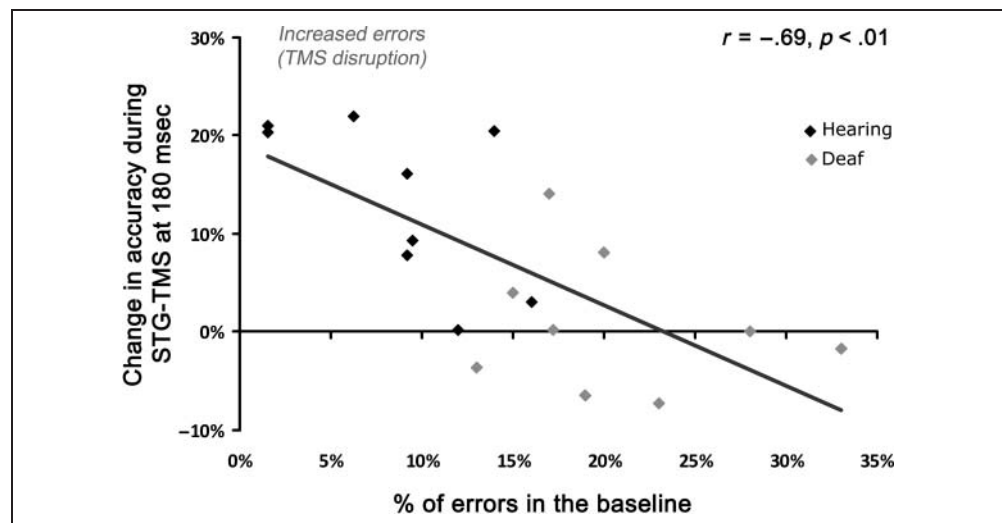
on deaf individuals; in particular, Levänen and Hamdorf (2001) found enhanced tactile sensitivity in deaf adults. However, the enhancement for the deaf individuals was limited to their ability to detect infrequent suprathreshold changes in a stream of frequent stimuli. This task is quite different from ours, because stimulation was perceived bilaterally through a plastic tube. In addition, an auditory noise was used to prevent the hearing subjects from hearing the stimuli, and this might have interfered with their performance. In this study, tactile temporal processing, as measured by means of vibrotactile stimuli, differed in deaf and hearing individuals. There are strong similarities between skin sensation of vibration and hearing, because these two sensory modalities are sensitive to the very same kind of physical property, namely oscillatory patterns generated by mechanical pressure. This kind of physical stimulus is much different from that determining visual experience. Moreover, there are several examples of acoustic influence in the perception of touch (see Soto-Faraco & Deco, 2009, for an extensive review), confirming that temporal frequency is a fundamental property shared by audition and touch (Yau, Olenczak, Dammann, & Bensmaia, 2009). Therefore, when tactile temporal processing is evaluated, it is not surprising to find a lower performance in congenitally deaf people than in normal hearing individuals, although other kinds of tactile stimuli/tasks can be processed/performed as efficiently as in hearing subjects. On a broader multisensory perspective, our results highlight the impact of audition on vibrotactile perception, pointing out to the functional interplay between these senses that seem to relay on a common neural basis within precise time constraints in terms of neural processing.

The deprived auditory cortex would contribute to tactile processing at an early stage. We suggest that the early recruitment of STG for tactile processing may reflect unmasking of preexisting direct cross-modal connections between SI and STG in response to auditory deprivation (Pascual-Leone, Amedi, Fregni, & Merabet, 2005). In line with this, individuals with prelingual hearing impairment, undergoing cochlear implant (CI) in adulthood, might initially report vibrotactile sensations from their CI, an apparently absent phenomenon in CI patients with postlingual-onset impairment (McFeely, Antonelli, Rodriguez, & Holmes, 1998). The involvement of STG in the early tactile analysis suggests that this typically multisensory cortex (Musacchia & Schroeder, 2009; Calvert, 2001) may have expanded its responsiveness to somatosensory stimulation in the absence of competing auditory input (Auer et al., 2007). Additional studies of individuals becoming deaf at different ages should clarify this issue.

