

A Double Dissociation between Anterior and Posterior Superior Temporal Gyrus for Processing Audiovisual Speech Demonstrated by Electroencephalography

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Abstract

Human speech can be comprehended using only auditory information from the talker's voice. However, comprehension is improved if the talker's face is visible, especially if the auditory information is degraded as occurs in noisy environments or with hearing loss. We explored the neural substrates of audiovisual speech perception using electrocorticography, direct recording of neural activity using electrodes implanted on the cortical surface. We observed a double dissociation in the responses to audiovisual speech with clear and noisy auditory component within the superior temporal gyrus (STG), a region long known to be important for speech perception. Anterior STG showed greater neural activity to audiovisual speech with clear auditory component, whereas posterior STG showed similar or greater neural activity to audiovisual speech in which

the speech was replaced with speech-like noise. A distinct border between the two response patterns was observed, demarcated by a landmark corresponding to the posterior margin of Heschl's gyrus. To further investigate the computational roles of both regions, we considered Bayesian models of multisensory integration, which predict that combining the independent sources of information available from different modalities should reduce variability in the neural responses. We tested this prediction by measuring the variability of the neural responses to single audiovisual words. Posterior STG showed smaller variability than anterior STG during presentation of audiovisual speech with noisy auditory component. Taken together, these results suggest that posterior STG but not anterior STG is important for multisensory integration of noisy auditory and visual speech. ■

INTRODUCTION

Human speech perception is multisensory, combining auditory information from the talker's voice with visual information from the talker's face. Visual speech information is particularly important in noisy environments in which the auditory speech is difficult to comprehend (Ross, Saint-Amour, Leavitt, Javitt, & Foxe, 2007; Bernstein, Auer, & Takayanagi, 2004; Sumby & Pollack, 1954). Although visual speech can substantially improve the perception of noisy auditory speech, little is known about the neural mechanisms underlying this perceptual benefit.

Speech varies on a timescale of milliseconds, requiring the brain to accurately integrate auditory and visual speech with high temporal fidelity. However, the most popular technique for measuring human brain activity, BOLD fMRI, is an indirect measure of neural activity with a temporal resolution on the order of seconds, making it difficult to accurately measure rapidly changing neural responses to speech. To overcome this limitation, we recorded from the brains of participants implanted with electrodes for the treatment of epilepsy. This technique, known as electro-

corticography, allows for the direct measurement of activity in small populations of neurons with millisecond precision. We measured activity in electrodes implanted over the superior temporal gyrus (STG), a key brain area for speech perception (Mesgarani, Cheung, Johnson, & Chang, 2014; Binder et al., 2000), as participants were presented with audiovisual speech with either clear or noisy auditory or visual components.

The STG is functionally heterogeneous. Regions of anterior STG lateral to Heschl's gyrus are traditionally classified as unisensory auditory association cortex (Rauschecker, 2015). In contrast, regions of posterior STG and STS are known to be multisensory, responding to both auditory and visual stimuli including faces and voices, letters and voices, and recordings and videos of objects (Reale et al., 2007; Miller & D'Esposito, 2005; Beauchamp, Lee, Argall, & Martin, 2004; van Atteveldt, Formisano, Goebel, & Blomert, 2004; Foxe et al., 2002; Calvert, Campbell, & Brammer, 2000).

On the basis of this distinction, we hypothesized that anterior and posterior regions of STG should differ in their electrocorticographic response to clear and noisy audiovisual speech. We expected that auditory association areas in anterior STG should respond strongly to speech with a clear auditory component but show

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a reduced response to the reduced information available in speech with noisy auditory component. Multisensory areas in posterior STG should be able to use the clear visual speech information to compensate for the noisy auditory speech, resulting in similar responses to speech with clear and noisy auditory components.

A related set of predictions comes from theoretical models of Bayesian integration. In these models, sensory noise and the resulting neural variability is independent in each modality. Combining the modalities through multisensory integration results in a decreased neural variability (and improved perceptual accuracy) relative to unisensory stimulation (Fetsch, Pouget, DeAngelis, & Angelaki, 2012; Knill & Pouget, 2004). Bayesian models predict that unisensory areas, such as those in anterior STG, should have greatly increased variability as the sensory noise in their preferred modality increases. Multisensory areas, like those in posterior STG, should be less influenced by the addition of auditory noise, resulting in similar variability for speech with clear and noisy auditory components.

METHODS

Participant Information

All experimental procedures were approved by the institutional review board of Baylor College of Medicine. Five human participants with refractory epilepsy (3 women, mean age = 31 years) were implanted with subdural electrodes guided by clinical requirements. Following surgery, participants were tested while resting comfortably in their hospital bed in the epilepsy monitoring unit.

Stimuli, Experimental Design, and Task

Visual stimuli were presented on an LCD monitor positioned at 57-cm distance from the participant, and auditory stimuli were played through loudspeakers positioned next to the participant's bed. Two video clips of a female talker pronouncing the single syllable words "rain" and "rock" with clear auditory and visual components (AV) were selected from the Hoosier Audiovisual Multitalker Database (Sheffert, Lachs, & Hernandez, 1996). The duration of each video clip was 1.4 sec, and the duration of the auditory stimulus was 520 msec for "rain" and 580 msec for "rock." The auditory word onsets were 410 msec for "rain" and 450 msec for "rock" after the video onset. The face of the talker subtended approximately 15° horizontally and 15° vertically.

Speech stimuli were consisted of four conditions: Speech with clear auditory and visual components (AV), clear visual but noisy auditory components (AnV), clear auditory but noisy visual components (AVn), and finally noisy auditory and noisy visual components (AnVn).

