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Separable processing of consonants and vowels

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There are two views about the nature of consonants and vowels. One view holds that they are categorically distinct objects that play a fundamental role in the construction of syllables in speech production[1–3]. The other view is that they are convenient labels for distinguishing between peak (vowel) and non-peak (consonant) parts of a continuous stream of sound that varies in sonority (roughly the degree of openness of the vocal apparatus during speech)[4–6], or that they are summary labels for bundles of feature segments[7,8]. Taking the latter view, consonants and vowels do not have an independent status in language processing. Here we provide evidence for the possible categorical distinction between consonants and vowels in the brain. We report the performance of two Italian-speaking aphasics who show contrasting, selective difficulties in producing vowels and consonants. Their performance in producing individual consonants is independent of the sonority value and feature properties of the consonants. This pattern of results suggests that consonants and vowels are processed by distinct neural mechanisms, thereby providing evidence for their independent status in language production.

AS, a right-handed 41-year-old woman, became aphasic due to ischemic cerebrovascular damage. A computerized tomography scan showed lesions in the left parietal and temporal lobes, and a small lesion in the right parietal lobe. IFA, a right-handed 52-year-old woman, suffered a vascular stroke that resulted in damage to the left supramarginal, angular and superior temporal gyri. The two patients showed similar clinical profiles. They showed no visual, auditory, somatosensory, motor or articulatory deficits; their verbal spans were severely reduced (3 forward and 3 backward for AS, and 3 forward and 2 backward for IFA); and their spontaneous speech was fluent but paraphasic. On a series of assessment tests[9] they scored very well on phonemic discrimination and auditory word-recognition tasks, but performed poorly on oral naming, reading and repetition tasks (ranging from 40% to 70% correct for AS and 50% to 65% correct for IFA). Performance on the latter tasks was characterized by phonological, morphological, lexical and semantic (only in naming) errors. Both patients could be classified as conduction aphasics. A striking feature of their speech-production performance was contrasting patterns of error rates on vowels relative to consonants: AS made many more errors on vowels and IFA made many more errors on consonants[10–12].

To document the suspected double dissociation of selective damage in producing consonants and vowels, AS and IFA were asked to repeat large numbers of words. From an initial corpus of 5,079 (46.3% of total) and 2,671 (43.7% of total) errors produced by AS and IFA, respectively, we analysed the substitution errors, as these were the predominant error type (65.51% for AS and 58.37% for IFA; Table 1). The analyses considered only non-word responses involving three or fewer phoneme substitutions ('Simple Phonological' errors in Table 1). The final error corpus analyses included 771 errors for AS and 939 errors for IFA. The other responses included primarily morphological errors, but also lexical substitution errors (tasca (pocket) → tassa (tax)) and other more complex non-word responses (tracceremo (we will trace) → /trokkomano/). These errors were excluded because they could arise from independent causes (in the case of morphological and lexical substitution errors) or were too complex for unambiguous analysis.

Substitution errors were distributed unequally for consonants and vowels for the two patients, but in opposite directions (Table 2). AS produced nearly three times as many errors on vowels as on consonants and IFA produced nearly five times as many errors on consonants as on vowels. The contrast in performance between the two patients is clearest when we consider their percentage of errors for each phoneme position in words of the same consonant/vowel

Table 1 Error distribution (number of errors and percentage error)

		AS		IFA	
Error type	Examples	*N*	%	*N*	%
Substitutions	salire (to climb) → savite	3,327	65.51	1,559	58.37
Deletions	salire → sare	287	5.65	381	14.26
Insertions	salire → savilire	295	5.81	386	14.45
Other types	salire → salte, sarile	645	12.70	182	6.81
Fragments	salire → fa…	446	8.78	146	5.47
No responses		79	1.56	17	0.64
Total errors		5,079	100.00	2,671	100.00
		AS		IFA	
Substitution errors by response type	Examples	*N*	%	*N*	%
Simple phonological	salire → solire, sotive, etc.	771	23.17	939	60.23
Complex phonological	salire → tolote, satuvo, etc.	450	13.53	212	13.60
Targets with glide phonological	olio (oil) → omio	109	3.28	93	5.97
Inflections and other morphological	salire → salito (climbed)	1,833	55.09	246	15.78
Lexical	salire → solare (of the sun)	150	4.51	69	4.43
Stress	salire → salevò	14	0.42	0	0.00
Total errors		3,327	100.00	1,559	100.00

