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SINCE THE DISCOVERY BY BROCA in 1863 that damage to the left cerebral hemisphere in men led to disruption of language (aphasia), clinicians, scientists, educators, and the public alike have been fascinated with the topic of hemispheric asymmetry. Research across remarkably diverse scientific fields has focused on better understanding which cognitive functions are lateralized to which cerebral hemisphere, whether there are differences between males and females in brain organization for these functions, whether hemispheric asymmetry is unique to humans, and how and why cerebral asymmetry evolved.

That the left hemisphere (LH) is dominant for most humans for verbal processing and the right hemisphere (RH) for most nonverbal acoustic processing is a foundational tenet of our understanding of cerebral organization and asymmetry of higher cortical function (Kimura 1961; Milner 1962). There have been many different theories and scientific approaches directed toward explaining these observations. Common across all of these studies is the finding that males are more likely than females to have speech and language lateralized to the LH, are more likely to suffer long-term aphasia after damage to the LH, and are more likely to have developmental language-based learning disorders. There are many comprehensive books and review articles synthesizing this vast research literature (cf. Hugdahl and Westerhausen 2010; Patel 2008).

Scientific questions focused on hemispheric asymmetry, specifically as it pertains to speech and language, are among the most studied and perhaps most contentious topics in cognitive neuroscience. Impassioned debate has raged for over half a century as to whether the neural mechanisms underlying speech perception comprise a uniquely human, domain-specific, specialized "closed" system (Liberman and Mattingly 1989) that is encapsulated in the LH in a "speech organ" (Chomsky 1972) or "speech module" (Fodor 1983) or, rather, domain-general, sharing many of the same sensory, perceptual, and cognitive mechanisms used by humans as well as other species for analyzing complex acoustic signals (Efron 1963; Kuhl and Miller 1975; Schwartz and Tallal 1980; Tallal 2004; Zatorre et al. 2002).

In their classic paper, "A Specialization for Speech Perception," Liberman and Mattingly (1989) wrote, "The processes that underlie perception of consonants and vowels are specifically phonetic, distinct from those that localize sources and assign auditory qualities to the sound from each source….The phonetic module has certain properties in common with modules that are 'closed' (for example, sound localization or echo ranging in bats) and, like other members of this class, is so placed in the architecture of the auditory system as to preempt information that is relevant to its special function. Accordingly, this information is not available to such 'open' modules as those for pitch, loudness, and timbre" (p. 489).

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Contrary to this view of language as a "closed," specialized module, in another classic paper, "Temporal Perception, Aphasia and Déjà Vu," Robert Efron (1963) provided some of the earliest data suggesting that language may share various aspects of auditory processing, specifically temporal processing, by showing that both are selectively impaired in men with left, but not right, hemisphere brain lesions leading to aphasia. In important ways, these two classic studies provided the impetus for decades of comparative studies across species aimed explicitly at investigating hemispheric asymmetries for specific acoustic cues that may also have relevance for speech. There is now a rich body of research focused on teasing out how the auditory system organizes different acoustic features and how these features are used in ecologically meaningful ways in species ranging from song birds (Nottebohm and Arnold 1978) and bats (Suga and Jen 1976) to rodents (Fitch et al. 1993), nonhuman primates (Joly et al. 2012; Rauschecker and Scott 2009), and humans (Abrams et al. 2008; Giraud et al. 2007; Zatorre et al. 2002).

