Categorical encoding of speech sounds: beyond auditory cortices

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Abstract

What processes lead to categorical perception of speech sounds? Investigation of this question is hampered by the fact that categorical speech perception is normally confounded by acoustic differences in the stimulus. By using ambiguous sounds, however, it is possible to dissociate acoustic from perceptual stimulus representations. We used a binaural integration task, where the inputs to the two ears were complementary so that phonemic identity emerged from their integration into a single percept. Twenty-seven normally hearing individuals took part in an fMRI study in which they were presented with an ambiguous syllable (intermediate between /da/ and /ga/) in one ear and with a meaning-differentiating acoustic feature (third formant) in the other ear. Multi-voxel pattern searchlight analysis was used to identify brain areas that consistently differentiated between response patterns associated with different syllable reports. By comparing responses to different stimuli with identical syllable reports and identical stimuli with different syllable reports, we disambiguated whether these regions primarily differentiated the acoustics of the stimuli or the syllable report. We found that BOLD activity patterns in the left anterior insula (AI), the left supplementary motor cortex, the left ventral motor cortex and the right motor and somatosensory cortex (M1/S1) represent listeners' syllable report irrespective of stimulus acoustics. The same areas have been previously implicated in decision-making (AI), response selection (SMA), and response initiation and feedback (M1/S1). Our results indicate that the emergence of categorical speech sounds implicates decision-making mechanisms and auditory-motor transformations acting on sensory inputs.

Keywords: Speech perception; Auditory; MVPA; fMRI; Dichotic listening

Significance statement

A central question in psycholinguistic research is whether speech sounds are neutrally coded as abstract perceptual units that are distinct from the sensory cues from which they are derived. One challenge for most studies of perception is to overcome that perceptual interpretations of sensory stimuli may be confounded by physical properties of the stimuli. Here, we use functional magnetic resonance imaging (fMRI) and multi-voxel pattern analysis (MVPA) to address the question of where in the cerebral cortex syllable percepts emerge during binaural integration. By controlling for physical stimulus acoustics, we find that the perceptual report of syllables arises in higher-order non-auditory cortical areas. This opens up the possibility that these areas determine the syllables we hear.

1 Introduction

The mapping of sensory information onto common categories is a fundamental feature of human cognition. For example, we can identify a familiar person on different photographs even if taken from different angles. Likewise, we can map speech sounds onto common words even if uttered from different speakers. Categorical perception in speech was described first by Liberman and colleagues (1957) who showed that synthetic syllables along the continuum between prototypes (e.g., /ba/ vs /da/) were perceived categorically despite their linear acoustic variations. However, it remains unclear how the brain maps the large variety of sensory signals to a limited number of invariant categories.

The neural mechanisms that underlie categorical speech perception have been attributed to different brain regions (Myers et al., 2009). One view is that phonetic invariance is based on acoustic stimulus processing (Blumstein and Stevens, 1981; Diehl et al., 2004) in the auditory association cortex (e.g. the superior temporal gyrus (STG) and the superior temporal (STS)). Evidence comes from studies which identified phonetic representations in STG/STS using fMRI and intracranial recordings (Formisano et al., 2008; Chang et al., 2010; Kilian-Hütten et al., 2011; Mesgarani et al., 2014; Arsenault and Buchsbaum, 2015; Yi et al., 2019; Levy and Wilson, 2020).

Alternatively, the acoustic input may be mapped onto motor patterns or gestures used in producing speech (Liberman et al., 1967). Evidence comes from fMRI studies showing activation (Pulvermüller et al., 2006; Hervais-Adelman et al., 2012) and phoneme identity representations (Lee et al., 2012; Chevillet et al., 2013; Du et al., 2014; Evans and Davis, 2015; Cheung et al., 2016) in motor cortex. Converging evidence is provided by non-invasive brain stimulation studies which perturbed phoneme perception when applied directly over the motor cortex (D'Ausilio et al., 2009; Möttönen and Watkins, 2009; Smalle et al., 2015).