Error type: classification into main error types of the total errors for the two patients AS and IFA. Substitution errors by response type: gives the breakdown of substitution errors: simple phonological, involving $\leqslant 3$ phonemes; complex phonological, involving >3 phonemes; targets with glide phonological, affecting a target word containing a glide (these errors are scored separately because of the uncertain phonological status of glides); inflections and other morphological, resulting in a word morphologically related to the target; lexical, resulting in another word; stress, involving a stress shift in addition to a segmental substitution. Only simple phonological errors were included in further analyses.

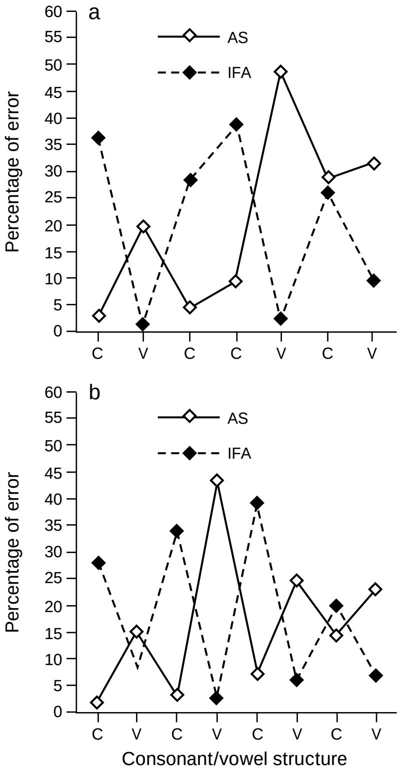

Figure 1 Performance in repetition of a set of words seven or eight phonemes in length. The figure illustrates the complementary performance of the two patients in repetition of items matched for length in number of phonemes and syllable structure. **a**, The data reported refer to items like 'pastore' (shepherd); **b**, the data reported refer to items like 'minatore' (miner).

(C/V) structure. As shown in Fig. 1, the percentage errors on consonants and vowels produced by AS and IFA for words of the same C/V structure are almost in complementary distribution.

Although these results establish that AS and IFA show contrasting selective impairments for vowels and consonants, they are not sufficient to establish that the two types of sounds are categorically distinct objects. It could be argued that damage to a mechanism that is responsible for processing the more sonorous (AS) or less sonorous (IFA) sounds would result in the observed double dissociation. However, this view also predicts that the percentage of errors within the consonant class should vary as a function of sonority[13]: AS should make more errors on the more sonorous than the less sonorous consonants and IFA should show the opposite pattern. We tested this prediction by correlating the percentage of errors for individual consonants with their respective sonority indices[5]. For this and the following analysis we considered only simple C/V syllables, so as not to bias the opportunity of errors for consonant substitutions. This is necessary because consonants of different sonority values are distributed unequally across positions within syllables. For both patients, the correlations between sonority values and the error rates were near zero (Table 3). Furthermore, AS was no more likely to produce incorrectly a less rather than a more sonorous segment, and IFA was no more likely to produce incorrectly a more rather than a less sonorous segment. The absence of a correlation between the sonority values of consonants and the probability of making an error on a consonant or producing the consonant in error is not because the range of sonority variation within consonants is too narrow. If anything, liquids (/l/, /r/) are much more similar in sonority to vowels than they are to stop consonants (/p/, /t/): liquids are classified as sonorants in phonetic analyses of speech[2,8]. Thus, these results show that a deficit to a sonority-based processing mechanism is not the cause of the observed double dissociation.

