

Brainstem origins for cortical ‘what’ and ‘where’ pathways in the auditory system

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We have developed a data-driven conceptual framework that links two areas of science: the source–filter model of acoustics and cortical sensory processing streams. The source–filter model describes the mechanics behind speech production: the identity of the speaker is carried largely in the vocal cord source and the message is shaped by the ever-changing filters of the vocal tract. Sensory processing streams, popularly called ‘what’ and ‘where’ pathways, are well established in the visual system as a neural scheme for separately carrying different facets of visual objects, namely their identity and their position/motion, to the cortex. A similar functional organization has been postulated in the auditory system. Both speaker identity and the spoken message, which are simultaneously conveyed in the acoustic structure of speech, can be disentangled into discrete brainstem response components. We argue that these two response classes are early manifestations of auditory ‘what’ and ‘where’ streams in the cortex. This brainstem link forges a new understanding of the relationship between the acoustics of speech and cortical processing streams, unites two hitherto separate areas in science, and provides a model for future investigations of auditory function.

Introduction

Over the past 20 years, increasing attention has been paid to the functional organization of sensory systems. Across modalities, sensory systems route different aspects of the input into discrete processing streams; in other words, a particular stimulus, whether a seen object, a heard sound or a felt touch, is not processed in the brain as a unit. Rather, different qualities of the stimulus (e.g. what it is, where it is coming from, and who or what is producing it) are processed separately, yet simultaneously, by different neural mechanisms before the stimulus is consciously perceived as a whole. Here, we present a novel way of looking at the origin of well-known what/where cortical processing streams – one that postulates a subcortical precursor to specialized speech processing in the cortex.

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Sensory processing streams

In 1983, a seminal article published in this journal described two parallel processing streams in the visual system, the ventral and dorsal pathways [1]. These streams are responsible for object identification (e.g. color and shape) and object location (e.g. position and motion), respectively, and have popularly become known as ‘what’ and ‘where’ pathways. This separation, evident early in parvocellular and magnocellular ganglion cells in the retina [2], continues throughout the afferent pathway via the thalamus to visual cortex. Evolutionarily, the dorsal ‘where’ pathway developed first [3]. It is also more responsive to multimodal stimulation than the ventral ‘what’ pathway [4,5].

A similar functional dichotomy in the auditory system has been proposed [6]. As in the visual system, auditory research has focused on the identity versus the location or motion of an auditory object [7,8]. How speech decoding fits into this functional and anatomical division remains a matter of debate. This is not surprising, given the complexity of the speech signal that simultaneously carries a wealth of information conveying both message and identity cues. Although both the ‘what’ and the ‘where’ pathways have been implicated in speech perception, there is a tendency to relegate the perception of location or motion alone to the ‘where’ pathway and that of auditory object identity to the ‘what’ pathway. For communication calls, including speech, many studies have found activation in the ‘what’ pathway [9–13] but some ‘where’ pathway involvement has also been noted [13–15]. Belin and Zatorre have proposed recently that the ‘where’ pathway, rather than merely being responsible for detection of location or motion in space, is also focused on spectral motion – that is, ‘where in frequency’ [14]. They draw a parallel between light moving across the visual field in the retina with the ‘movement’ of acoustic stimulation across the frequency-mapped basilar membrane in the cochlea. This information provides the essential building blocks for distinguishing consonants, vowels and phonemes that ultimately compose the message. Spectral motion in speech-like stimuli can selectively activate secondary auditory pathway regions that are analogous to visual cortical sites activated by visual motion [15]. Further support for this latter what/where demarcation comes from experiments showing

that cortical lesions can selectively disrupt either the understanding of linguistic content (word deafness) or the recognition of speech prosody, the latter often with accompanying amusia (tone deafness) [16,17]. The way in which sound is transformed into these putative pathways has not been previously addressed.