Further, invariant categorical percepts may arise from decision-making mechanisms, i.e. acoustic-to-phoneme mapping is seen as an active cognitive process wherein multiple hypotheses regarding the interpretation of the acoustic pattern are tested (Magnuson and Nusbaum, 2007). Evidence is provided by studies finding invariant neural responses in frontal areas involved in executive processing like the inferior frontal gyrus (Hasson et al., 2007; Myers et al., 2009; Lee et al., 2012). Eventually, it was proposed that invariant percepts arise from mapping the speech input onto higher-level phonological representations. In this case, invariant neural responses to speech sounds of the same category emerge in parietal areas, such as the

left angular gyrus (Blumstein et al., 2005) and the left supramarginal gyrus (Caplan et al., 1995; Zevin and McCandliss, 2005; Raizada and Poldrack, 2007).

A major methodological challenge is to identify brain regions in which neural activity tracks the perceived speech rather than its sensory properties. For instance, if physically different stimuli are used as exemplars of different categories, the perceptual representation of the stimulus is confounded with its physical properties. One approach to overcome this problem is to employ ambiguous stimuli that can elicit different percepts in order to identify brain regions that represent the perceptual report of the participant given the same acoustic stimulus (Kilian-Hütten et al., 2011; Lee et al., 2012). This approach, however, weights perceptual representations resulting from maximal sensory uncertainty more strongly, which may not generalize well to situations with higher sensory evidence.

We presented ambiguous (intermediate between /ga/ and /da/) and unambiguous stimuli (clear /ga/ vs. /da/) together with a meaning-differentiating speech feature (high vs low F3) in a binaural integration paradigm. In the ambiguous condition, the input to each ear was incomplete but complementary so that the perceived syllable identity emerged from the combination of the inputs into a single percept. In the unambiguous condition, the stimulus could be interpreted based on monaural input alone (see Fig. 1).

We used fMRI and searchlight MVPA (Kriegeskorte et al., 2006) to identify brain areas which differentiated between different syllable reports (/ga/ and /da/). In contrast to previous studies (Kilian-Hütten et al., 2011; Lee et al., 2012), we aimed to identify regions that consistently differentiate perceptual reports of both unambiguous and ambiguous stimuli. We tested whether the identified brain regions carry information about the perceived speech (/da/ vs /ga/ response) alone, or its acoustic properties (high vs low F3).

2 Material & Methods

2.1 Participants

Twenty-seven right-handed listeners with no history of hearing impairment (M=21.89 years, SD=3.14, 8 male) took part. The present analysis is based on a dataset collected as part of our previous research on the influence of transcranial brain stimulation on binaural integration (Preisig et al., 2021). All participants had normal or corrected-to-normal visual acuity. The participants reported no history of neurological, psychiatric, nor hearing disorders. All participants had normal hearing (hearing thresholds of less than 25 dB HL at 250, 500, 750,

1000, 1500, 3000, and 4000 Hz, tested on each ear using pure tone audiometry) and no threshold difference between the left ear (LE) and the right ear (RE) larger than 5dB for any of the tested frequencies. All participants gave written informed consent prior to the experiment. This study was approved by the local research ethics committee (CMO region Arnhem-Nijmegen) and was conducted in accordance with the principles of the latest Declaration of Helsinki.

2.2 Experimental Design and Task

The dataset reported in this article comprised four task fMRI runs and one fMRI run with passive listening. The data from four additional task runs during which participants underwent non-invasive brain stimulation are reported elsewhere (Preisig et al., 2021).

Each task fMRI run comprised 128 trials, 88 trials included the presentation of an auditory stimulus (4 trials included sham ramps which were thus discarded). The detailed description of auditory stimuli can be found in our previous reports (Preisig and Sjerps, 2019; Preisig et al., 2020, 2021). Each task fMRI run included 60 binaural integration trials for which the F3 frequency of the RE stimulus was set at the individual category boundary and 24 unambiguous control trials for which the F3 component of the RE stimulus supported 12 times a clear /da/ and 12 times a clear /ga/ interpretation (see Fig. 1). For binaural integration trials, the LE stimulus was 30 times the high F3 and 30 times the low F3. For control trials, LE stimulus included a F3 cue with the same F3 frequency as the RE stimulus. Control trials did not require interhemispheric integration for disambiguation because they could be readily identified based on monaural input alone, i.e., the unambiguous /da/ or /ga/ stimulus presented to the RE.