Worth mentioning, the stimulation of the parietal operculum, namely the OP1 and OP4 areas, did not impair the temporal processing of touches, either in the deaf individuals or in the hearing participants. This finding is in broadly agreement with the results of a recent fMRI study in humans (Hegner et al., 2010), showing that the parietal operculum is more involved in the processing of the spatial-related information of tactile stimuli than in the processing of temporal (frequency)-related information (but see also Iguchi et al., 2007). However, the parietal operculum, together with the insula bilaterally, seems to be selectively involved in haptic texture processing (Stilla & Sathian, 2008) or tactile roughness perception (Roland, O'Sullivan, & Kawashima, 1998; Ledberg, O'Sullivan, Kinomura, & Roland, 1995), which seems to require frequency discrimination. Possibly, the lack of TMS effects is because of the bilateral contribution of the parietal operculum.

There is, however, an alternative interpretation, namely that the auditory modality might have some special status as compared with other senses with respect to the encoding of temporal information. This would provide an additional reference point for time perception, as has been shown in studies comparing visual and auditory time perception (Guttman, Roy, & Blake, 2005). The absence of such an auditory representation in deaf individuals would result in an impairment extending to tactile stimulus processing. In this case, although the processing of superficial somatosensory qualities of a stimulus would be unimpaired in deaf individuals, they may lack the ability to generate a secondary representation to facilitate their judgments in the temporal domain. This possibility deserves further investigation and could also shed light on the debate concerning dedicated and intrinsic models of time perception (Ivry & Schlerf, 2008).

Finally, it has to be acknowledged the possibility, as briefly mentioned earlier, that factors other than the spatial-temporal distinction could account for our results, because the energy differences due to stimulus duration could not eventually equate those due to varying numbers of stimulus points, as in the spatial task.

In conclusion, the lack of experience with speech might impact on the development of abilities in the temporal domain (Emmorey, 2002). A critical role of language in making comparisons of brief temporal durations has been postulated (Van Allen, Benton, & Gordon, 1966). The sensory systems influence each other during perceptual development (Lewkowicz & Ghazanfar, 2009) and our findings extend this notion for tactile perception, demonstrating that the lost sense plays a preferential role in "instructing" the others—that is, audition for temporal processing. The resulting cross-modal breakdown cannot be overcome or might even be supported by cross-modal plastic brain changes.

Notes

1. The choice of the temporal and spatial tasks was guided by preliminary behavioral experiments conducted in hearing individuals. In those pilot experiments, we systematically changed the parameters of the tactile stimuli in both tasks to opportunely match their level of difficulty, and to obtain at least a 10% of errors in both tasks.

2. To assess the effect of early exposure to sign language, in the two main TMS experiments, for each experimental condition (including the baseline, i.e., no-TMS) the sensitivity and the response criterion of each of the two deaf nonsigners were compared with that of the deaf signers by means of t tests (Crawford & Garthwaite, 2005). No significant difference emerged ($p > .3$ for all comparisons). However, this result needs to be confirmed with larger sample sizes.

REFERENCES

Auer, E. T., Jr., Bernstein, L. E., Sungkarat, W., & Singh, M. (2007). Vibrotactile activation of the auditory cortices in deaf versus hearing adults. *NeuroReport, 18,* 645–648.

Bastings, E. P., Gage, H. D., Greenberg, J. P., Hammond, G., Hernandez, L., Santago, P., et al. (1998). Co-registration of cortical magnetic stimulation and functional magnetic resonance imaging. *NeuroReport, 9,* 1941–1946.

Bolognini, N., & Maravita, A. (2007). Proprioceptive alignment of visual and somatosensory maps in the posterior parietal cortex. *Current Biology, 17,* 1890–1895.

Bolognini, N., Papagno, C., Moroni, D., & Maravita, A. (2010). Tactile temporal processing in the auditory cortex. *Journal of Cognitive Neuroscience, 22,* 1201–1211.

Bolognini, N., Rossetti, A., Maravita, A., & Miniussi, C. (2011). Seeing touch in the somatosensory cortex: A TMS study of the visual perception of touch. *Human Brain Mapping,* doi: 10.1002/hbm.211723.

Bross, M. (1979). Residual sensory capacities of the deaf: A signal detection analysis of a visual discrimination task. *Perceptual and Motor Skills, 48,* 187–194.

Bross, M., & Sauerwein, H. (1980). Signal detection analysis of visual flicker in deaf and hearing individuals. *Perceptual and Motor Skills, 51,* 839–843.

Burton, H., Sinclair, R. J., & McLaren, D. G. (2008). Cortical network for vibrotactile attention: A fMRI study. *Human Brain Mapping, 29,* 207–221.