It could also be argued that selective damage to the sets of features that discriminate among vowels and among consonants, respectively, would result in the observed double dissociation. This view would predict that damage to the features that discriminate among vowels (the dorsal features high, low and back) should result not only in an impairment in processing vowels, but also in greater difficulty for those consonants that are distinguished on the basis of those features (/k/, /g/, /l/, /r/)[6]. However, the error rates for the latter consonants did not differ from those for other consonants (7.9% versus 11.7%, and 27.5% versus 28.3% for AS and IFA, respectively).

Three clear facts have emerged from our analysis of the error performance of patients AS and IFA. First, consonants and vowels can be damaged independently of each other. Second, the distribution of error rates for consonants is not a function of their sonority value. Third, the distribution of errors for consonants is not a function of their dependence on features that distinguish among both vowels and consonants. These three facts have clear implications for theories of speech production and their representation of phonological processes in the brain. The fact that consonants and vowels can be damaged independently of each other rules out, as a general cause of such deficits, an explanation based on the argument

Table 2 Error distribution by segmental position

		Number of segment errors	Number of segments in words	Error rate
AS	Vowel	737	2,736	0.269
	Consonant	318	3,434	0.093
	Total	1,055		
IFA	Vowel	181	3,397	0.053
	Consonant	1,173	4,159	0.282
	Total	1,354		

Analyses of 771 responses for AS and 939 responses for IFA. Number of segment errors, individual phoneme substitutions produced by each patient. Number of segments in words, occurrences of consonants and vowels in the error corpus. Error rate, ratio of segment errors to the number of segments in the words. The proportions of anticipation and perseveration errors for vowels (AS: 54%; IFA: 57%) and consonants (AS: 30%; IFA: 37%) were comparable for the two patients. Analysis of the substituted consonants and vowels revealed similar patterns for the two patients. In both cases, substitutions which were phonologically close (such as /t/ → /d/) and distant (such as /t/ → /s/) from the target response were equally represented.

Table 3 Sonority effect analyses

Consonant type	Sonority scale	% error for each target consonant type		% of consonant type produced as an error	
		AS	IFA	AS	IFA
r	8	7.65	21.54	9.12	26.60
l	7	11.27	39.29	32.39	35.71
ʎ	7	16.67	16.67	16.67	5.56
m	6	14.97	14.00	14.97	20.67
n	6	11.36	30.09	11.82	22.57
ɲ	6	15.79	33.33	0.00	8.33
s	5	12.99	30.16	40.26	16.67
ʃ	5	0.00	28.57	0.00	0.00
v	4	8.37	28.99	10.23	32.61
z	4	28.57	19.00	19.00	82.80
f	3	4.76	29.03	0.00	22.58
tʃ	3	5.66	24.76	0.00	43.81
ʤ	3	4.76	29.11	3.57	16.46
b	2	16.00	37.70	6.00	14.75
d	2	9.32	57.94	10.56	17.06
g	2	14.00	65.12	8.00	6.98
p	1	8.33	17.65	4.17	20.00
t	1	16.00	17.25	6.59	38.00
k	1	2.38	14.62	17.86	33.08
Spearman's rho		0.16 ns	0.01 ns	0.27 ns	–0.12 ns
Partial correlation		0.14 ns	–0.15 ns	0.32 ns	–0.13 ns

Two sets of correlations are reported for each patient. One is between sonority value[5] and the percentage of errors for each target consonant segment (first two columns). The other is between sonority value and the percentage of occurrences of consonant types produced as errors (last two columns). Error percentages are calculated against the total number of occurrences of each consonant in each set. For each set, a partial correlation was computed with the frequency of occurrence of each consonant in the language partialled out. ns, not significant.

that consonants are more difficult to produce than vowels. More importantly, this fact and the fact that error performance depends neither on the sonority value of individual phonemes nor on their feature properties suggest that consonants and vowels are categorically distinct objects at some level of representation even though they are not categorically distinguishable at a phonetic level. This conclusion is consistent with recent experimental work in speech production with neurologically intact speakers, which has shown that phonological encoding operates over segments (consonants and vowels) and not features[14]. Evidence consistent with the possibility that consonants and vowels are represented categorically in perception is provided by the results of a study that stimulated the left superior temporal gyrus of patients with implanted subdural electrode arrays[15]. Stimulation impaired discrimination of consonants but not vowels. Importantly, the disruptive effect of the stimulation was equal across all consonants tested, independently of their sonority.