During task fMRI, each trial was 3 s long (equal to the repetition time of the fMRI sequence) and started with the acquisition of a single fMRI volume (TA = 930 ms). The auditory stimulus was presented approximately 1750 ms after trial onset (Preisig et al., 2021). The presentation of the auditory stimulus lasted 250ms. The participant's response window corresponded to the interval from auditory stimulus onset to 70 ms before the onset of the next trial.

The passive listening fMRI run consisted of 336 trials, 96 trials included auditory stimuli: 48 binaural integration trials and 48 unambiguous trials. Passive listening trials were 2 s long (equal to the repetition time of the fMRI sequence). The auditory stimulus was presented between 1450 and 1550 ms after trial onset. The presentation of the auditory stimulus lasted 250ms.

For additional details on the stimulus presentation see Preisig et al. (2021).

2.3 MRI data acquisition and preprocessing

Anatomical and functional MRI data were acquired with a 3-Tesla Siemens Prisma scanner using a 64-channel head coil. A 3-dimensional high-resolution T1-weighted anatomical volume was acquired using a 3D MPRAGE sequence with the following parameters: repetition time (TR) / inversion time (TI) / echo time (TE) = 2300/1100/3ms, 8° flip angle, FOV 256x216x176 and a 1x1x1 mm isotropic resolution. Parallel imaging (iPAT = GRAPPA) was used to accelerate the acquisition. The acquisition time (TA) of the T1-weighted images was 5 min and 21 sec.

fMRI data was acquired with sparse imaging to minimize the impact of EPI gradient noise during presentation of auditory stimuli (Hall et al., 1999). For this purpose, a delay was introduced in the TR during which the auditory stimuli were presented. This delay was 2070ms during task fMRI and 1070 ms during the passive listening run. For task fMRI each run included 128 echo planar imaging (EPI) volumes. The passive listening run included 336 EPI volumes. Each scan comprised 66 slices of 2mm thickness which were acquired using a interleaved acquisition sequence with multi-band acceleration (TR_{task}: 3000 ms, TR_{passive listening}: 2000 ms, TA: 930 ms, TE: 34 ms, flip angle: 90 deg, matrix size: 104x104x66, in plane resolution: 2x2x2mm, Multi-band accel. factor: 6x).

fMRI data were pre-processed in SPM12 (<http://www.fil.ion.ucl.ac.uk/spm>). Preprocessing included the following steps: (1) functional realignment and unwarping, (2) co-registration of the structural image to the mean EPI, (3) normalization of the structural image to a standard template, (4) application of the normalization parameters to all EPI volumes, and (5) spatial smoothing using a Gaussian kernel with a full-width at half maximum of 8 mm.

2.4 Univariate analyses

For the univariate analyses, voxel-wise BOLD activity was modeled by means of a single subject first-level General Linear Model (GLM) using normalized and spatially smoothed images. The model included one regressor coding the onsets of the auditory stimuli and one regressor coding the onset of the participants' button presses during task fMRI. The onsets of the button presses during task fMRI were modelled to account for the BOLD signal variability resulting from different response latencies. For each run, six realignment regressors accounting for movement-related effects and a constant term per functional imaging run were included in the model.

For each participant, T-contrasts (all auditory stimuli > implicit baseline) were computed to identify brain regions that responded significantly to auditory stimuli during passive listening and task. Contrast maps from each subject were summarized at the group level using a one-sample t-test (Fig. 2 & Fig. 3). Based on the task-evoked activation map, a binary mask was generated at a voxelwise threshold of $p < .001$.

2.5 Multi voxel pattern analysis (MVPA)

The MVPA analysis was carried out in subjects' native image space using realigned and unwrapped EPI images (Kriegeskorte et al., 2006). A first-level design matrix was specified including one regressor per condition: unambiguous /da/ report, unambiguous /ga/ report, ambiguous /da/ report, ambiguous /ga/ report. Further, the model included a regressor coding the onset of the participants' button presses. As above, six realignment regressors were further included to account for movement-related effects and a constant term per functional imaging run.