To create speech stimuli with a noisy auditory component, the auditory component of the speech stimulus

was replaced with noise that matched the spectrotemporal power distribution of the original auditory speech. The total power of this speech-specific noise was equated to the total power of the original auditory speech (Schepers, Schneider, Hipp, Engel, & Senkowski, 2013). This process generated speech-like noise.

To create speech stimuli with a noisy visual component, the visual component of the speech stimulus was blurred using a 2-D Gaussian low-pass filter (MATLAB function *fspecial*, filter size = 30 pixels in each direction). Each video frame (image size = 200 × 200 pixels) was filtered separately using 2-D correlation (MATLAB function *imfilter*). Values outside the bounds of the images were assumed to equal the nearest image border. These filter settings resulted in highly blurred videos.

Thirty-two to 56 repetitions of each condition were presented in random sequence. Each 5.4-sec trial consisted of a single 1.4-sec video clip followed by an ISI of 4 sec during which a fixation cross on a gray screen was presented. Participants pressed a mouse button to report which word was presented.

Electrode Localization and Recording

Before surgery, T1-weighted structural MRI scans were used to create cortical surface models (Figure 1A) with FreeSurfer (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999) and visualized using SUMA (Argall, Saad, & Beauchamp, 2006). Participants underwent a whole-head CT after the electrode implantation surgery. The postsurgical CT scan and presurgical MR scan were aligned using AFNI (Cox, 1996), and all electrode positions were marked manually on the structural MR images. Electrode positions were then projected to the nearest node on the cortical surface model using the AFNI program *SurfaceMetrics*. Resulting electrode positions on the cortical surface model were confirmed by comparing them with the photographs taken during the implantation surgery.

A 128-channel Cerebus amplifier (Blackrock Microsystems, Salt Lake City, UT) was used to record from subdural electrodes (Ad-Tech Corporation, Racine, WI) that consisted of platinum alloy discs embedded in a flexible silicon sheet. Electrodes had an exposed surface diameter of 2.3 mm and were located on strips or grids with interelectrode distances of 10 mm. An inactive intracranial electrode implanted facing the skull was used as a reference for recording. Signals were amplified, filtered (low-pass: 500 Hz, Butterworth filter with order 4; high-pass: 0.3 Hz, Butterworth filter with order 1) and digitized at 2 kHz.

Electrophysiological Data Analysis

Data were analyzed in MATLAB 8.5.0 (MathWorks, Inc. Natick, MA) using the FieldTrip toolbox (Oostenveld,

(R Core Team, 2015) to perform a linear mixed effect (LME) analysis of the relationship between the neural response and both fixed and random factors that may influence the response. For the main LME analyses (Tables 1–5), the fixed factors were the location of each electrode (Anterior or Posterior), the presence or absence of auditory noise (Clear A or Noisy A), and the presence or absence of visual noise Clear V or Noisy V. The random factors were the mean response of each electrode across all conditions and the stimulus exemplar. The use of stimulus exemplar as a random factor accounts for differences in response to individual stimuli and allows for inference beyond the levels of the factors tested in the particular experiment (i.e., generalization to other stimuli).

For each fixed factor, the LME analysis produced an estimated effect in units of the dependent variable and a standard error relative to a baseline condition (equivalent to beta weights in linear regression). For the main LME analyses, the baseline condition was always the response to AV speech in anterior electrodes. The full results of all LME analyses and the baseline condition for each analysis are shown in the tables and table legends.

Additional Experiment: Varying Levels of Auditory Noise

In an additional control experiment, we recorded responses to audiovisual speech with varying levels of auditory noise. Similar to the main experiment, for each auditory word, noise that matched the spectrotemporal power distribution of the auditory speech was generated, then noise and the original auditory speech were added together with different weights while keeping the total power constant (Schepers et al., 2013). We parametrically increased the amount of auditory noise in 11 steps from 0% to 100% in 10% increments. Forty-two to 44 repetitions were presented for each noise level. The participant's task was to discriminate between four different words: Rain, Rock, Neck, and Mouth.

Model Creation

A simple Bayesian model was constructed to aid in interpretation of the data (Figure 6) using a recently developed model of human multisensory speech perception (Magnotti & Beauchamp, 2017). Briefly, the high-dimensional neuronal response vector is conceptualized as a point in 2-D space. In this space, the x axis represents auditory feature information and the y axis represents visual feature information. Speech tokens are located at a fixed point in this space (shown in Figure 6 as the black dot at the center of each ellipse). For each presentation of an audiovisual speech stimulus, the brain encodes the auditory and visual information with noise. Over many trials, we characterize the distribution of the encoded speech stimulus as an ellipse. The axes of the ellipse correspond to the relative

precision of the representation along each axis. Modalities are encoded separately, but through extensive experience with audiovisual speech, encoding a unisensory speech stimulus provides some information about the other modality. Although the results are robust across a range of parameters, for demonstration purposes, we assume that the variability of the preferred to non-preferred modality for audiovisual speech with a clear auditory component is 2:1 (shown in Figure 6 as the asymmetry of the ellipses in the auditory and visual representations). The integrated representation is formed according to Bayes rule, which combines the two modalities into a single representation that has smaller variance than either of the component modalities: $\Sigma_{AV} = (\Sigma_A^{-1} + \Sigma_V^{-1})^{-1}$ (Ma, Zhou, Ross, Foxe, & Parra, 2009). For audiovisual speech with noisy auditory component, we assume that the variability in the auditory representation increases by 150% while keeping the relative variability at the same ratio of 2:1 (shown in Figure 6 as larger ellipse). We model the visual representation of speech with noisy auditory component as being either identical to the representation of speech with a clear auditory component or with a gain term that reduces variability by 50% (with the relative variability remaining at 2:1). The multisensory representation is calculated in the same fashion with and without gain.

