



AUDITORY PERCEPTION OF SEGMENTAL FEATURES: A FUNCTIONAL-NEUROANATOMIC STUDY

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Abstract—This study investigated the extent to which segmental feature perception depends on left-hemisphere mechanisms, as previously claimed. We used direct cortical electrical interference to examine purported lateralisation differences in the perception of stop consonants and vowels and in stop consonant voicing and place-of-articulation. Electrical interference was applied through indwelling subdural electrode arrays covering the lateral left perisylvian cortex of six patients with normal speech perception and language abilities. Extensive screening of the temporal lobe and other cortical regions revealed auditory syllable discrimination errors at only one posterior temporal site in each patient. Patients were significantly more impaired in detecting consonant differences than vowel differences, but showed no evidence of selective voicing or place-of-articulation impairments when pairs were contrasted in syllable-initial position. Moreover, discrepancies in patients' ability to detect place-of-articulation and voicing differences in syllable-final position were attributed to syllable context effects. These findings concur with previous claims concerning the relative importance of the left hemisphere for consonant perception, and further suggest that stop consonant processing is supported by a small region of the left posterior temporal lobe. Conversely, despite the specificity of electrical interference effects, our data do not support previous claims for the neurofunctional independence of stop consonant feature detectors, and furthermore suggest that no single feature may account for the lateralisation of stop consonant perception.

INTRODUCTION

THE EXTRACTION of acoustic information from the auditory speech signal is considered critical for normal auditory language comprehension, yet the functional and neural mechanisms responsible for this process remain largely unspecified. Evidence from dichotic listening experiments and from studies of speech perception in aphasic patients have suggested that acoustic cues to vowels and consonants are processed differently [1-3]. The steady-state formants of vowels are thought to be perceived by either cerebral hemisphere, while the rapidly changing frequency information associated with certain classes of consonants has generally been thought to require the specialised resources of the left hemisphere [4, 5].

Stop consonants (/p,t,k,b,d,g/) have been associated with left-hemisphere processing more than other consonant classes [6]. In articulatory terms, the acoustic parameters of stop consonants correspond to two primary phonetic features: voicing and place-of-articulation. Voicing refers to the presence or absence of glottal pulsing during stop closure release (/b-p/; /d-t/; /g-k/), while place-of-articulation specifies the location of stop consonant closure within the vocal tract (/p-t-k/; /b-d-g/).

Evidence that stop consonants are processed along both acoustic dimensions derives from the well-documented feature number effect, whereby listeners discriminate stop consonants contrasted by both voice *and* place-of-articulation (i.e. /b-t/) better than those contrasted by the

single feature of voice *or* place [1, 7–9]. The feature number effect has commonly been interpreted as evidence for the existence of independent feature processing mechanisms.

More recently, it has been suggested that the lateralisation of stop consonant perception reflects the processing requirements of one particular phonetic feature, namely place-of-articulation [5, 10, 11]. Previous perceptual studies have isolated formant transitions as a salient acoustic cue to the perception of place-of-articulation [12, 13]. Unlike acoustic cues to voicing, formant transitions involve frequency modulations that occur over relatively short time intervals. The detection of brief acoustic cues required to perceive place-of-articulation differences is precisely the type of processing for which the left hemisphere is thought to be specialised [5, 10]. Accordingly, the perception of place-of-articulation would be expected to be more vulnerable to impairment with left-hemisphere damage than the perception of stop consonant voicing. A number of studies of speech perception in aphasic patients have reported such a feature type effect [7, 8]. Aphasic patients, especially posterior aphasics, appear to have more difficulty discriminating place than voicing in consonant–vowel–consonant (CVC) speech pairs, where these two features were contrasted in syllable–initial and syllable–final positions [7].

Although this finding suggests that discrimination of stop consonant place-of-articulation is more dependent on left-hemisphere resources than is voicing, different results are reported when syllable context is taken into consideration. DENES and SEMENZA [14] found no differences when comparing aphasic patients' accuracy of discrimination for place and voicing in syllable–initial position. Similarly, a recent cortical stimulation study of speech perception in epilepsy patients reported no significant differences between patients' discrimination of voicing and place contrasts in syllable–initial position [15].