Source and filter

In an attempt to disentangle the ‘what’ and ‘where’ of speech perception, it is helpful to consider the acoustics of the speech signal itself. The literature on speech production provides a useful dichotomy to describe the acoustics of speech. The source–filter model states that the vibration of the vocal folds reacting to airflow from the lungs is the sound source. Everything else – vocal tract, oral cavity, tongue, lips and jaw – comprises the filter [18]. Broadly speaking, linguistic content – vowels and consonants – is transmitted by particular filter shapes, whereas nonlinguistic information, such as tone of voice, relies largely on characteristics of the source. In the what/where-in-frequency dichotomy, spectral motion is confined to short-term changes in frequency, such as the fast-moving frication and stops that mold consonants and the formant transitions that shape vowels, not to the slower phrase-length or sentence-length pitch changes that signal linguistic prosody. A related classification of speech components is as ‘information-bearing elements’ versus ‘information-bearing parameters’ [19], which can be described as largely spectral or temporal in nature, respectively [20]. In music, a parallel to the source–filter model of speech can be drawn. In a musical instrument, the vibrating item (e.g. a reed or string) is the source and the shape of the instrument (e.g. oboe or cello) is the filter. Thus, the acoustics associated with the filter would fall under the realm of the ‘where’ pathway; the source information would be handled by the ‘what’ pathway.

Brainstem response to speech

The evoked brainstem potential – fluctuations in voltage recordable from scalp electrodes in humans – consists of both transient and sustained components in response to a complex sound such as a speech syllable. The response functions as a gauge both of spectrum encoding – which is indicative of the overarching organization scheme of the auditory pathway – and of periodicity encoding. The transient onset response is akin to the well-documented clinical measure that is used with click or tonal stimuli as a tool for assessing both peripheral hearing and retrocochlear damage such as tumors of the auditory nerve or brainstem [21]. Much of its clinical value lies in its replicability and reliability within an individual. Moreover, the specificity of generation sites (early waves at <3 ms arising from action potentials in the auditory nerve; later waves at >3 ms reflecting postsynaptic activity in rostral brainstem structures) provides valuable diagnostic information [22]. Frequency encoding is manifested in speech-evoked auditory responses in both the latency [23–25] and the amplitude [26] of transient responses. The sustained frequency-following response (FFR), although not widely used as a clinical tool, has also been studied [27–34]. It is a phase-locked response that

‘follows’ the waveform of the stimulating sound up to a frequency of ~1000 Hz [30]. The FFR is such a reliable phase-locker that when the speech-evoked FFR, recorded directly from subcortical structures, is amplified and ‘played back’ through a loudspeaker, it is recognizable as identifiable speech [35]. The source of the scalp-recorded FFR is still a matter of debate, but the posterior brainstem is certainly involved – probably the lateral lemniscus and/or inferior colliculus [28,30]. It must be noted that, although the FFR is a sustained response, it might be considered a series of repeated transients. Thus, the FFR can be treated as a measure of both periodicity and spectral processing. These two aspects of the FFR are important for disentangling the response waveform with respect to source and filter aspects of the speech sound, and for understanding the subsequent relaying of information into parallel sensory processing streams.

Our group has extensively characterized the brainstem response to a 40-ms syllable, /da/ [36]. Figure 1 illustrates both time–voltage (bottom) and time–frequency (top) plots of /da/. Although short, the syllable is acoustically complex, beginning with an unvoiced, aharmonic and relatively broadband frication, followed by a harmonically rich and spectrally dynamic voiced transition to the vowel. Acoustically, the ‘source’ is the fundamental frequency (F_0) of the utterance, ramping from 100 Hz to 120 Hz (in the case of a male speaking with a slight upward inflection). The ‘filter’ is manifested acoustically by (i) the initial frication (tongue at the roof of the mouth blocking airflow, followed by a release of the blockage) resulting in the ‘d’ sound, and (ii) a shift in the articulators (lowering of the tongue and widening of the mouth) transforming the initial ‘d’ into the ‘ah’. This filtering of the source selectively accentuates certain harmonics (overtones) of the fundamental, resulting acoustically in prominent peaks in the spectrum, the formants. The relative spacing of these formants is unique to a particular vowel.