We constrained our MVPA analysis to areas that significantly responded to sound during task fMRI at the group level. For each participant, an individual task-evoked activation map was created by warping the group-level mask (for details see univariate analyses) into the subject's native space using the inverse normalization parameters.

Afterwards, we conducted an MVPA searchlight analysis (sphere radius 8mm, equivalent to 251 voxels) within sound responsive areas to identify brain regions in which different syllable reports (/da/ vs /ga/) elicited distinct spatial BOLD response patterns. To evaluate the representational consistency across unambiguous and ambiguous stimuli, an encoding model was specified using the TDT toolbox (Hebart et al., 2015) such that the fitted regression coefficients (beta values) from the unambiguous trials were used for the training and the beta values from ambiguous trials were used for the test set.

For statistical inference, we computed the crossnobis distance between the response patterns associated with /da/ and /ga/ syllable reports. The crossnobis distance is the cross-validated version of the Mahalanobis distance (multivariate noise normalized Euclidean distance) (Kriegeskorte et al., 2006; Walther et al., 2016). Here, we computed the crossnobis distance using a leave-one-run-out procedure (Allefeld and Haynes, 2014). In each of four cross-validation folds, the beta-value maps derived from unambiguous trials from three fMRI runs were cross-validated against the beta-value maps including ambiguous trials from the left-out run. Cross-validation ensures that the distance is zero if two voxel patterns are not statistically

different from each other, making crossnobis distance a suitable summary statistic for group-level inference (e.g. with the one-sample t-test). Note that because of this cross-validation, the crossnobis distance can take negative values if its true value is close to zero in the presence of noise (Sohoglu et al., 2020).

For group-level inference, individual crossnobis distance maps were normalized and smoothed (using a Gaussian kernel with a full-width at half maximum of 8 mm) and then entered into a group level random-effects analysis using permutation-based nonparametric statistics in SNPM (<http://www2.warwick.ac.uk/fac/sci/statistics/staff/academic-research/nichols/software>).

Family-wise error correction (FWE) for multiple comparisons across voxels was applied at a threshold of $p < .05$.

3 Results

3.1 Binaural integration

Twenty-seven participants listened to ambiguous syllables (intermediate between /ga/ and /da/), whose perceived identity depends upon binaural integration, and to unambiguous syllables (clear /ga/ vs. /da/) that could be readily interpreted based on monaural input (for details see Material & Methods). During task fMRI, participants reported on every trial whether they heard a /da/ or a /ga/ syllable.

Behavioral analyses indicated that participants reliably integrate the speech feature (high vs low F3) in the binaural integration condition. Participants answered on average with $25.40 \pm 2.80\%$ (mean $\pm$ SEM) /ga/ responses and $70.60\% \pm 3.00\%$ /da/ responses to ambiguous syllables combined with the high F3 and $75.00\% \pm 3.5\%$ /ga/ responses and $20.70\% \pm 3.10\%$ /da/ responses for ambiguous syllables combined with the low F3.

The probability of reporting an unambiguous stimulus with low or high F3 respectively as a /ga/ or /da/ syllable was high: Participants gave on average $84.4\% \pm 2.2\%$ /da/ responses to unambiguous /da/ stimuli, and $87.4 \pm 1.8\%$ (mean $\pm$ SEM) /ga/ responses were registered for unambiguous /ga/ stimuli.

Figure 1. Adapted from (Preisig et al., 2021). (Center) Schematic illustration of the processing pathway underlying binaural integration. The green line indicates the propagation of acoustic input from the left ear to the right auditory cortex and from the right ear to the left auditory cortex. The black line illustrates the interhemispheric connection between the auditory cortices via the corpus callosum. (Left) Sound pressure waveform and corresponding sound spectrogram of the non-speech acoustic feature (F3) presented to the left ear. (Upper left) High F3 supporting a /da/ interpretation. (Lower left) Low F3 supporting a /ga/ interpretation. (Right) Sound pressure waveform and corresponding spectrogram of the syllables presented to the right ear. (Upper right) Ambiguous speech sound intermediate to the syllables /da/ and /ga/. (Lower right) Unambiguous /ga/ and /da/ syllables. The red lines in the spectrogram highlight the spectral area of stimulus manipulation.