The differential effects of syllable context offer one explanation for these apparently conflicting results. The perception of phonetic features is known to be influenced by syllable position [16, 17]. This is particularly relevant for the perception of stop consonant voicing, for which an additional perceptual cue is available in the form of vocalic lengthening before syllable–final voiced consonants. Despite such well-documented contextual effects, previous studies of speech perception in aphasic patients have generally studied segmental processing independent of syllable context.

It is not known, therefore, whether place-of-articulation perception is more difficult for aphasic patients than voicing because of i) its unique dependence on left-hemisphere processing, or ii) the influence of syllabic context on the perception of phonetic features, in particular voicing. To explore these issues further, we studied the effects of electrical interference on patients' ability to discriminate segmental features contrasted in different syllabic contexts.

METHODS

Patients

Six right-handed patients, three female and three male, were selected from a larger pool of epilepsy patients undergoing cortical function mapping as part of a routine clinical diagnostic procedure for possible surgical treatment of intractable partial complex seizures. Patients' demographic characteristics are summarised in Table 1.

All six patients met the following criteria for inclusion in this study: i) full-scale IQ ratings above 85, as assessed by the Wechsler Adult Intelligence Scale-Revised [18]; ii) no history or evidence of hearing or oral-motor disorders; iii) left-hemisphere dominance for speech as confirmed by intracarotid amobarbital injection [19, 20]; iv) age of seizure onset after that of language onset (i.e. not earlier than 5 years of age); and v) no evidence of structural brain abnormalities, as determined by MRI scanning (1.5 Tesla, 5 mm slice T1- and T2-weighted images). These latter two criteria were incorporated to exclude patients in whom epilepsy, or its underlying etiology, had affected the

Table 1. Characteristics of patient population

Patient	Age	Sex	Handedness/Language dominance by WADA	FSIQ (V/PIQ)	Age of seizure onset	Seizure focus
Patient 1	24	F	Right-handed/ Left-dominant	121 (113/123)	18	Left basal temporal
Patient 2	36	F	Right-handed/ Left-dominant	97 (91/109)	22	Left mid-hippocampal
Patient 3	15	F	Right-handed/ Left-dominant	92 (85/97)	8	Left anterior basal temporal
Patient 4	34	M	Right-handed/ Left-dominant	95 (98/92)	10	Left anterior temporal
Patient 5	17	M	Right-handed/ Left-dominant	98 (96/112)	13	Left anterior basal temporal
Patient 6	23	M	Right-handed/ Left-dominant	112 (105/118)	10	Left basal temporal

neurofunctional organisation of language functions [21–23]. All patients gave informed consent for research testing in compliance with the protocols approved by our institution's clinical investigations committee.

Stimuli and task

Thirty consonant–vowel–consonant (CVC) verbal stimuli were recorded from an adult, male native speaker of American English onto audio cassette tape in a professional recording studio. Each CVC syllable was composed of stop consonants and one of seven different vowels (/i, l, e, ε, æ, A, u/). Stimuli were roughly divided between words ($N = 17$) and non-words ($N = 13$). To standardise the order and timing of stimulus presentation, the 30 CVC monosyllables were digitised at 44 kHz, 16 bits per sample, using commercially available speech digitisation software [24]. The digitised samples were stored on computer (Macintosh IIx) and output through a speaker (Realistic Model 32–2031A) for testing. To ensure that no significant degradation of the speech signal had occurred, six normal volunteers, blinded to the purpose of the study, were asked to label the CVC stimuli. There was 100% agreement in their responses.

An auditory syllable discrimination task was developed comprising 60 CVC pairs drawn from the set of digitised stimuli. An AX format was selected, rather than the more traditional ABX format, to ensure adequate time for presentation of stimuli and elicitation of response during the electrical stimulation period (5 seconds). Fifty of the 60 pairs were contrasted by any one of the following: i) syllable–medial vowel ($N = 10$); ii) syllable–initial consonant ($N = 20$); or iii) syllable–final consonant ($N = 20$). In syllable–initial and final positions, consonants were contrasted either by the feature of voicing ($N = 7$) or place-of-articulation ($N = 7$), or by both voicing and place-of-articulation ($N = 6$). To avoid promoting a single response strategy, 10 of the 60 pairs contained two of the same stimuli. A constant interval of 400 milliseconds separated each item in a pair, and each pair was presented at 5-second intervals.