RESULTS

Across participants, a total of 27 speech-responsive electrodes were identified on the STG. Using the posterior border of Heschl's gyrus as an anatomical landmark, 16 of these electrodes were located over anterior STG and 11 electrodes were located over posterior STG (Figure 1A). We hypothesized that the presence of noise in the speech stimulus (Figure 1B–E) might differentially affect responses in anterior and posterior electrodes. To test this hypothesis, we used the response amplitude in the gamma band as the dependent measure and fit a LME model with electrode location (Anterior vs. Posterior), the presence or absence of auditory noise in the stimulus (Clear A vs. Noisy A), and the presence or absence of visual noise in the stimulus (Clear V vs. Noisy V) as fixed factors. To account for overall differences in response amplitude across electrodes and stimulus exemplars, these were added to the model as random factors.

Amplitude of the Responses to Clear and Noisy Speech

As shown in Table 1, there were three significant effects in the LME model. There was a small but significant effect of electrode location ($p = .01$) driven by a smaller overall response in posterior electrodes (Anterior vs. Posterior: $136 \pm 27\%$ vs. $101 \pm 24\%$, mean signal change from baseline averaged across all stimulus conditions $\pm SEM$) and

Table 1. Linear Mixed-effects Model of the Response Amplitude

<i>Fixed Effects</i>	<i>Estimate</i>	<i>SE</i>	<i>df</i>	<i>t</i>	<i>p</i>
Baseline	183.1	24.8	33.7	7.4	10^{-8}
Auditory noise (An)	-109.6	13.5	188	-8.1	10^{-13}
Posterior location × An	140.6	21.2	188	6.6	10^{-10}
Posterior location	-101	38.7	34.2	-2.6	.01
Visual noise (Vn)	21.6	13.5	188	1.6	.11
An × Vn	-13.3	19.1	188	-0.7	.49
Posterior location × Vn	-8.9	21.2	188	-0.4	.67
Posterior location × An × Vn	3.6	29.9	188	0.1	.91

Results of an LME model of the response amplitude. The fixed effects were the location of each electrode (Anterior vs. Posterior), the presence or absence of auditory noise (An) in the stimulus and the presence or absence of visual noise (Vn) in the stimulus. Electrodes and stimulus exemplar were included in the model as random factors. For each effect, the model estimates (in units of percent signal change) for that factor are shown relative to baseline, the response in anterior electrodes to clear audiovisual speech (AV stimulus condition). The “SE” column shows the standard error of the estimate. The degrees of freedom (“df”), *t* value, and *p* value derived from the model were calculated according to the Satterthwaite approximation, as provided by the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2015). The baseline is shown first; all other effects are ranked by absolute *t* value. Significant effects are shown in **bold**. The significance of the baseline fixed effect is grayed-out because it was prespecified: only electrodes with significant amplitudes were included in the analysis.

two larger effects: the main effect of auditory noise ($p = 10^{-14}$) and the interaction between auditory noise and the location of the electrode ($p = 10^{-10}$). Speech with clear auditory components evoked a larger response than speech with noisy auditory components (Clear A, consisting of the average of the AV and AVn conditions, $151 \pm 27\%$ vs. Noisy A, consisting of the average of the AnV and AnVn conditions, $93 \pm 14\%$, mean \pm SEM across electrodes) driving the main effect of auditory noise. However, the response patterns were very different in anterior and posterior electrodes, leading to the significant interaction in the LME model (Figure 2A). Speech with clear auditory components evoked a larger response than speech with noisy auditory component in anterior electrodes (Clear A vs. Noisy A: $194 \pm 39\%$ vs. $78 \pm 16\%$, mean \pm SEM across electrodes) but speech with clear auditory components evoked a smaller response than speech with noisy auditory component in posterior electrodes ($88 \pm 23\%$ vs. $115 \pm 25\%$).

To determine if the interaction between electrode location and the response to auditory noise was consistent, we plotted the amplitude of the response to Clear A versus Noisy A for all electrodes using one symbol per electrode (Figure 2B). All of the anterior electrodes lay above the line of equality, indicating uniformly larger responses for Clear A, and all of the posterior electrodes lay on or below the line of equality, indicating similar responses for Clear A and Noisy A.

To examine the interaction between location and auditory noise in a single participant, we examined two electrodes: an anterior electrode located just anterior to the A–P boundary and an adjacent electrode located 10 mm more posterior, just across the anterior–posterior boundary (Figure 2C and D). In the anterior electrode, the response to Clear A speech was much larger than the

response to Noisy A speech (Clear A vs. Noisy A: $461 \pm 35\%$ vs. $273 \pm 21\%$, mean across trials \pm SEM; unpaired *t* test across trials: $t(147) = 4.6$, $p = 10^{-6}$), whereas in the adjacent posterior electrode, the response to Clear A speech was similar to the response to Noisy A speech (Clear A vs. Noisy A: $313 \pm 21\%$ vs. $349 \pm 18\%$, $t(147) = 1.3$, $p = .2$). Hence, two electrodes located on either side of the anterior–posterior boundary showed very different patterns of responses to Clear A and Noisy A speech.