Figure 2 illustrates the scalp-recorded brainstem response to /da/ in a typical normal-hearing individual, together with the stimulus (top). Waves I, III and V are standard nomenclature for the onset response complex. Wave A is also a prominent part of the onset complex. Waves C to F are sequential response peaks, unique to this particular syllable. (Wave B, which is infrequently seen, is absent in this subject.) Wave O is a response to the offset of the sound. The particular pattern of voltage fluctuations varies depending on the stimulus but, across individuals, the response pattern to a particular utterance is highly replicable.

Not all peaks are created equal

In Figure 2, it should be apparent that the response resembles the stimulus time–voltage waveform, at least in the latter (vowel) portion. Closer examination of the relationship between stimulus and response reveals two discrete categories of response (Box 1). Waves V and A signal the onset of sound at the brainstem (lateral lemniscus/inferior colliculus). Wave C is probably a response to the onset of the vowel – the release of the tongue from the roof of the mouth. Wave O is a response to the cessation of sound. Together, these transient peaks,

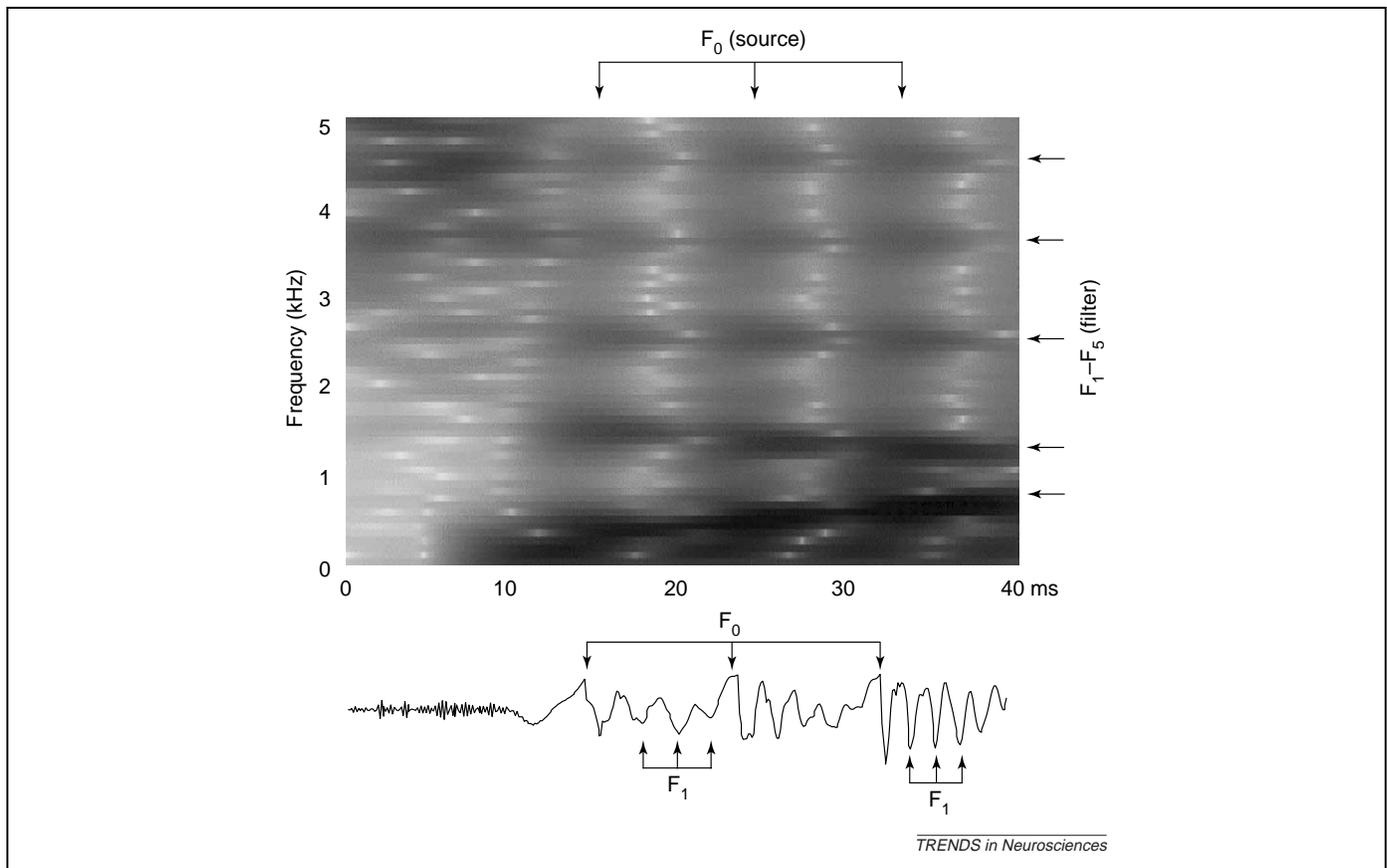


Figure 1. Five-formant synthesized /da/: time–frequency (broadband spectrogram) and time–voltage plots. Fundamental frequency, a source cue, is visible in the spectrogram as vertical striations corresponding in time to the major F_0 peaks in the time–voltage plot. The five formants (F_1 – F_5), high-energy bands resulting from the filter characteristics of the vocal cavity, are the darker horizontal stripes seen from ~10 ms to 40 ms (the largest and lowest in frequency, F_1 , is also indicated in the time–voltage plot). In the time–frequency plot, the consonant burst is the diffuse dark area in the high-frequency range of the first 10 ms.

the timing of which is sensitive to stimulus spectrum, comprise responses to the acoustic filter characteristics of the syllable. Also belonging to the filter group are the small higher-frequency fluctuations between waves D, E and F. Their spacing corresponds in frequency to that of the first formant (F_1) of the stimulus, which, along with F_2 , primarily shapes the vowel sound /a/. F_2 and the higher formants in the /da/ are, however, beyond the phase-locking frequency limit of the brainstem and not evident in the response. Peaks D, E and F comprise the second class of response, which represents