Clinical procedures

In each patient, a 6×8 (Patients 1, 2, and 5) or an 8×8 (Patients 3, 4, and 6) electrode array was surgically placed in the subdural space over the lateral left cortical surface according to a pre-established clinical protocol [25]. This array covered the temporal, inferior frontal, and anterior parietal regions. A separate 2×8 array was placed over the basal temporal regions of all patients. One patient (Patient 6) had additional arrays placed over the frontal and occipital regions resulting in coverage of most of the lateral left cortex (see Fig. 1).

Electrodes were 10 millimeters apart (center-to-center) in a rectangular pattern, embedded in medical-grade silastic. The array was composed of platinum iridium disks, 3 millimeters in diameter, with 2–3 millimeters exposed. Electrode locations were determined from intraoperative photographs, plain skull films, and three-dimensional reconstructions of each patient's brain from MRI. Electrode positions were normalised across patients by use of the Talairach atlas [26], with particular reference to the Sylvian fissure and the anterior–posterior distance along the superior portion of the temporal lobe.

Electrical interference testing procedures

Cortical stimulation testing procedures have been described elsewhere [15, 19]. Briefly, electrical interference was produced by 300-microsecond square-wave pulses, of alternating polarity, generated at a rate of 50 pulses per second between horizontally adjacent electrode pairs. We established a threshold current for sensorimotor effects or afterdischarges (if any) before testing. If no sensorimotor effects or afterdischarges were present, the current was set to

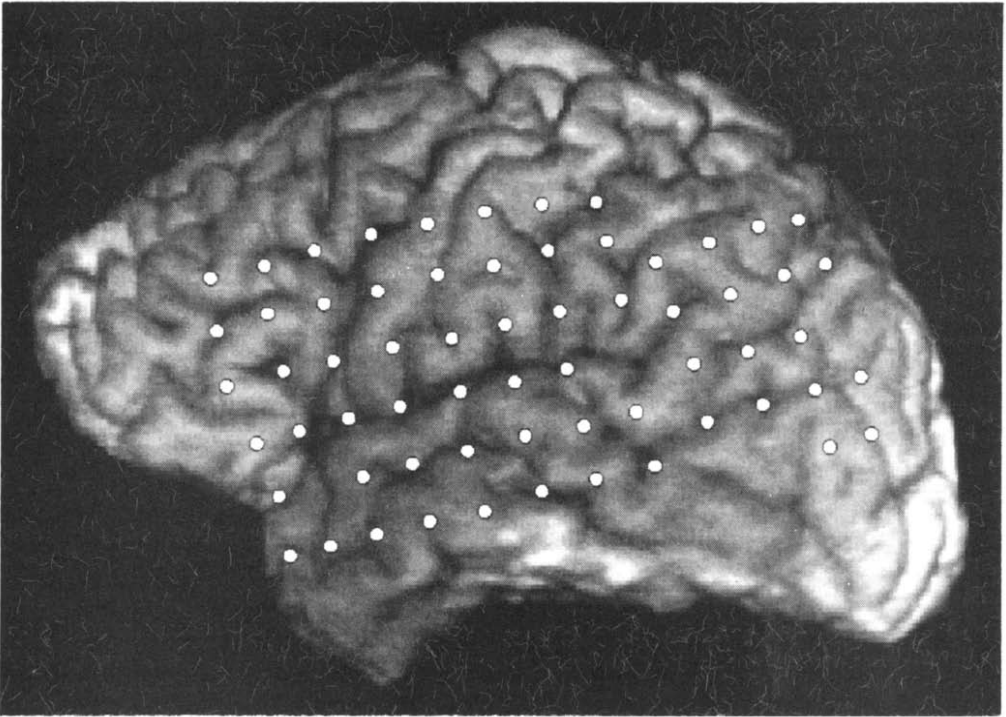


Fig. 1. Superimposed 3-dimensional CT-MRI reconstruction of subdural electrode array coverage in Patient 6. (Note: center-to-center, inter-electrode distance is 1 cm; exposed electrode surface is 2 mm.)

a maximal level of 15 milliamps. Otherwise, we tested at the next lowest current level that did not yield sensorimotor effects or afterdischarges. Stimulus pairs were presented 1 second after current onset. Stimulus presentation and response occurred under electrical stimulation, constituting a single trial. The current remained active for 5 seconds, or until a response was made.