To examine the effect of anatomical location on the response to Clear A and Noisy A speech in more detail, we calculated each electrode’s location in a reference frame defined by the STG (Figure 2E) and the difference in the electrode’s response amplitude to Clear A and Noisy A speech (Clear A – Noisy A). First, we examined electrodes sorted by their medial-to-lateral position on the STG and observed no discernible pattern (Figure 2F). Second, we examined electrodes sorted by their anterior-to-posterior position on the STG (Figure 2G). Anterior electrodes showed uniformly positive values for Clear A – Noisy A (Clear A) whereas posterior electrodes showed zero or negative values for Clear A – Noisy A. However, we did not observe a gradient of responses between more anterior and more posterior electrodes, suggesting a sharp transition across the A–P boundary rather than a gradual shift in response properties along the entire extent of the STG. To quantify this observation, we tested two simple models. In the discrete model, there was a sharp transition between response properties on either side of the A–P boundary; in the continuous model, there was a gradual change in response properties across the entire extent of the STG.

For the discrete model, we fit the amplitude versus location points with two constants ($y = b$; horizontal lines with a fixed mean and zero slope, one mean for the anterior electrodes and one for the posterior electrodes;

the coordinates of each electrode. The average location in standard space of the Heschl's gyrus landmark, the boundary between the anterior and posterior STG ROIs, was $y = -27 \pm 2$ (mean across participants $\pm SD$). The mean position in standard space of all anterior electrodes was ($x = \pm 66, y = -18, z = 6$), whereas for posterior electrodes the mean position was ($x = \pm 67, y = -34, z = 12$).

Variability of the Responses to Clear and Noisy Speech

Theoretical models predict that combining the information available about speech content from the auditory and visual modalities should reduce neural variability (Fetsch et al., 2012; Knill & Pouget, 2004); see discussion and Figure 6 for more details. We hypothesized that the presence of noise in the speech stimulus might differentially affect the response variability in anterior and posterior electrodes. To test this hypothesis, we fit the same LME model used to examine response amplitude, except that response variability (CV) was used as the dependent measure. As shown in Table 2, there were three significant effects in the LME model, including an effect of electrode location ($p = .02$) driven by a larger overall response variability in posterior electrodes than in anterior electrodes (Anterior vs. Posterior: $0.85 \pm 24\%$ vs. 0.99 ± 0.1 , mean CV averaged across all stimulus conditions $\pm SEM$). The other two effects showed a larger effect size: the main effect of auditory noise ($p = 10^{-6}$) and the interaction between auditory noise and the location of the electrode ($p = 10^{-8}$).

Speech with Noisy A resulted in larger response variability than speech with Clear A (Clear A vs. Noisy A: 0.89 ± 0.06 vs. 0.93 ± 0.06 , mean $\pm SEM$ across electrodes) driving the main effect of auditory noise in the model. However, the response patterns were very different in anterior and posterior electrodes, leading to the significant interaction (Figure 3A). Speech with noisy auditory compo-

nent resulted in a larger response variability than speech with clear auditory component in anterior electrodes (Clear A vs. Noisy A: 0.73 ± 0.05 vs. 0.96 ± 0.1 , mean $\pm SEM$ across electrodes) but speech with a noisy auditory component resulted in a smaller response variability than speech with a clear auditory component in posterior electrodes (Clear A vs. Noisy A: 1.1 ± 0.1 vs. 0.9 ± 0.1).

To determine if the interaction between electrode location and the response variability for auditory noise was consistent, we plotted the variability of the response to Clear A versus Noisy A for all electrodes using one symbol per electrode (Figure 3B). Most of the anterior electrodes lay below the line of equality, indicating larger variability for Noisy A, whereas most of the posterior electrodes lay above the line of equality, indicating smaller variability for noisy A.

To demonstrate the effect at the single electrode level, we examined the interaction between location and auditory noise in a single participant, we examined two electrodes: an anterior electrode and a posterior electrode (Figure 3C and D). Figure 3C shows the normalized responses for a single anterior electrode for single trials of speech with clear and noisy auditory components. In this anterior electrode, there was variability across trials in both conditions, but the variability was much greater for speech with a noisy auditory component than for speech with a clear auditory component (Clear A vs. Noisy A: 1.1 vs. 1.7, unpaired t test across normalized trial amplitudes: $t(221) = 5.4, p = 10^{-7}$). In a posterior electrode from the same participant (Figure 3B), the opposite pattern was observed: The variability was much greater for speech with a clear auditory component than for speech with a noisy auditory component (Clear A vs. Noisy A: 1.4 vs. 0.9, $t(221) = 5, p = 10^{-6}$). Hence, two electrodes located on either side of the anterior-posterior boundary showed very different patterns of response variability.

To examine the effect of anatomical location on variability, we calculated the difference in each electrode's variability to Clear A and Noisy A speech (CV for

Table 2. Linear Mixed-effects Model of the Response Variability

<i>Fixed Effects</i>	<i>Estimate</i>	<i>SE</i>	<i>df</i>	<i>t</i>	<i>p</i>
Baseline	0.76	0.1	29.8	8	10^{-8}
Posterior location \times An	-0.59	0.1	179.9	-5.7	10^{-7}
Auditory noise (An)	0.31	0.07	180.4	4.6	10^{-5}
Posterior location	0.35	0.14	39.8	2.5	.02
Posterior location \times Vn	-0.13	0.1	179.5	-1.3	.2
Posterior location \times An \times Vn	0.15	0.15	179.5	1	.31
An \times Vn	0.03	0.09	179.6	0.3	.77
Visual noise (Vn)	0.01	0.06	179.5	0.1	.89

Results of an LME model of the response variability measure as CV. The baseline for the model was the response in anterior electrodes to clear audiovisual speech (AV stimulus condition). Baseline is shown first; all other effects are ranked by absolute t value. Significant effects are shown in **bold**.