In their recent article, Washington and Kanwal (2012) add a provocative new finding by demonstrating that, like humans, mustached bats show sex-dependent hemispheric asymmetries for processing frequency-modulated (FM) sounds in the auditory cortex. Suga and colleagues classically demonstrated that the auditory cortex of the mustached bat contains a map of echolocation signals that is largely consistent across animals (Suga and Jen 1976). Kanwal and colleagues later showed that single auditory cortical neurons in this species are equally capable of processing both echolocation and communication signals (Esser et al. 1997; Kanwal 1999), a finding that directly refutes Liberman and Mattingly's (1989) hypothesized "closed" system for echolocation and communicative signals in the bat. In their recent study, Washington and Kanwal (2012) recorded single-unit cortical activity from the right and left primary auditory cortex (A1) in awake bats in response to the presentation of constant-frequency (CF) tone bursts and linear FM sweeps that are contained within their echolocation and/or communication sounds (Kanwal and Rauschecker 2007; Washington and Kanwal 2008). In response to CF tone bursts, they found that, whereas the distribution of responses to frequency was not significantly different across hemisphere for either sex, there were significant differences in temporal response parameters (such as latencies) in males, but not in females. For males, neurons in the LH were also significantly more responsive to fast-rate FMs relative to those in the RH. For females, there were no significant hemispheric differences in neuronal response to fast-rate FMs, with neurons in both hemispheres being comparable to those in the LH of males. They also found that, for males, neurons in the RH were significantly less responsive to broadband FMs relative to those in the LH. For females, again, there were no significant hemispheric differences. These data on fast vs. slow FM rates derived from single-cell recordings in bats are compatible with both behavioral and lesion studies in rats showing sex-dependent hemispheric asymmetry for processing tone sequences, with only males showing LH asymmetry based on rate of stimulus presentation (Fitch and Tallal 1993). Their data on broad vs. narrow FM bandwidths, at least in males, also are consistent with enhanced spectral resolution in the RH (Boemio et al. 2005; Zatorre and Belin 2001), which has been used to explain deficits in music perception (Milner 1962) and detecting prosodic variation (Robinson and Fallside 1991) following RH lesions.

While these studies show that humans are not the only species to have sex-dependent hemispheric asymmetry for specific aspects of auditory processing, it is quite another thing to show that similar processes underlie sex-dependent hemispheric asymmetry for speech in humans. Historically, the majority of studies in humans that have investigated hemispheric asymmetry for verbal compared with nonverbal auditory processing have confounded phonetic and acoustic variables. Whereas most speech stimuli used in these studies incorporated very rapidly changing spectrotemporal acoustic spectra, most nonverbal stimuli (i.e., musical tones, environmental sounds) did not. In an attempt to disambiguate phonetic and acoustic cues, Tallal and Newcombe (1978) used computer-synthesized speech for the first time to investigate hemispheric asymmetries for verbal and nonverbal auditory processing in men with chronic LH or RH focal brain lesions. They developed three sets of stimuli: *1*) complex tone sequences separated by varying interstimulus intervals (ISI), *2*) synthesized steady-state vowels, and *3*) consonant-vowel syllables synthesized with varying duration formant (spectrotemporal) transitions. Contrary to the expectation that LH lesions would lead to speech-specific deficits and RH lesions to nonverbal auditory processing deficits, the results showed that men with LH damage, but not RH damage, were impaired in their ability to respond correctly to rapidly changing acoustic stimuli, regardless of whether stimuli were verbal or nonverbal. Aphasic patients with LH lesions were selectively impaired in responding to tone sequences that were presented rapidly in succession (ISIs <150 ms), but not with longer ISIs. Similarly, they were impaired in discriminating between speech stimuli (/ba/ vs. /da/) with 40-ms-duration formant transitions but significantly less so on the same syllables with 80-ms-duration formant transitions and vowels that were acoustically steady state. Importantly, the degree of impairment in processing rapidly presented tone sequences correlated highly with the degree of language comprehension impairment. A similar pattern of results was also found in subsequent studies using the same stimuli within a dichotic listening paradigm with healthy adults. A significantly greater right ear (LH) advantage was found for speech syllables with 40-ms compared with 80-ms formant transitions (Schwartz and Tallal 1980) as well as tone sequences presented with brief (mean = 20 ms) but not longer ISI durations, and only for males (Brown et al. 1999).