Experimental testing procedures

To establish baseline performance levels, we first tested patients on the syllable discrimination task without electrical interference. We then performed clinical mapping in each patient to plan for resection surgery. The clinical battery administered at each electrode pair included a modified version of the Token test [27] to measure auditory comprehension. Fifteen one-step verbal commands were spoken by a trained clinical technician. Visual cuing from lips and other articulators was avoided. Because auditory comprehension is considered more vulnerable to impairment than lower-level speech perceptual functions, such as discrimination [1, 15], we used the Token test to identify electrode pairs for further speech perceptual testing. Although low-level speech perceptual deficits are not thought to occur in the absence of auditory comprehension deficits [28], we attempted to ensure that our screening procedure was valid. To do so, we administered an abbreviated version of the syllable discrimination task ($N = 15$), with stimuli that were similar but not identical to those in the experimental task. These stimuli were administered at all electrode pairs in Patient 6, who had the most extensive subdural array coverage (see Fig. 1). As predicted, syllable discrimination was not selectively impaired at any site where auditory comprehension remained intact, thereby validating the use of auditory comprehension as a screen for the possible presence of lower-level speech perceptual deficits.

We administered the syllable discrimination task at all electrode pairs where auditory comprehension was found to be impaired during clinical testing. We tested patients individually in quiet but not soundproof conditions. Syllable stimuli were presented binaurally through foam ear tips (Etymotic Research, ER1) inserted directly into the ear canal. Comfortable volume levels were determined separately for each patient. Patients responded to each auditorily presented stimulus pair by circling *Same* or *Different* on a response form. Patients' responses and markers indicating current and stimulus onset were recorded onto video tape for later analysis. To ensure maintenance of baseline performance levels between stimulated trials, we also tested patients periodically without electrical interference.

Scoring and analysis

Trials accompanied by afterdischarges (fewer than 1% per patient) were excluded from analysis. Responses made after the 5-second period of electrical current were scored as incorrect. Responses made during the electrical stimulation period were scored as correct or incorrect relative to each patient's baseline (without electrical interference) responses to the same items.

The ceiling effects obtained at baseline eliminated variance within cells, thereby precluding use of parametric statistical inferences based on the distributions of the test scores. Consequently, paired comparisons between each patient's baseline and electrical interference performance were performed with McNemar's test [29]. Logistic regressions were computed to determine the magnitude of the relationship between error rate and segmental feature and to assess the consistency of that relationship across patients. Likelihood-based approximate 95% confidence intervals for the odds ratios were calculated by inverting likelihood ratio tests [30]. The Mantel-Haenszel test [29], a score test based on the conditional likelihood function, and, therefore, less sensitive to problems arising from small sample sizes, was also used to specify any effects that small sample sizes may have had on our conclusions.

RESULTS

Without electrical interference, all patients performed at perfect (5/6: 100%) or near perfect levels (1/6: 96.6%) on the auditory syllable discrimination task. Patients also performed at ceiling on the Token test.

With electrical interference, patients' performance on the Token test was impaired with stimulation of 3–4 electrode pairs per patient in the temporal and frontal regions. Syllable discrimination was impaired at only one of these pairs in each patient, as determined by paired comparisons between each patient's baseline and electrical interference performance on the syllable task (for all patients, Mantel-Haenszel odds ratio = infinity, approximate p -value ≤ 0.008 ; McNemar's test). This site of syllable discrimination impairment was located on the lateral left posterior temporal cortex, in the superior or middle temporal gyrus of each patient (see Fig. 2).

Patients' discrimination accuracy at this site varied as a function of the particular segmental features tested. Proportional scores for each segmental feature tested are summarised in Table 2. Logistic regressions were performed with these scores. The odds ratios and their corresponding confidence intervals (CI) are displayed in Table 3.