Table 4. Linear Mixed-effects Model of the Response Onset

<i>Fixed Effects</i>	<i>Estimate</i>	<i>SE</i>	<i>df</i>	<i>t</i>	<i>p</i>
Baseline	81.5	9.2	27.6	8.8	10⁻⁹
Posterior location	17.6	13.6	41.3	1.3	.2
Posterior location × An	-9.1	9.8	187.9	-0.9	.35
An × Vn	-7.1	8.8	187.9	-0.8	.42
Auditory noise (An)	-2.6	6.3	187.9	-0.4	.68
Visual noise (Vn)	-2.6	6.3	187.9	-0.4	.68
Posterior location × An × Vn	5	13.9	187.9	0.4	.72
Posterior location × Vn	-1.3	9.8	187.9	-0.1	.9

Results of an LME model of the response onset. The baseline for the model was the response in anterior electrodes to clear audiovisual speech (AV stimulus condition). Baseline is shown first; all other effects are ranked by absolute *t* value. No factors were significant. Significant effects are shown in **bold**.

interactions (Table 4 and Figure 4D). For the LME model with time-to-peak as the dependent measure (Table 5 and Figure 4E), there was a significant main effect of auditory noise ($p = 10^{-9}$) and an interaction between auditory noise and electrode location ($p = 10^{-4}$) driven by a longer time-to-peak for Clear A speech (Clear A vs. Noisy A: 229 ± 6 msec vs. 197 ± 10 msec, mean across electrodes $\pm SEM$), more so in anterior electrodes (Clear A vs. Noisy A: 232 ± 9 msec vs. 183 ± 14 msec) than posterior electrodes (Clear A vs. Noisy A: 224 ± 6 msec vs. 216 ± 12 msec).

Relationship between Neuronal Responses and Perceptual Accuracy

Participants performed a task that required them to respond to the identity of the word present in each trial. Across participants, only AnVn trials consistently gen-

erated enough errors to compare correct and incorrect trials (AV: $99 \pm 3\%$, AVn: $98 \pm 3\%$, AnV: $81 \pm 20\%$, AnVn: $63 \pm 15\%$; % correct, mean across participants $\pm SD$). To determine the relationship between neuronal response amplitude and behavioral accuracy within AnVn trials, an LME model was constructed with response amplitude as the dependent measure, electrode location (Anterior vs. Posterior), and behavioral accuracy (Correct vs. Incorrect) as fixed factors and stimulus exemplar, participant, and electrode (nested within participant) as random factors (Table 6). In the LME model, the only significant effect was an interaction between electrode location and behavioral accuracy ($p = .01$) driven by smaller amplitudes in correct trials for anterior electrodes (Correct vs. Incorrect: $84 \pm 15\%$ vs. $93 \pm 20\%$, mean gamma power signal change relative to baseline across electrodes $\pm SEM$) but larger amplitudes in correct trials for posterior electrodes (Correct vs. Incorrect: $122 \pm 27\%$ vs. $106 \pm 26\%$). A similar model with CV as the dependent measure did not show any significant effects (Table 7).

Potential Confound: Intelligibility

We observed very different neuronal responses to audiovisual speech with noisy auditory component in anterior compared with posterior electrodes, attributing this difference to the differential contributions of anterior and posterior STG to multisensory integration. However, we used only high levels of auditory noise in our audiovisual speech stimuli. To determine how the level of auditory noise influenced the effect, in one patient we presented audiovisual speech with 11 different levels of auditory noise and examined the neural response in two electrodes located on either side of the anterior–posterior boundary (Figure 5A). First, we examined how these data compared with our previous results by collapsing the 11 different levels of noise into just two categories “low noise” (0–40% noise levels) and “high noise” (50–100% noise levels)

Table 5. Linear Mixed-effects Model of the Response Peak Time

<i>Fixed Effects</i>	<i>Estimate</i>	<i>SE</i>	<i>df</i>	<i>t</i>	<i>p</i>
Baseline	234.3	10.4	36	22.6	10⁻¹⁶
Auditory noise (An)	-46.5	7.4	187.9	-6.3	10⁻⁹
Posterior location × An	45.5	11.5	187.9	3.9	10⁻⁴
Posterior location	-12.5	15.8	41.6	-0.8	.44
Posterior location × Vn	8.7	11.5	187.9	0.8	.45
Visual noise (Vn)	-3.9	7.4	187.9	-0.5	.6
Posterior location × An × Vn	-8.4	16.3	187.9	-0.5	.61
An × Vn	-4.9	10.4	187.9	-0.5	.64

Results of an LME model of the response peak time. The baseline for the model was the response in anterior electrodes to clear audiovisual speech (AV stimulus condition). Baseline is shown first; all other effects are ranked by absolute *t* value. Significant effects are shown in **bold**.

Table 6. Linear Mixed-effects Model of the Effect of Accuracy on Response Amplitude

<i>Fixed Effects</i>	<i>Estimate</i>	<i>SE</i>	<i>df</i>	<i>t</i>	<i>p</i>
Baseline	105.2	36.1	4.2	2.9	.04
Incorrect responses × Posterior location	-25.6	10.2	65.8	-2.5	.01
Incorrect responses	11.3	6.6	66.1	1.7	.09
Posterior location	19.6	21.8	22.8	0.9	.38

Results of an LME model on the relationship between response amplitude and behavioral accuracy for auditory noise, visual noisy audiovisual speech (AnVn stimulus condition). The fixed effects were the location of each electrode (Anterior vs. Posterior) and the behavioral accuracy of the participant's responses (Correct vs. Incorrect). Participants, electrodes nested in participants, and stimulus exemplar were included in the model as random factors. The baseline for the model was the response in anterior electrodes for correct behavioral responses. Baseline is shown first; all other effects are ranked by absolute *t* value. Significant effects are shown in **bold**.