Caetano, G., & Jousmaki, V. (2006). Evidence of vibrotactile input to human auditory cortex. *Neuroimage, 29,* 15–28.

Calvert, G. A. (2001). Crossmodal processing in the human brain: Insights from functional neuroimaging studies. *Cerebral Cortex, 11,* 1110–1123.

Cohen, J. (1973). Eta-squared and partial eta-squared in fixed factor anova designs. *Educational and Psychological Measurement, 33,* 107–112.

Cohen, L. G., Bandinelli, S., Sato, S., Kufta, C., & Hallett, M. (1991). Attenuation in detection of somatosensory stimuli by transcranial magnetic stimulation. *Electroencephalography and Clinical Neurophysiology, 81,* 366–376.

Crawford, J. R., & Garthwaite, P. H. (2005). Testing for suspected impairments and dissociations in single-case studies in neuropsychology: Evaluation of alternatives using Monte Carlo simulations and revised tests for dissociations. *Neuropsychology, 19,* 318–331.

Eickhoff, S. B., Amunts, K., Mohlberg, H., & Zilles, K. (2006). The human parietal operculum: II. Stereotaxic maps and correlation with functional imaging results. *Cerebral Cortex, 16,* 268–279.

Emmorey, K. (Ed.) (2002). *Language, cognition and the brain. Insights from sign language research*. London: Erlbaum.

Emmorey, K., Allen, J. S., Bruss, J., Schenker, N., & Damasio, H. (2003). A morphometric analysis of auditory brain regions in congenitally deaf adults. *Proceedings of the National Academy of Sciences, U.S.A., 100,* 10049–10054.

Green, D., & Swets, J. (1966). *Signal detection theory and psychophysics*. New York: Wiley.

Guttman, S. E., Roy, L. A., & Blake, R. (2005). Hearing what the eyes see: Auditory encoding of visual temporal sequences. *Psychological Science, 16,* 228–235.

Hamalainen, H., Kekoni, J., Sams, M., Reinikainen, K., & Näätänen, R. (1990). Human somatosensory evoked potentials to mechanical pulses and vibration: Contributions of SI and SII somatosensory cortices to P50 and P100 components. *Electroencephalography and Clinical Neurophysiology, 75,* 13–21.

Hari, R., Hamalainen, H., Hamalainen, M., Kekoni, J., Sams, M., & Tiihonen, J. (1990). Separate finger representations at the human second somatosensory cortex. *Neuroscience, 37,* 245–249.

Harris, J. A., Miniussi, C., Harris, I. M., & Diamond, M. E. (2002). Transient storage of a tactile memory trace in primary somatosensory cortex. *Journal of Neuroscience, 22,* 8720–8725.

Hegner, Y. L., Lee, Y., Grodd, W., & Braun, C. (2010). Comparing tactile pattern and vibrotactile frequency discrimination: A human fMRI study. *Journal of Neurophysiology, 103,* 3115–3122.

Heming, J. E., & Brown, L. N. (2005). Sensory temporal processing in adults with early hearing loss. *Brain and Cognition, 59,* 173–182.

Herwig, U., Schonfeldt-Lecuona, C., Wunderlich, A. P., von Tiesenhausen, C., Thielscher, A., Walter, H., et al. (2001). The navigation of transcranial magnetic stimulation. *Psychiatry Research, 108,* 123–131.

Iguchi, Y., Hoshi, Y., Nemoto, M., Taira, M., & Hashimoto, I. (2007). Co-activation of the secondary somatosensory and auditory cortices facilitates frequency discrimination of vibrotactile stimuli. *Neuroscience, 148,* 461–472.

Ivry, R. B., & Schlerf, J. E. (2008). Dedicated and intrinsic models of time perception. *Trends in Cognitive Neuroscience, 17,* 273–280.

Kowalska, J., & Szelag, E. (2006). The effect of congenital deafness on duration judgment. *Journal of Child Psychology and Psychiatry, 47,* 946–953.

Ledberg, A., O'Sullivan, B. T., Kinomura, S., & Roland, P. (1995). Somatosensory activations of the parietal operculum of man. A PET study. *European Journal of Neuroscience, 7,* 1934–1941.

Levänen, S., & Hamdorf, D. (2001). Feeling vibrations: Enhanced tactile sensitivity in congenitally deaf humans. *Neuroscience Letters, 301,* 75–77.

Levänen, S., Jousmaki, V., & Hari, R. (1998). Vibration-induced auditory-cortex activation in a congenitally deaf adult. *Current Biology, 8,* 869–872.