The conclusion that consonants and vowels are represented autonomously does not imply that sonority does not play a role in speech production. The sonority gradient plays a crucial role in determining consonant ordering within the onset and coda of a syllable and in determining syllable boundary. Furthermore, sonority has been used to explain various patterns of speech errors in aphasia[16–18] and it has been shown to play a direct role in the distribution of consonant errors produced by a non-fluent aphasic patient with frontal lobe damage[13]. The contrasting sets of results suggest that sonority and C/V structure information are used at different levels of the speech production process.

Finally, we considered the possible functional motivation for representing consonants and vowels independently and categorically. The distinction between consonants and vowels plays a crucial role in determining the prosodic structure of speech and in the organization of syllables[1,16,17]. It has been proposed that syllable structure is not stored directly with our knowledge of the sounds of words but is computed 'on-line' during speech[19,20]. This on-line process is necessary because the domain of syllabification is not the lexical word (where syllable structure might be represented) but the phonological word[21]. As a consequence syllable boundaries often straddle word boundaries—parts of one word are syllabified with parts of an adjacent word. For example, the phrase 'understand it' is syllabified as un-der-stan-dit and not as un-der-stand-it[21]. The independent representation of C/V structure could serve as the basis for this syllabification process by using this information to assign segments to nucleus and non-nucleus positions in a syllable. ☐

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Noradrenaline in the ventral forebrain is critical for opiate withdrawal-induced aversion

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Cessation of drug use in chronic opiate abusers produces a severe withdrawal syndrome that is highly aversive, and avoidance of withdrawal or associated stimuli is a major factor contributing to opiate abuse[1,2]. Increased noradrenaline in the brain has long been implicated in opiate withdrawal[3], but it has not been clear which noradrenergic systems are involved. Here we show that microinjection of β-noradrenergic-receptor antagonists, or of an α2-receptor agonist, into the bed nucleus of the stria terminalis (BNST) in rats markedly attenuates opiate-withdrawal-induced conditioned place aversion. Immunohistochemical studies revealed that numerous BNST-projecting cells in the A1 and A2 noradrenergic cell groups of the caudal medulla were activated during withdrawal. Lesion of these ascending medullary projections also greatly reduced opiate-withdrawal-induced place aversion, whereas lesion of locus coeruleus noradrenergic projections had no effect on opiate-withdrawal behaviour. We conclude that noradrenergic inputs to the BNST from the caudal medulla are critically involved in the aversiveness of opiate withdrawal.

Opiate withdrawal results in marked hyperactivity of central noradrenergic neurons[3,4]. There is evidence that increased noradrenaline is involved in various aspects of the withdrawal response[3], but it has not been determined where and how increased noradrenaline release contributes to the opiate withdrawal syndrome. The bed nucleus of the stria terminalis (BNST), a component of the extended amygdala[5], has the highest density of noradrenergic inputs in the brain[6], and is anatomically connected with other brain areas implicated in drug abuse[5]. We therefore hypothesized that the BNST may be an important site for the actions of noradrenaline during opiate withdrawal.

To determine whether noradrenaline afferents to the BNST are stimulated by opiate withdrawal, we injected a retrograde tract-tracer into the BNST and used triple labelling for the tracer, for tyrosine hydroxylase (a marker for noradrenergic neurons), and for Fos-related antigens (FRAs; a marker of cellular activation). Consistent with previous studies[7], we found numerous retrogradely