similar to our initial analysis of Clear A and Noisy A audiovisual speech (Figure 5B). The responses were similar to that observed with just two levels of noise (compare Figure 5B and Figure 2A). An LME model fit to the data across the different noise levels (Table 8) showed significant effects of noise level ($p = 10^{-16}$), electrode location ($p = 10^{-16}$), and an interaction between noise level and location ($p = 10^{-16}$), driven by significantly greater response in anterior electrodes to low noise stimuli (Low vs. High: $248 \pm 13\%$ vs. $124 \pm 8\%$, mean across trials $\pm SEM$) and similar responses in posterior electrodes to low and high noise conditions (Low vs. High: $95 \pm 5\%$ vs. $115 \pm 5\%$). Next, we examined the response to each different level of auditory noise. In the anterior electrode, increasing levels of auditory noise led to smaller responses, whereas in the posterior electrode, increasing levels of auditory noise led to similar or slightly larger gamma band responses (Figure 5C). We quantified this by fitting a line to the anterior and posterior electrode responses at 11 different auditory noise levels. The anterior electrode fit was significant ($R^2 = .9, p = 10^{-6}$) with a negative slope ($m = -24$), whereas the posterior electrode fit was not significant ($R^2 = .07, p = .4$) with a slightly positive slope ($m = 1.32$).

The participant performed at a high level of accuracy even in trials with a high level of auditory noise (zero errors) demonstrating that the visual speech information was able to compensate for the increased levels of auditory noise.

DISCUSSION

We observed a double dissociation in the responses to audiovisual speech with clear and noisy auditory components for both amplitude and variability measures. In anterior STG, the amplitude of the high-gamma response was greater for speech with clear auditory components than for speech with noisy auditory components, whereas in posterior STG, responses were similar or slightly greater for speech with noisy auditory component. In anterior STG, the CV across single trials was greater for speech with noisy auditory component, whereas in posterior STG, it was greater for speech with clear auditory components.

These data are best understood within the framework of Bayes optimal models of multisensory integration (Alais & Burr, 2004; Ernst & Banks, 2002) and speech perception (Bejjanki, Clayards, Knill, & Aslin, 2011; Ma et al., 2009). In these models, different sensory modalities are posited to contain independent sources of environmental and sensory noise. Because of the independence of noise sources across modality, Bayesian integration results in a multisensory representation that has smaller variance than either of the unisensory variances (Fetsch et al., 2012; Knill & Pouget, 2004).

Recently, a Bayesian model of causal inference in audiovisual speech perception was proposed (Magnotti & Beauchamp, 2017). Figure 6 shows an application of this model to our data. We assume that anterior STG contains

Table 7. Linear Mixed-effects Model of the Effect of Accuracy on Response Variability

<i>Fixed Effects</i>	<i>Estimate</i>	<i>SE</i>	<i>df</i>	<i>t</i>	<i>p</i>
Baseline	1	0.19	7	5.4	10^{-3}
Posterior location	-0.13	0.2	31.3	0.6	.53
Incorrect responses	0.02	0.11	67.1	0.2	.86
Incorrect responses × Posterior location	0.01	0.17	66.5	0.1	.95

Results of an LME model on the relationship between response variability (CV) and behavioral accuracy for noisy auditory and noisy visual speech (AnVn stimulus condition). The baseline for the model was the response in anterior electrodes for correct behavioral responses. Baseline is shown first; all other effects are ranked by absolute *t* value. No factors were significant. Significant effects are shown in **bold**.