In all cases, patients discriminated pairs contrasted by vowels better than pairs contrasted by stop consonants (odds ratio 3.52; CI [1.56,9.00]), and words better than non-words (odds ratio 1.63; CI [1.08,3.31]). Moreover, pairs contrasted by two stop consonant features (i.e. voicing *and* place-of-articulation) were discriminated better, in both syllable–initial (odds ratio 2.27; CI [1.06,5.02]) and syllable–final position (odds ratio 2.48; CI [1.18,5.43]) than pairs contrasted by a single feature (i.e. voicing *or* place-of-articulation).

Comparing patients' overall performance in discriminating pairs contrasted by either place-of-articulation or voicing, without regard to syllable position, revealed significantly more place-of-articulation errors than voicing errors (odds ratio 2.47; CI [1.35,4.58]). However, when syllable position was taken into consideration, a different pattern of results emerged. Although patients detected voicing contrasts better than place contrasts in syllable–final position (odds ratio 3.86; CI [1.58,10.1]), no significant differences were obtained in syllable–initial position (odds ratio 1.862; CI [0.746,4.76]).

Thus, for all but one comparison, the odds ratios differed significantly from 1, permitting rejection of null hypotheses. The only comparison that was not significant was that of voicing versus place in syllable–initial position.

To determine whether our small sample sizes may have affected the conclusions above, the data were also analysed by Mantel-Haenszel tests. The results from the Mantel-Haenszel tests

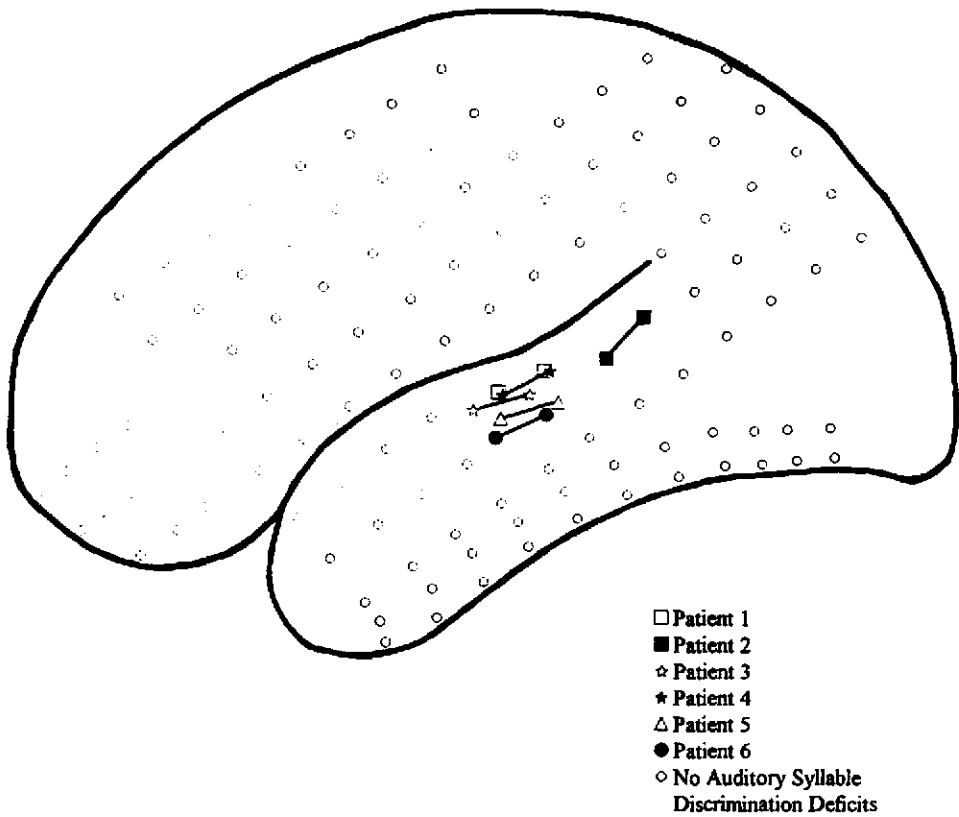


Fig. 2. Localisation of auditory syllable discrimination deficits. Electrode positions associated with discrimination deficits were normalised across patients. Other electrode sites are represented schematically. Syllable discrimination was tested at all temporal lobe electrode sites in each patient. (Note: because electrode locations were normalised across patients, certain electrodes appear to be superimposed.)