3.2 Auditory activation during passive listening and task

In order to localize areas that respond to our syllable stimuli in the absence of any task and motor response, we mapped auditory-evoked activity during passive listening. Further, we also mapped the areas that were additionally activated by the task (see Figure 3B). For this purpose, we examined BOLD responses on all trials, contrasted with the baseline (see Methods). During passive listening and task, whole-brain analysis revealed an extended bilateral brain network including the bilateral supratemporal plane, inferior frontal areas, and motor cortical areas (see Fig. 2). In the task blocks, we observed more extensive activation in these cortical areas and

additional occipital as well as subcortical activation. Based on the task-evoked activation map, a binary mask was generated at a voxelwise threshold of $p < .001$ for subsequent searchlight MVPA.

Figure 2. Results of the univariate analyses. For each participant, T-contrasts (all trials > baseline) were computed to identify brain regions that responded significantly to auditory stimuli and the task. Contrast maps from each subject were statistically assessed at the group level using a one-sample t-test. Based on this map of sound- and task-evoked responses, a binary mask was computed at a voxelwise threshold of $p < .001$. Numbers refer to the slice position in z direction.

3.3 Categorical representations outside of the auditory cortices

We used a searchlight procedure (Kriegeskorte et al., 2006) to compute the cross-validated Mahalanobis distance (hereafter crossnobis distance). The crossnobis distance here refers to the Euclidean distance after multivariate noise normalization (Walther et al., 2016) between the BOLD response patterns associated with different perceptual reports (/da/ vs /ga/). BOLD response patterns were extracted separately for unambiguous and ambiguous stimulus trials and

constrained to areas significantly responding to sound at the group level (see auditory task-evoked activation mask) in participants' native brain space.

We computed the crossnobis distance between /da/ and /ga/ reports as the arithmetic product of the perceptual distances in unambiguous and ambiguous stimuli.

$$(\text{/da/ report}_{\text{unambiguous}} - \text{/ga/ report}_{\text{unambiguous}}) \times (\text{/da/ report}_{\text{ambiguous}} - \text{/ga/ report}_{\text{ambiguous}})$$

In this way, we sought to identify BOLD patterns that consistently differentiated perceptual reports across unambiguous stimuli and ambiguous stimuli. Thus, BOLD response patterns which consistently differentiated /da/ vs. /ga/ reports in both unambiguous and ambiguous stimuli yielded greater distances, while inconsistent BOLD patterns yielded smaller distances.

Group-level analysis (random-effects analysis using permutation-based nonparametric statistics) of normalized and smoothed distance maps revealed significant ($p < .05$ FWE-corrected) BOLD activity patterns in the left AI, the left SMA, the left vMC, and the right M1/S1 that reliably represented the participants' syllable report (see Fig. 3 & Table S1). The results of a similar analysis in unambiguous stimuli are presented in Fig S1. It should be noted that, as physical stimulus and its perceptual interpretation were confounded in this whole-brain analysis, the observed categorical response patterns could be driven by the stimulus acoustics, the syllable percept, or both.

Figure 3. Results of the MVPA searchlight analyses projected onto a canonical MNI single-subject brain. (A) In the highlighted regions, the average crossnobis distance associated with different syllable reports was found to be significantly larger than zero at $p_{FWE} < .05$. (B) The clusters presented in (A) are thresholded here at $p_{unc} < .001$ and overlaid on regions activated during auditory stimulus presentation and passive listening (light blue color) and regions activated during auditory stimulus presentation and task (dark blue color).

3.4 Acoustic or phonemic representation?

In follow-up analyses, we tested whether categorical patterns derived from the unambiguous stimuli in the localized regions generalize better to the stimulus percept (/da/ vs /ga/) within the same acoustic stimulus, or to the presented acoustic stimulus (high vs low F3) within the same stimulus percept.