vibrations of the vocal folds – the source. Notice that the interpeak intervals correspond precisely to the wavelength of the F_0 of the utterance. These FFR peaks involve the encoding of periodicity, and are prominent enough to provide reliable latency measurements. Additionally, the FFR, encompassing F_0 and F_1 peaks, can be viewed in the frequency domain, thereby quantifying the amount of neural activation at particular frequencies in the stimulus. Furthermore, the fidelity of the response to its evoking stimulus permits direct stimulus-to-response correlations. Thus, both transient and sustained measurements of the FFR are possible. Overall, the brainstem response reflects acoustic characteristics of the speech stimulus with remarkable precision in both frequency and time domains. These separate source and filter characteristics occur simultaneously in the speech signal, yet can be viewed independently in the response patterns of brainstem neurons.

Although each response component originates in the brainstem, we have demonstrated a consistent pattern of dissociation between those belonging to the source and filter classes. In a group of normal subjects, response components within a class, but not between classes, are highly correlated [36]. Source-class responses are relatively immune to background noise [36–38] and increased repetition rates [38]. By contrast, these stresses degrade filter-class responses. A similar dissociation is seen in an animal model [39]. Further evidence of a dissociation between these two response classes comes from individuals with language-based learning disorders who demonstrate abnormalities in filter-class responses, despite normal source-class and click-evoked brainstem responses [37,38,40–42]. This biological marker of abnormal brainstem timing is consistent with message-type deficits observed perceptually, and the implication of the dorsal (where) pathway in dyslexia [43,44]. Moreover, targeted training programs designed to improve language skills in underachieving children lead to increased stimulus-to-response correlations, apparently due to more robust F_1 encoding [45]. Together, these findings point towards misencoding in subcortical structures as a possible origin for speech message decoding difficulties – both in poor listening conditions and in clinical populations. More research into brainstem encoding of ‘source’ cues in individuals with paralinguistic decoding difficulty (e.g. in autism or nonverbal learning disability) is warranted.