Lewkowicz, D. J., & Ghazanfar, A. A. (2009). The emergence of multisensory systems through perceptual narrowing. *Trends in Cognitive Science, 13,* 470–478.

McFeely, W. J., Jr., Antonelli, P. J., Rodriguez, F. J., & Holmes, A. E. (1998). Somatosensory phenomena after multichannel cochlear implantation in prelingually deaf adults. *The American Journal of Otology, 19,* 467–471.

McGurk, H., & MacDonald, J. (1976). Hearing lips and seeing voices. *Nature, 264,* 746–748.

Merabet, L. B., & Pascual-Leone, A. (2010). Neural reorganization following sensory loss: The opportunity of change. *Nature Review Neuroscience, 11,* 44–52.

Musacchia, G., & Schroeder, C. E. (2009). Neuronal mechanisms, response dynamics and perceptual functions of multisensory interactions in auditory cortex. *Hearing Research, 258,* 72–79.

Nava, E., Bottari, D., Zampini, M., & Pavani, F. (2008). Visual temporal order judgment in profoundly deaf individuals. *Experimental Brain Research, 190,* 179–188.

Neville, H., & Bavelier, D. (2002). Human brain plasticity: Evidence from sensory deprivation and altered language experience. *Progress in Brain Research, 138,* 177–188.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9,* 97–113.

Pascual-Leone, A., Amedi, A., Fregni, F., & Merabet, L. B. (2005). The plastic human brain cortex. *The Annual Review of Neuroscience, 28,* 377–401.

Pascual-Leone, A., Walsh, V., & Rothwell, J. (2000). Transcranial magnetic stimulation in cognitive neuroscience—virtual lesion, chronometry, and functional connectivity. *Current Opinion in Neurobiology, 10,* 232–237.

Poizner, H., & Tallal, P. (1987). Temporal processing in deaf signers. *Brain and Language, 30,* 52–62.

Porro, C. A., Martinig, M., Facchin, P., Maieron, M., Jones, A. K., & Fadiga, L. (2007). Parietal cortex involvement in the localization of tactile and noxious mechanical stimuli: A transcranial magnetic stimulation study. *Behavioural Brain Research, 178,* 183–189.

Roland, P. E., O'Sullivan, B., & Kawashima, R. (1998). Shape and roughness activate different somatosensory areas in the human brain. *Proceedings of the National Academy of Sciences, U.S.A., 95,* 3295–3300.

Rossi, S., Hallett, M., Rossini, P. M., & Pascual-Leone, A. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology, 120,* 2008–2039.

Schurmann, M., Caetano, G., Hlushchuk, Y., Jousmaki, V., & Hari, R. (2006). Touch activates human auditory cortex. *Neuroimage, 30,* 1325–1331.

Seyal, M., Siddiqui, I., & Hundal, N. S. (1997). Suppression of spatial localization of a cutaneous stimulus following transcranial magnetic pulse stimulation of the sensorimotor cortex. *Electroencephalography and Clinical Neurophysiology, 105,* 24–28.

Smith, K. M., Mecoli, M. D., Altaye, M., Komlos, M., Maitra, R., Eaton, K. P., et al. (2011). Morphometric differences in the Heschl's gyrus of hearing impaired and normal hearing infants. *Cerebral Cortex, 21,* 991–998.

Soto-Faraco, S., & Deco, G. (2009). Multisensory contributions to the perception of vibrotactile events. *Behavioural Brain Research, 196,* 145–154.

Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: Current issues from the perspective of the single neuron. *Nature Reviews Neuroscience, 9,* 255–266.

Stilla, R., & Sathian, K. (2008). Selective visuo-haptic processing of shape and texture. *Human Brain Mapping, 29,* 1123–1138.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotactic atlas of the human brain*. Stuttgart: Thieme Verlag.

Van Allen, M. W., Benton, A. L., & Gordon, M. C. (1966). Temporal discrimination in brain-damaged patients. *Neuropsychologia, 4,* 159–167.

Walsh, V., & Pascual-Leone, A. (2003). *Transcranial magnetic stimulation: A neurochronometrics of mind*. Cambridge, MA: MIT Press.

Yau, J. M., Olenczak, J. B., Dammann, J. F., & Bensmaia, S. J. (2009). Temporal frequency channels are linked across audition and touch. *Current Biology, 19,* 561–566.