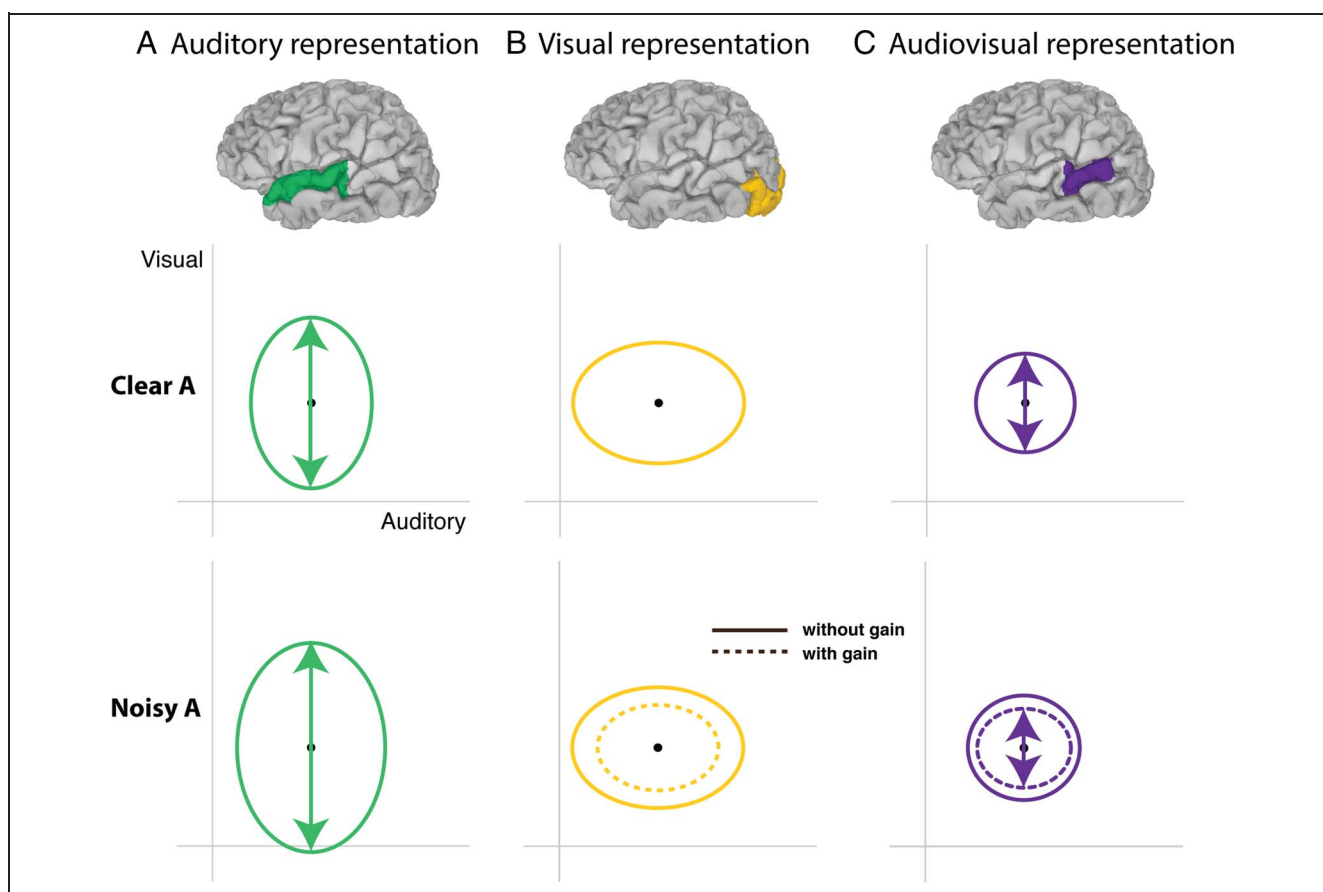


Figure 6. Bayesian model of audiovisual speech with auditory noise. (A) The model assumes that a neural representation of the auditory component of audiovisual speech exists in anterior STG (top row: brain region colored green). The high-dimensional neural representation is projected onto a 2-D space (middle and bottom rows) in which the x axis represents auditory feature information and the y axis represents visual feature information. The stimulus representation is shown as an ellipse indicating the cross-trial variability in representation of an identical physical stimulus due to sensory noise. For audiovisual speech with clear auditory component (Clear A) in anterior STG (green ellipse in middle row), there is less variability along the auditory axis and more variability along the visual axis, indicated by the shape of the ellipse. For audiovisual speech with noisy auditory component (Noisy A) in anterior STG (green ellipse in bottom row), there is greater variability along both axes due to the added stimulus noise (see Methods for details). (B) The model assumes that a neural representation of the visual component of audiovisual speech exists in lateral extrastriate visual cortex (top row: brain region colored yellow). In the visual representation, there is less variability along the visual axis and more variability along the auditory axis, indicated by the shape of the ellipse. For audiovisual speech with noisy auditory component (Noisy A), the visual component of the speech is identical, so the representation should be identical (yellow ellipse in bottom row). However, evidence from Schepers et al. (2015) demonstrates that response in visual cortex to Noisy A speech is actually greater than to Clear A speech, suggesting an increase in gain due to attentional modulation or other top-down factors. The representation with gain modulation is shown with the dashed yellow ellipse. (C) The model assumes that a neural representation that integrates both auditory and visual components of audiovisual speech exists in posterior STG (top row: brain region colored purple). Because of the principles of Bayesian integration, this representation has smaller variability than either the auditory representation or the visual representation (compare size of purple ellipse in each row with green and yellow ellipses). Assuming gain modulation, the integrated representation of Noisy A speech (dashed purple ellipse in bottom row) has smaller variability than the representation of Clear A speech (purple ellipse in middle row).

that increase the gain in visual cortex, similar to attentional modulation in which representations in visual cortex are heightened and/or sharpened by spatial or featural attention (Maunsell & Treue, 2006; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). This gain increase would be adaptive because it would increase the likelihood of decoding speech from visual cortex under conditions of low or no auditory information, at the cost of additional deployment of attentional and neural resources. We implemented this gain modulation in our Bayesian model as reduced variance in the visual representation for Noisy A compared with

Clear A speech. When this visual representation with reduced variance is integrated with the noisy auditory representation, the resulting multisensory representation becomes more focal for Noisy A than Clear A speech, a fit to the observed increased amplitude and reduced variability for Noisy A compared with Clear A speech in posterior STG.

Although the Bayesian model provides a conceptual framework for understanding how multisensory integration could affect the amplitude and variance of neuronal population responses, it is agnostic about the actual stimulus features important for integration. We did not

observe a main effect of visual noise (or an interaction between visual noise and auditory noise) LME on amplitude and variance (Tables 1 and 2). Most of the relevant information provided by the visual signal during auditory–visual speech perception is related to the timing of mouth opening and closing relative to auditory speech. The blurring procedure used to generate the noisy visual speech may leave this timing information intact.

Our Bayesian model also does not make explicit predictions about the latency or duration of the neuronal response. However, we observed the same pattern of double dissociation between anterior and posterior STG for response duration as in other response measures. At the high levels of auditory noise used in our experiments, the auditory representation contains little useful information, so it would be adaptive for top–down modulation to decrease both the amplitude and duration of activity in the anterior STG for Noisy A speech. Interestingly, the absolute duration of the response in posterior STG during Noisy A speech was the same as the absolute duration of the response in anterior STG during Clear A speech (210 msec), raising the possibility that this is the time frame of the selection process in which the competing unisensory and multisensory representations are selected for perception and action.

An interaction between electrode location and response amplitude was also observed in an analysis of perceptual accuracy (only speech with both noisy auditory and noisy visual component generates enough errors for this analysis). In anterior electrodes, responses were larger for incorrect trials, whereas in posterior electrode responses were larger for correct trials. This supports the idea that posterior electrodes are particularly important in the perception of noisy speech, with larger amplitude indicating a more focal peak of activity in the population code and less uncertainty about the presented stimulus.