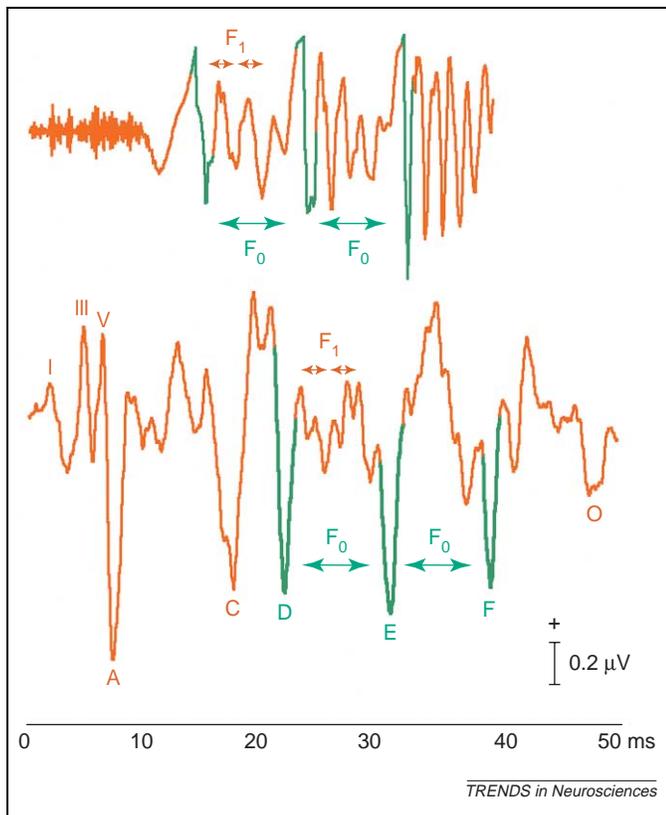


Figure 2. Similarities between acoustic speech and its electrical response recorded from the brainstem. Top: time–voltage plot of the stimulus /da/. Bottom: brainstem response to /da/. Waves D, E and F are ‘source’ peaks, arising from the fundamental frequency of the stimulus. Other labeled waves are ‘filter’ peaks. Higher-frequency formants are not visible in the response owing to the low-pass filter characteristic of the brainstem. Neural conduction accounts for a delay of ~ 7 ms between stimulus features and corresponding response components. Thus, the fundamental frequency (F_0 , green) peaks at ~ 15 ms, ~ 24 ms and ~ 33 ms in the stimulus correspond to waves D (22 ms), E (31 ms) and F (40 ms), respectively, in the response. (The figure shows an average of responses to 3000 repetitions of alternating-polarity stimuli, presented to right ear via insert earphone with an interstimulus interval of 51 ms. A silver–silver chloride electrode at vertex was referenced to the earlobe; sampling rate was 20 kHz, band-pass filtered from 100 to 3000 Hz.)

Overall, multiple lines of evidence support the existence of two classes of brainstem response that correspond to source and filter characteristics of the signal.

Subcortical and cortical streams?

The ‘source’ characteristics of speech are closely linked to nonlinguistic information, such as sex, emotional state, attitude and recognition of the speaker as an auditory object. ‘Filter’ characteristics are almost wholly related to linguistic content – the consonants and vowels that comprise the code of language and, hence, constitute the building blocks of the message. The two classes of

Box 1. Brainstem response classes

‘Source’ responses

Transient FFR: waves D, E and F
Sustained FFR: fundamental frequency (F_0)

‘Filter’ responses

Onset: waves V, A and C
Offset: wave O
Sustained FFR: first formant (F_1)