For this purpose, we recomputed the crossnobis distance between syllable reports within each stimulus class (high; low F3) separately. The converse was also calculated – the distance between each acoustic stimulus, within each syllable report (/da/; /ga/). In both cases the distances were cross-validated as previously, against the syllable reports in unambiguous stimuli. We found better generalization to the stimulus percept in the aforementioned areas, as reflected by larger crossnobis distances between different syllable percepts than between different stimulus acoustics (percept: $1.297 \times 10^6 \pm 3.332 \times 10^5$; acoustic: $-3.210 \times 10^5 \pm 3.635 \times 10^5$, mean $\pm$ SEM, *Shapiro-Wilk Test of Normality* $p < .001$, *Paired-samples Wilcoxon Sign Rank Test*, $Z = 2.033$, $p = .042$, effect size: $r = .40$). In all brain regions but the left vMC, the distances between different syllable percepts were significantly different from zero (*One sample Wilcoxon Tests*, left AI: $Z = 2.375$, $p_{\text{holm}} = .035$; left SMA: $Z = 2.983$, $p_{\text{holm}} = .006$; left vMC: $Z = 0.855$, $p_{\text{holm}} = .785$; right M1/S1: $Z = 2.733$, $p_{\text{holm}} = .013$), whereas distances between acoustically different stimuli did not show any significant difference from zero ($p_{\text{uncorrected}} > .305$). We found no statistically significant difference in the crossnobis distance between categories across different brain regions (left AI: $4.291 \times 10^5 \pm 1.134 \times 10^5$; left SMA: $4.273 \times 10^5 \pm 1.110 \times 10^5$; left vMC: $2.720 \times 10^5 \pm 8.421 \times 10^4$; right M1/S1: $8.228 \times 10^5 \pm 1.613 \times 10^5$, mean $\pm$ SEM, *Friedman ANOVA*. $\chi^2(3) = 6.543$, $p = .088$, effect size: $W = .10$). Pairwise post-hoc comparisons revealed that the crossnobis distance between categories was significantly larger between different syllable percepts than between different stimulus acoustics in the left SMA (*Paired-samples Wilcoxon Sign Rank Test*, $Z = 2.572$, $p_{\text{holm}} = .041$, effect size: $W = .56$), but not the other regions ($p_{\text{uncorrected}} > .023$) (see Fig. 4).

Figure 4. (A) Follow-up MVPA analysis constrained to the regions presented in Figure 3. In green, crossnobis distance between /da/ vs /ga/ percept within the same acoustic stimulus ($p_{unc} < .01$) is shown, overlaid on the group map presented in Fig 3. At the same threshold, we found no significant clusters for the crossnobis distance maps between high vs low F3 acoustic stimulus. (B) Average crossnobis distance extracted from the regions presented in Figure 3 form categorical patterns representing the distance between different acoustic stimuli (magenta) and different syllable percepts (green). * $p < .01$ Paired-samples Wilcoxon test, corrected for multiple comparisons (Holm-Bonferroni).

4 Discussion

In the present study, we aimed to identify a level of neural representation where speech sounds are coded as abstract categorical perceptual units that are invariant to the sensory signals from which they are derived. For this purpose, we first localized brain regions which consistently discriminated the syllable reports evoked by different unambiguous and ambiguous stimuli. We then assessed whether these regions discriminated primarily the acoustics of the stimuli or the syllable report. Our results show that the perceptual report of the syllable arises in a set of regions which include the left SMA, the left AI, the left vMC and the right M1/S1. These regions are outside of what is traditionally regarded as auditory or phonological processing areas, such as the auditory cortex. For the interpretation of these findings, it is important to keep in mind that a task (listeners had to report the syllable they perceived by button press) typically embeds perception in a context of decision-making. The neural representations that we identified in our experiment may hence reflect: (1) the auditory percept, (2) categorization of percept into syllable, i.e., decision-making, (3) motor response planning and execution, or (4) a combination of different processes along this hierarchy. In the following section we will discuss these alternative interpretations in the light of previous findings in these brain regions.