Table 2. Proportion correct responses under electrical interference (chance = 0.50)

	Syllable-initial consonant			Syllable-medial vowel	Syllable-final consonant		
	voice	place	voice and place		voice	place	voice and place
Pt 1	0.42	0.33	0.57	1.0	0.66	0.44	0.71
Pt 2	0.62	0.33	0.57	0.66	0.83	0.44	0.71
Pt 3	0.62	0.50	0.71	0.83	0.66	0.33	0.71
Pt 4	0.50	0.33	0.71	0.83	0.66	0.25	0.71
Pt 5	0.50	0.33	0.71	0.83	0.66	0.44	0.85
Pt 6	0.37	0.33	0.57	0.66	0.66	0.33	0.57

confirmed the likelihood-based results in all cases. For all but one comparison, $p \leq 0.026$. The only non-significant difference was obtained for patients' performance discriminating voice and place contrasts in syllable-initial position ($p = 0.161$), a finding that is also consistent with the likelihood-based analysis.

Logistic regressions were also performed to evaluate the consistency of these results across

Table 3. Logistic regressions calculated to assess the magnitude and consistency of the relationship between patient performance and segmental feature. Odds ratios corresponding to each comparison are presented in order of magnitude from higher to lower. Likelihood-based approximate confidence intervals for the odds ratios were calculated by inverting likelihood ratio tests

Features contrasted	Odds ratio maximum likelihood estimate	Lower 95% confidence limit	Upper 95% confidence limit
Voice vs. place syllable-final	3.86	1.57	10.10
Vowel vs. consonant	3.52	1.56	9.0
2 vs. 1 feature syllable-final	2.48	1.18	5.43
Voice vs. place (overall)	2.47	1.36	4.58
2 vs. 1 feature syllable-initial	2.27	1.06	5.02
Voice vs. place syllable-initial	1.86	0.75	4.76
Words vs. non-words	1.63	1.08	3.31

patients. No statistically significant interactions were obtained between patient and discrimination accuracy for any of the segmental features tested.

DISCUSSION

These findings reveal distinct lateralisation differences in the processing of stop consonants and vowels. Specifically, stop consonant discrimination was significantly more impaired than vowel discrimination when electrical interference was applied to the lateral left cortex of all six patients.

Previous attempts to localise stop consonant perception more precisely within the left cerebral cortex have identified the perisylvian region, and especially the temporal lobe, as a critical area [1, 31, 32]. These investigations, however, were generally based on studies of individual patients presenting with irreversible and relatively extensive ischaemic cerebral damage precluding more exact localisation. Precise localisation was accomplished in the present study by use of electrical interference and by screening multiple sites within the left perisylvian region, particularly the temporal lobe. As a result, we were able to localise stop consonant discrimination deficits to a single site in the posterior temporal lobe of each patient. This site encompassed a relatively small area ($\sim 1 \text{ cm}^2$), at a strikingly similar location in all patients (see Fig. 2). Stop consonant discrimination appears, therefore, not only to be more lateralised than vowel perception, but also to be localised to a relatively confined region within the left posterior temporal lobe.

It has been postulated that consonant perception is more lateralised than vowel perception because the left hemisphere is specialised for processing brief acoustic cues, such as stop consonant formant transitions which are shorter in duration than the steady-state formants of vowels [10, 13]. Formant transitions have also been identified as one of the primary acoustic cues to stop consonant place-of-articulation [12, 13]. Based on this association, it has been claimed that detection of stop consonant place-of-articulation is more vulnerable to impairment with left hemisphere lesions than other stop consonant features, such as voicing [5, 10]. Although it has been reported that aphasic patients demonstrate more difficulty detecting

place-of-articulation than voicing [5], the opposite pattern, or no feature type effects has also been reported [14, 33]. We found no significant differences in our patients' accuracy in discriminating either feature in syllable-initial position. This finding is not compatible with the view that detection of place-of-articulation is intrinsically more dependent than voicing on left-hemisphere processing and, therefore, more vulnerable to impairment. Furthermore, our patients showed impaired perception of both place and voicing, suggesting that left-hemisphere mechanisms are important for the detection of both stop consonant features. The inference of a lack of independence between these two stop consonant features is predicated upon the anatomic resolution of the cortical stimulation which has been assessed at approximately 1 cm² [34–37]. We cannot, therefore, exclude the possibility that a finer level of anatomic detail would result in the separability of feature type. However, these electrical interference data do help establish upper boundaries on the extent to which such potential dissociations can be claimed.