Anterior versus Posterior Anatomical Specialization

There was a strikingly sharp boundary between the anterior and posterior response patterns, suggesting that anterior and posterior STG are functionally distinct. We divided STG at the posterior border of Heschl’s gyrus (mean $y = -27$), a landmark that also has been used in previous neuroimaging studies of speech processing (Okada et al., 2010; Specht & Reul, 2003; Hickok & Poeppel, 2000). A functional division in STG near Heschl’s gyrus is consistent with the division of the auditory system into two processing streams, one of which runs anterior–ventral from Heschl’s gyrus and one of which runs posterior–dorsal (Pickles, 2015; Rauschecker, 2015). These two streams are often characterized as specialized for processing “what” or object identity features (anterior–ventral) and “where” or object location features (posterior–dorsal) by analogy with the different streams of visual processing (Mishkin & Ungerleider, 1982). However, these labels do not

neatly map onto an anterior preference for clear speech and a posterior preference for noisy speech (Leonard & Chang, 2014) and may reflect preferences for different rates of spectrotemporal modulation (Hullett, Hamilton, Mesgarani, Schreiner, & Chang, 2016).

Although we are not aware of previous studies examining changes in the neural variability to Clear A and Noisy A audiovisual speech, a number of neuroimaging studies have reported A–P differences in the amplitude of the neural response to Clear A and Noisy A audiovisual speech. Stevenson and James (2009) presented clear audiovisual speech and audiovisual speech with noise added to both modalities (noisy auditory + noisy visual), contrasting both against a standard baseline condition consisting of simple visual fixation. Anterior regions of STG/STS showed greater responses to clear than noisy audiovisual speech (Figure 5C and Table 3 in their paper, $y = -20$ compared with $y = -18$ in this study, mean across left and right hemispheres). Their results slightly differ from ours because they showed that posterior STG/STS (Figure 5D and Table 1 in their paper, $y = -37$, compared with $y = -34$ in this study) displays relatively weak responses to moderately noisy speech. This could be explained by their use of noisy auditory + noisy visual speech versus our use of noisy auditory + clear visual speech: If posterior regions respond to both auditory and visual speech information, degraded visual information might be expected to reduce response amplitudes in posterior regions.

Consistent with these results, Lee and Noppeney (2011) found that anterior STG/STS ($y = -16$, their Table 2) showed significant audiovisual interactions only for clear speech, whereas posterior STG/STS (mean $y = -36$, Table 2 in their paper) showed interactions for both clear and noisy audiovisual speech.

Bishop and Miller (2009) reported greater responses to clear versus noisy audiovisual speech in anterior regions of STG (Table 1 in their paper, $y = -13$ mean across left and right hemispheres), whereas McGettigan and colleagues (2012) reported greater responses for clear than noisy audiovisual speech in both anterior STG ($y = -12$, Table 1 in their paper) and posterior STG ($y = -42$).

Although most neuroimaging studies have reported greater responses to clear than noisy audiovisual speech, two studies have reported the opposite result of greater responses to noisy speech in the STG (Callan et al., 2003; Sekiyama, Kanno, Miura, & Sugita, 2003). However, the interpretation of these studies is complex. Sekiyama and colleagues tested clear and noisy speech consisting of incongruent audiovisual speech (including McGurk syllables) that are known to evoke responses in STS that are both different from congruent syllables and vary markedly from participant to participant (Erickson et al., 2014; Nath & Beauchamp, 2012). Callan and colleagues performed an analysis in which they first subtracted the response to auditory-only clear speech from the response to audiovisual clear speech, then subtracted

the response to auditory-only noisy speech from the response to audiovisual noisy speech, and finally subtracted the two differences. Without a direct comparison between clear and noisy audiovisual speech, it is possible that the reported preference for noisy audiovisual speech was driven by the intermediate analysis step in which the auditory-only response was subtracted from the audiovisual response. For instance, even if clear and noisy audiovisual speech evoked the exact same response, a weak response to auditory-only noisy speech and a strong response to auditory-only clear speech (a pattern observed in a number of studies, see below) would result in the reported greater response to noisy audiovisual speech.

The idea of an A–P double dissociation is also generally supported by the neuroimaging literature examining brain responses to clear and noisy auditory-only speech, although the many differences in the stimulus materials, task manipulations, and data analysis strategies makes direct comparisons difficult. Obleser, Zimmermann, Van Meter, and Rauschecker (2007) reported a double dissociation, with posterior regions ($y = -26$, Table 1 in their paper) preferring noisy speech to clear speech, whereas anterior regions ($y = -18$) preferred clear speech to noisy speech. A double dissociation was also reported by Du, Buchsbaum, Grady, and Alain (2014): Anterior regions of STG ($y = -15$, Table S2 in their paper) showed greater BOLD amplitude with less auditory noise, whereas posterior regions ($y = -32$) showed greater BOLD amplitude with more auditory noise. Similarly, Wild, Davis, and Johnsrude (2012) found that anterior regions of STG ($y = -12$, Table 1 in their paper) preferred clear to noisy speech, whereas posterior regions ($y = -30$) preferred noisy speech to clear speech.

Single dissociations consistent with an anterior preference for clear speech are also common in the literature. Scott, Blank, Rosen, and Wise (2000) found that anterior regions ($y = -12$) showed greater response amplitudes for clear speech, whereas posterior regions ($y = -38$, Figure 2A in their paper) showed similar response amplitudes. Giraud and colleagues (2004) also reported greater response amplitudes for clear than noisy speech in anterior STG (Table 1 in their paper, $y = -4$ mean across left and right hemispheres) but not posterior STG.

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