4.1 Auditory perception

Speech perception is typically seen as a hierarchical process because stronger activation is found in high-order auditory areas to complex information-bearing stimuli, such as speech and music, than to simple stimuli, such as pure tones (Schönwiesner and Zatorre, 2009; Leaver and Rauschecker, 2010; Norman-Haignere et al., 2015). Therefore, it is a commonly held belief that low-level acoustic features are extracted in early auditory areas, which are later transformed into more complex and speech-specific representations in the nonprimary cortex in the superior temporal gyrus (Rauschecker and Scott, 2009; Brodbeck et al., 2018). In this study, we found no area that represented the acoustic difference (high vs low F3) in our stimuli. This might be explained by the relatively subtle acoustic difference between our stimuli that may be difficult to resolve from the fMRI data. It is noteworthy that there is evidence that challenges this hierarchical processing structure, favoring parallel streams of auditory processing (Hackett et al., 2001; Jasmin et al., 2019; Hamilton et al., 2021).

4.2 Categorization of percept into syllable

Existing data suggest the involvement of numerous brain areas in processing of sublexical units, including pSTG/STS (Formisano et al., 2008; Chang et al., 2010; Kilian-Hütten et al., 2011;

Mesgarani et al., 2014; Arsenault and Buchsbaum, 2015; Yi et al., 2019; Levy and Wilson, 2020), IFG (Hasson et al., 2007; Myers et al., 2009; Lee et al., 2012; Chevillet et al., 2013; Du et al., 2014) as well as vMC (Du et al., 2014; Evans and Davis, 2015; Cheung et al., 2016) and premotor cortex (Chevillet et al., 2013). It has been shown that during listening the neural responses in the pSTG/STS (Mesgarani et al., 2014) and vMC (Cheung et al., 2016) show a similar spatial organization along acoustic features. This is interesting because Cheung and colleagues (2016) also found, that in contrast to listening, the neural responses in the vMC during speaking are organized along articulatory features. We found that the left vMC discriminates between syllable reports in ambiguous and unambiguous stimuli. However, when testing whether the left vMC discriminates syllable percepts while keeping the stimulus acoustics constant, we found no significant difference. Further, we found evidence for categorical representations of unambiguous stimuli in the left STS (Figure S1). These results indicate that categorical representations in the left vMC and STG/STS may dependent on the acoustic properties of the stimulus.

4.3 Syllable percepts emerge outside of the auditory cortices

The searchlight approach allowed us to identify areas discriminating syllable percepts that have rarely been associated with categorical speech perception: the left SMA and the left AI. In the midline motor areas, the strongest responses to auditory stimuli have been reported in pre-SMA and at the boundary area between pre-SMA and SMA (Lima et al., 2016). The latter overlaps with the area we identified in our study (Mayka et al., 2006; Kim et al., 2010). The SMA receives direct projections from the basal ganglia (Lehéricy et al., 2004; Akkal et al., 2007), the STG/STS (Luppino et al., 1993, 2001; Reznik et al., 2015), and the inferior-parietal (Luppino et al., 1993) and inferior-frontal cortices (Catani et al., 2012; Vergani et al., 2014). The SMA is not typically considered as a part of the speech and language network in the brain (Hickok and Poeppel, 2007; Friederici, 2011; Hagoort, 2014), despite its connections with this network. Although, SMA activity in response to speech and non-speech sounds has been reported in several studies (for reviews see (Hertrich et al., 2016; Lima et al., 2016)), the functional role of the SMA in auditory speech processing has remained elusive, possibly because SMA and pre-SMA are traditionally conceptualized as being linked to action-related processes, like speech motor control (Tourville and Guenther, 2011), rather than auditory processes (Lima et al., 2016).

The left AI cluster that we identified includes a portion of the dorsal anterior insula. Insula activity during speech perception has been reported in several studies (Benson et al., 2001;

Golestani and Zatorre, 2004; Aleman et al., 2005; Falkenberg et al., 2011) Particularly, the dorsal AI seems to be involved in speech perception, whereas other parts of the insula seem to contribute more to speech production (for a meta-analysis see (Oh et al., 2014)). Similar to the SMA, the insula has extensive connections with the auditory cortex, temporal pole, and superior temporal sulcus (Augustine, 1996; Oh et al., 2014), and is typically not considered to be involved in speech perception (Hickok and Poeppel, 2007; Friederici, 2011; Hagoort, 2014).

