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Japanese Quail Can Learn Phonetic Categories

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Japanese quail (*Coturnix coturnix*) learned a category for syllable-initial [d] followed by a dozen different vowels. After learning to categorize syllables consisting of [d], [b], or [g] followed by four different vowels, quail correctly categorized syllables in which the same consonants preceded eight novel vowels. Acoustic analysis of the categorized syllables revealed no single feature or pattern of features that could support generalization, suggesting that the quail adopted a more complex mapping of stimuli into categories. These results challenge theories of speech sound classification that posit uniquely human capacities.

LACK OF INVARIANCE IN THE RELATION between linguistic categories and the acoustic signal poses a central problem in the study of speech perception. Acoustic information specifying a phonetic segment varies substantially depending on surrounding segments, and the ease with which humans identify speech sounds in the face of this variability has encouraged many researchers to invoke uniquely human perceptual processes that give rise to phonetic categories.

Some have hypothesized the existence of a system, biologically distinct from the general human auditory system, that automatically assigns acoustically different speech sounds to the same category on the basis of common underlying articulatory events (*1*). Others suggest that, although a separate system is not necessary, humans may have evolved special sensitivities or sensory discontinuities in the auditory system to facilitate classification of linguistically significant vocal tract output (*2*). Finally, a logical possibility is that phonetic categories have no natural basis in either audition or articulation. Perhaps the human listener learns to group physically diverse speech tokens together on purely functional grounds. By this view, learning that [di] and [du] have the same initial segment is much like learning that upper- and lowercase "A" belong to the same orthographic category.

Experiments with nonhuman animals are particularly informative in assessing whether uniquely human processes are required for speech categorization. In almost all previous research with nonhumans, monkeys or chinchillas were trained in tasks that generally involved simple classification or discrimination of synthetic speech sounds varying on a well-defined dimension (*3*). In contrast, the present study examines the ability of an avian species to categorize naturally produced speech stimuli that vary on several relevant acoustic dimensions (*4*). None of the above hypotheses predicts appropriate phonetic categorization by nonhumans, which obviously lack both specific adaptations for perceiving human speech and the extensive exposure to language required to learn phonetic categories on a purely functional basis.

Japanese quail (*Coturnix coturnix*) were used as subjects in a categorization experiment (*5*). Three females were taught to discriminate natural [d]-vowel-[s] syllables from [b]-vowel-[s] and [g]-vowel-[s] syllables (*6*). The phonetic segments [b], [d], and [g] are all voiced stop consonants that differ only in place of articulation. In particular, [d] was chosen because it represents "the paradigm case of lack of acoustic invariance" (*7*). Despite extensive examination of the signal, researchers have not found a reliable acoustic correlate of [d] (*8*).

Quail first learned to discriminate [dis], [dus], [dæs], and [das] from [bis], [bus], [bæs], [bas] and from [gis], [gus], [gæs], [gas] in training sessions consisting of 48 positive and 48 negative trials (*9*). During positive trials, birds received food reinforcement for pecking a single lighted key during repeated presentation of [d] syllables; during negative trials, they were required to refrain from pecking for 10 seconds for presentation of [b] and [g] syllables to be terminated (*10*).

After reaching asymptotic performance for the [i], [u], [æ], and [a] contexts (*11*), birds were tested on novel syllables containing the vowels [ɪ], [ʊ], [ɛ], and [ʌ]. Each of eight novel vowel tokens was presented three times in a test session, with every novel vowel appearing in one positive and one negative syllable. For example, during one test session, the novel tokens were [dɪs], [dʊs], [dɛs], [dʌs], [bɪs], [bɛs], [gʊs], and [gʌs]. Birds could not receive food on novel [d] stimuli, and they did not need to cease pecking for presentation of the novel [b] and [g] stimuli to terminate. The 24 nonreinforced novel stimulus trials were interspersed with 96 nonnovel stimulus trials presented with the same reinforcement contingencies in effect as those during training sessions. Eight test sessions were carried out 2 or 3 days apart, separated by normal nonnovel sessions (Fig. 1 and Table 1).

All three quail pecked significantly more often to novel stimuli beginning with [d] than to those beginning with [b] or [g]. Bird 716 did not peck at all to the [gʊs] syllable. Quail recognized novel [d] stimuli as belonging to the same category as the [d] stimuli on which they were trained (*12*).

It could be argued that the vowel environments [ɪ], [ʊ], [ɛ], and [ʌ] were not sufficiently novel, since they may be loosely characterized as short or lax versions of the vowels used in training. Demonstration of category formation requires that discriminably different items be classified equivalently by the perceiver. To address this point, two of the same birds were tested in a second experiment with four more novel vowel environments including the diphthongs [eʸ], [oʷ], [oʸ], and retroflex [ɝ] (*13*). These vowels are acoustically quite distinct from the eight formerly used. Quail were trained for a few days on the test stimuli used in the first experiment. Critical test sessions were then carried out as before, except that trials with the four new test

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vowels were presented among trials with the eight vowels previously used. For both birds, performance with these four new vowel environments was essentially the same as that with the former novel vowels (Fig. 1, right side).