In the syllable-final position, the detection of place-of-articulation was more severely impaired than was perception of voicing. In the absence of a dissociation between place and voicing in syllable-initial position, differential lateralisation effects cannot readily account for this difference, as has been previously claimed [5, 10]. These differences can, however, be attributed to the effects of syllable context. Specifically, vowels preceding voiced consonants are typically lengthened, providing an additional cue to the presence of voicing that is not available for pre-vocalic consonants. Evidence that our patients were able to detect differences in vowel duration is provided by their relatively superior performance discriminating vowel contrasts that are characterised by intrinsic durational differences (i.e. /i-I/). Furthermore, our data confirm that patients were able to use contextual information, as evidenced by the effect of lexical status on their syllable discrimination accuracy. It is reasonable to assume, therefore, that patients were able to use the contextual information provided by pre-voicing vocalic lengthening to discriminate syllable-final voicing contrasts. Thus, syllable context effects adequately account for the finding that perceptual differences between voicing and place in our patients only occurred when these contrasts appeared in syllable-final position.

The lack of comparable performance differences in the discrimination of syllable-initial voicing and place contrasts challenges previous claims that perception of place-of-articulation is more vulnerable to impairment than voicing [7, 8]. We suggest that methodological differences may, in part, be responsible for this apparent discrepancy in results. Specifically, our data identified an interaction between syllable position and feature type. Most previous studies of feature discrimination in aphasic patients have not taken such interactional effects into consideration. As a result, it is difficult to determine whether previously reported perceptual differences between stop consonant place and voice reflect such interactional effects, or other as yet unidentified factors. It is noteworthy that studies where contextual effects were restricted to a single syllable position, as, for example, in CV (consonant-vowel) speech stimuli, have reported no significant differences for voicing and place discrimination [14, 15]. These results support previous claims that there are lateralisation differences in the processing of consonants and vowels. Data provide no evidence, however, that these differences reflect the specialised perceptual requirements of the single stop consonant feature of place-of-articulation.

Although a feature number effect (voice and place vs voice or place) was evident in our data, its interpretation requires some caution. The feature number effect has typically been interpreted as evidence for the existence of independent processing mechanisms [7–9]. However, additivity effects do not definitively establish processing independence. Increasing the number of feature differences may, for example, simply provide a single underlying processor with

additional information to augment its performance. Indeed, there was some evidence of co-dependence between place-of-articulation and voicing detection. Specifically, place-of-articulation and voicing errors co-occurred at the same sites, and did not occur independently at any other sites. This coincident functional and anatomic association of deficits in discriminating both features across all six patients further challenges the purported independence between voicing and place processing mechanisms.

Although stop consonant perception appears to be more dependent upon left-hemisphere processing than does vowel perception, the reason for this discrepancy remains to be determined. One recently proposed hypothesis suggests that the overall shape of the spectrum at the onset of stop closure release, as opposed to any single acoustic parameter, cues the listener to the identity of a stop consonant [38]. Because the spectral shape at closure release is not influenced by the following vocalic context, the mechanisms responsible for detecting such abrupt changes in spectral energy are thought to function independent of those subserving vowel perception. Moreover, acoustic properties associated with both voicing and place-of-articulation are thought to contribute, in an integrated fashion, to the overall spectral pattern. Accordingly, perceptual dissociations between these two features would not be expected to occur. Additional research is clearly needed to further validate this hypothesis.

In conclusion, our data support previous claims that stop consonant perception is more dependent on left-hemisphere processes than vowel perception. Furthermore, our results indicate that stop consonant discrimination is dependent on a relatively small region of the left posterior temporal lobe, thereby extending previous findings. Voicing and place-of-articulation deficits were both detected at the same posterior temporal site and did not differ significantly in magnitude. This suggests that the lateralisation of stop consonant perception cannot be attributed to the particular requirements of a single stop consonant feature. Instead, multiple aspects of stop consonants, which are perhaps integrated into the overall spectral patterns sampled by the listener, are dependent on similar, if not identical, left-hemisphere structures.

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