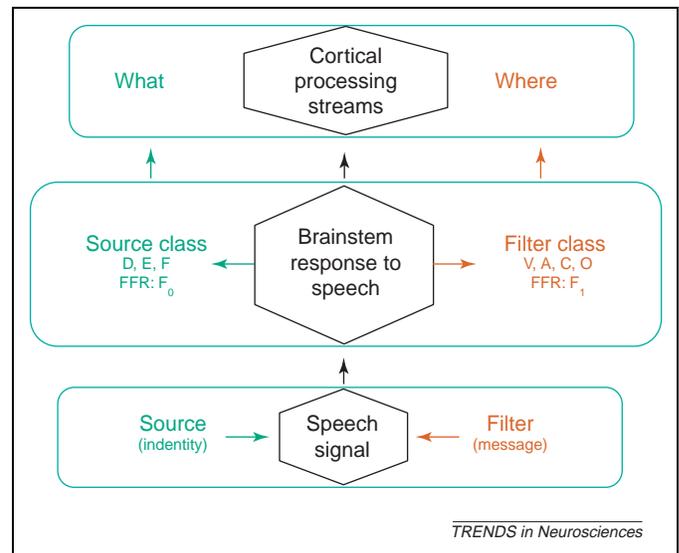


Figure 3. Model of the brainstem as a mediator between acoustic properties of speech and cortical processing streams. Bottom: a speaker encodes his or her thoughts into audible sounds by using the vocal tract to filter the sound of the vibrating vocal cords (the source). Although the filter is constantly changing to shape the sounds that compose the consonants and vowels of language (i.e. the message), the overall gestalt of the speaker as an auditory object remains the same. Middle: after the sounds are mechanically transduced into electrical signals in the cochlea of the listener, the auditory nerve relays the signal to the midbrain where both source and filter components of the signal are preserved. This preservation is quantifiable in different response components. Listed here are the main peaks in the response to /da/. Source-class responses consist of F_0 measures whereas filter-class responses reflect onset, offset and F_1 . Members of a response category vary together. Source-class responses are rate and noise resistant and are not disrupted in individuals with language-based learning disorders; filter-class responses are vulnerable. Top: separation of speech components in the brainstem is proposed as a precursor to the ‘what’ and ‘where’ streams in the cortex.

responses to an auditory speech signal measured from the brainstem are linked to the properties of speech that they convey. It could well be that the brainstem encoding of speech is a fundamental precursor to the divergence of the parallel processing streams identified in the cortex (Figure 3).

The idea of parallel processing streams in the auditory system is receiving increasing attention [6,8,11,13,46,47] and criticism [48]. It is unlikely that the separation is total (it is not total in the visual system [49]), but evidence for specialization in the auditory cortex and subcortex is mounting. Although ‘what’ certainly has a role in speech perception, it appears that, at a preconscious level, there could be a ‘where-in-frequency’ precursor in the brainstem attuned to the coding of the filter elements of the speech signal – those that comprise the building blocks of the message. Another functional separation seen in acoustic processing that is especially relevant to speech is that of hemispheric laterality. There is much evidence that the commonly held position that speech is processed on the left is not strictly true. Speech processing is bilateral, but certain aspects of the speech signal are preferentially treated in one hemisphere or the other [50]. Because the speech signal evolves on multiple timescales, a distinction in temporal integration windows has been postulated as the underlying cause for hemispheric specialization: the left hemisphere samples signals on a shorter timescale (20–40 ms) than the right (150–250 ms) [51]. The former timescale is more relevant to phonetic (segmental)

information [52], and thus most tasks involving speech comprehension invoke the left hemisphere preferentially. However, tasks designed to focus on longer-term (super-segmental) properties of speech, such as F_0 , result in a rightward lateralization [50]. Although it is not possible to disentangle left and right brainstem contributions in the far-field response recordings reported here, it is notable that the distinction between response classes falls along the same general nonlinguistic-source and linguistic-filter lines that mediate hemispheric laterality, and the early distinctions seen in the brainstem might be an antecedent to the eventual division seen between the two hemispheres.

The emerging model of subcortical specialization presented here could be incorporated into existing frameworks of auditory processing streams and is a useful way to consider the manner in which the speech code is dissected early in the auditory pathway. Future research can apply this model to further our understanding of the biological bases underlying hemispheric specialization, the encoding of musical signals, and auditory perception in various populations (e.g. the aged or hearing impaired). The existence of these proposed subcortical streams enriches the model of auditory system organization, and contributes to our understanding of organization of sensory systems in general.

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