4.4 The putative role of the SMA and AI in auditory decision making

Recent evidence suggests that SMA may play an important role for the categorization of auditory percepts into syllables, including decision-making. In a recent study, Morán and colleagues (2021) found categorical neural responses in rhesus monkeys, who were trained to categorize numerous complex sounds, including words. The authors recorded extracellular activity directly from SMA neurons and found robust categorical responses at both the single neuron and population levels. Most importantly, they observed that neural population coding shifted from acoustic to motor representations during the task suggesting that the SMA integrates acoustic information in order to form categorical signals that drive the behavioral response. Interestingly, the population activity in error trials reflected the behavioral decision, rather than the presented physical stimulus.

The left AI has been associated with decision making in a number of studies (for a review see (Droutman et al., 2015)). Particularly, the dorsal AI seems to be functionally implicated in cognitive control processes associated with decision-making including attention re-focusing, evaluation, action, and outcome processing (Droutman et al., 2015). Further, dorsal AI activation has been related to decision ambiguity (Huettel et al., 2006) and error awareness (Ullsperger et al., 2010). Recent evidence indicates that the anterior insula could serve as a gate for conscious access to sensory information (Huang et al., 2021).

We found two interesting distinctions between the BOLD patterns in the left SMA and the left AI. First, only the cluster in the left AI overlapped with areas which were activated during passive listening to the same stimuli (Fig. 3). Second, only in the left SMA, but not in the left AI, the crossnobis distances between syllable percepts were larger between different syllable percepts than between different stimulus acoustics. This indicates the responses in the left SMA, but not left AI, were invariant to the physical stimulus properties of the stimuli. Taken together, one may speculate about the processing hierarchy and the functional differences between the processing in AI and the SMA. The AI may be more relevant for the integration of auditory

evidence and the preparation of a perceptual representation, which is then strengthened to become an invariant representation in the SMA.

4.5 Motor response planning and execution

A possible alternative interpretation is that the effects reported in the SMA and the AI reflect merely task-related motor or domain-general cognitive processes, such as button presses or response selection (Zatorre et al., 1992; Kawashima et al., 1996). This view is supported by our observation that the right M1/S1 differentiated between different syllable percepts. However, it is likely that additional processes, other than button pressing, also contributed to the effect. This is supported by studies showing SMA (Benson et al., 2001; Scott et al., 2004; Warren et al., 2006; Jardri et al., 2007) and insula (Ackermann et al., 2001; Benson et al., 2001; Steinbrink et al., 2009; Hervais-Adelman et al., 2012) activation during passive listening. Further, there are studies showing activation in the SMA and the insula during auditory task on top of merely motor-execution related activity (Adank et al., 2013; Bestelmeyer et al., 2014; Sammler et al., 2015). Thus, our observed effect may reflect either task- and motor-execution-related activity, or tactile feedback. Our interpretation is further supported by results from the passive condition, which revealed activation in the anterior insula and pre-SMA during listening only.

4.6 Conclusion

Our finding that BOLD patterns discriminating different syllable reports occur in brain regions contributing to auditory processing, categorization of percept into syllables, i.e., decision-making, and motor response, suggests that the identified representations reflect a combination of various processes along this hierarchy.

Our finding that areas whose responses to speech stimuli discriminate between phonemic categories exist outside auditory cortical areas is consistent with the possibility that higher-order areas are instrumental in determining the syllables we hear, and that these regions feed abstract categorical representations back into the auditory association cortex (Formisano et al., 2008; Chang et al., 2010; Kilian-Hütten et al., 2011) and even to earlier auditory areas (Levy and Wilson, 2020).

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671

672 7 Supplementary Figures and Table

Figure S1. Results of the MVPA searchlight analyses within unambiguous stimuli, projected onto a canonical MNI single-subject brain. Numbers refer to the slice position in z direction.

Table S1: The results of the group-level analysis (random-effects analysis using permutation-based nonparametric statistics) of normalized and smoothed individual distance maps ($p < .05$ FWE-corrected).

	Coordinates			T score
	x	y	z	
right postcentral gyrus (PoG)	44	-28	44	6.45
left anterior insula (AI)	-30	20	14	6.35
left ventral motor cortex (vMC)	-38	4	42	5.67
left supplementary motor cortex (SMA)	-6	-8	52	5.22

Coordinates are in MNI space.