With the advent of functional neuroimaging [positron emission tomography (PET), functional magnetic resonance imaging (fMRI), magenetoencephalography (MEG)], many studies have explicitly explored the question of whether hemispheric asymmetries reflect domain-specific speech processing or rather more domain-general acoustic processing. Belin et al. (1998) computer synthesized a novel set of complex, nonverbal, acoustic stimuli that closely mimicked the spectrotemporal acoustic spectrum of consonant-vowel syllables. They then incorporated a rapid (40 ms) or slower (200 ms) spectrotemporal transition into these nonverbal stimuli. PET results from healthy adults demonstrated that even though neither set of these stimuli were perceived as speech, there was increased regional cerebral blood flow in left auditory regions for both types of stimuli, indicating that the LH has the capacity to process spectral change over a wide range of durations. However, activity in homologous regions of right auditory cortex was observed only for the stimuli with the slower transitions. A similar pattern of results was found in a PET study by Fiez et al. (1995), but in this case using speech syllables that either did or did not incorporate rapidly changing formant transitions as well as tone triplets separated by brief ISIs. They found that only those stimuli incorporating rapidly changing formant transitions or brief ISIs showed increased cerebral blood flow in the LH, regardless of whether they were verbal or nonverbal.

More comparable to the physiological recording techniques reported by Washington and Kanwal (2012) in bats, and potentially linking more closely animal and human research, are the electrophysiological findings of Liégeois-Chauvel et al. (1999). They recorded electrical potentials from the left and right side of the human auditory cortex using implanted electrodes. They observed that responses from left, but not right, Heschl's gyrus (A1) distinguished brief temporal differences in both speech and nonspeech sounds. Similarly, electrophysiological studies by Benasich and colleagues showed that infants with a family history of language learning impairments show reduced mismatch negativity (MMN) to tone sequences, selectively in the LH and selectively for sequences presented with brief (70 ms), but not longer (300 ms), ISIs. By following these infants longitudinally, they demonstrated that rapid auditory processing thresholds established in infancy, together with being male, predicted more than 93% correctly which of these infants would subsequently score in the impaired range in verbal (but not nonverbal) IQ when they were 36 mo old (cf. Benasich et al. 2002).

Taken together, data spanning over half a century, with the use of a large number of methodologies across multiple species, are consistent in finding that left auditory cortex responses are optimal for processing a range of temporal features relevant for processing phonological contrasts, whereas right auditory cortex has greater spectral resolution. Whereas I have focused here at the level of intrasyllabic phonemic analysis, it is important to emphasize that analysis of rapidly changing formant transitions also plays a critical role in accurate perception of fluent speech by binding together phonetic segments so that at rapid transmission rates the temporal order and segmentation of the ongoing acoustic waveform of speech may be preserved (Dorman et al. 1975). Similarly, although I have focused more on the LH asymmetries for broadband, rapid temporal processing reported recently by Washington and Kanwal (2012), their findings pertaining to asymmetries for narrowband, more slowly modulating signals have equal relevance for spectral processing important in music perception as well as for processing prosodic information in speech. Giraud et al. (2007) posited a potentially unifying interpretation of the data that takes into account both auditory and speech processes that depend on different, but nested, time windows. Using simultaneous electroencephalogram (EEG) and fMRI recordings from humans, they showed that spontaneous EEG power variations within the gamma range (phonemic rate) correlate best with left auditory cortical synaptic activity, whereas fluctuations within the theta range that are essential for tracking the amplitude envelope of speech (Goswami et al. 2002) correlate best with that in the RH. These data show that endogenous cortical rhythms provide temporal and spatial constraints on the neuronal mechanisms underlying speech perception.

The results reported by Washington and Kanwal (2012) in bats add to a growing body of behavioral, neuroimaging, and electrophysiological studies in humans that support an acoustic spectrotemporal (rather than speech specific) account of the nature of hemispheric asymmetry, including sex differences, in the pattern of asymmetries for analyzing complex sounds, of which speech is one example. Finally, it is important to point out that in addition to their theoretical significance, these findings also provide support for including explicit auditory spectrotemporal training, including musical training, within language intervention programs (Merzenich et al. 1996; Tallal and Gaab 2006). As such, these data have the potential to impact clinical intervention for patients with a broad variety of developmental and acquired disorders affecting central auditory processing, speech, and language.

DISCLOSURES

P. Tallal is a co-founder, director, and consultant for Scientific Learning Corporation, a neuroscience company that produces language and literacy training programs for struggling learners.

AUTHOR CONTRIBUTIONS

P.T. conception and design of research; P.T. analyzed data; P.T. interpreted results of experiments; P.T. drafted manuscript; P.T. edited and revised manuscript; P.T. approved final version of manuscript.

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