On what basis do these quail correctly categorize new tokens? The possibility that their categorization is based on a knowledge of articulatory commonalities can be excluded. Moreover, if quail treated the training categories as physically and auditorily arbitrary sets of stimulus tokens, with functional equivalence defined only with respect to the value that a stimulus carries in predicting reinforcement, then correct generalization to novel tokens would not be expected. Therefore, performance must reflect the use of acoustic or auditory commonalities among the [d] syllables not shared with the [b] or [g] syllables.

Although some invariant acoustic property of [d] may be detected by quail, rigorous acoustic analysis does not reveal what it is. Examination of spectrograms, waveforms, amplitude envelopes, and spectral cross sections disclosed no invariant property. In measurements of voice onset time, second-formant onset frequency, burst frequency, and burst amplitude, extensive overlap between [d], [b], and [g] tokens was observed. None of these properties could, by itself, support appropriate categorization.

Perhaps some more global invariant acoustic property gives rise to categorization. For example, it has been proposed that short-time spectra sampled at the onset of stop consonants may exhibit gross spectral properties that specify consonantal place of articulation (*14*). Accordingly, frequency spectra were measured at the onsets of all stimuli after multiplying by a 26-msec raised-cosine window. The energy level for [b] syllables was either fairly uniform across frequency or else declined slightly with increased frequency. The distribution of energy for [d] spectra was also generally diffuse, but the level tended to increase with frequency. For [g] syllables, there was usually at least one broad central spectral prominence that varied in frequency depending on the following vowel. These generalizations did not hold for every stimulus; however, a few [d]'s had the central peak characteristic of [g]'s (for example, [doʷs] and [dɝs], and the energy distribution for some [g]'s was diffuse with no major peak (for example, [gis] and [goʷs]). Significantly, performance for these exceptional stimuli was as good as that for stimuli with more characteristic gross spectral shapes.

Alternatively, the [d] category may have no single invariant acoustic property; rather, quail may use some combination of stimulus properties to categorize syllables. There are two ways in which such a category could be formed. The first is that initial consonantal information may depend on the type of vowel that follows. In an earlier study using the same stimulus tokens used in these experiments, human subjects appear to have waited for acoustic information specifying the vowel type (such as, high or low) before categorizing the preceding voiced stop (*15*). The second is that these phonetic categories are examples of polymorphous concepts (*16*), with no single necessary or sufficient condition for class membership. Instances of such concepts can at best be described as having a family resemblance (*17*). Natural concepts are almost always polymorphous, and the ability to form polymorphous concepts has been demonstrated in pigeons (*18*).

The quail data are consistent with those from a growing number of studies carried out over the past decade, in which concept formation by nonhumans has been demonstrated for various visual stimuli. For example, after learning to discriminate among slides depicting trees, people, or oak leaves, pigeons correctly classified novel instances of these categories (*19*). Just as with phonetic categories, these visual categories are apparently not definable in terms of any single stimulus dimension.

The data presented here do not reveal the basis for the quails' categorization. They do, however, call to mind the cautionary message of C. Lloyd Morgan's canon: never opt

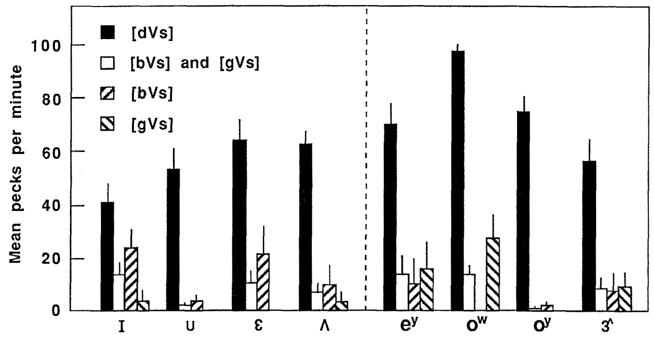

Fig. 1. Peck rates for positive and negative test stimuli for bird 716 for each vowel context, and the standard error is indicated. Each [d]-vowel-[s] ([dVs]) token was presented in 24 trials, and [bVs] and [gVs] tokens were each presented on 12 trials (*9*). The average trial duration was 30 seconds.

Table 1. Peck rates for positive and negative novel test stimuli as well as for nonnovel training stimuli for each bird. Novel [dVs] tokens were presented for three trials during each of eight test sessions, while novel [bVs] and [gVs] tokens were each presented for three trials during four of the eight test sessions. Training stimuli were presented in multiple trials during test sessions with reinforcement contingencies operative, so that close comparisons between test and training stimuli is not warranted.

	[ɪ]	[ʊ]	[ɛ]	[ʌ]	All test sessions	All training stimuli	[eʸ]	[oʷ]	[oʸ]	[ɝ]	All test sessions	All training stimuli
Bird 716												
[d]	41.7	53.4	63.8	62.3	55.3	63.6	70.5	97.1	73.8	56.0	74.4	82.1
[b]	23.3	3.5	22.0	9.8	14.7	7.1	10.5	0.0	1.3	7.6	4.9	8.4
[g]	4.3	0.0	0.3	3.8	2.1	4.5	15.9	27.3	0.0	8.8	13.0	7.5
[b/g]	13.8	1.8	11.1	6.8	8.4	5.8	13.2	13.6	0.7	8.2	8.9	8.0
Bird 730												
[d]	47.7	71.5	66.8	85.5	67.9	116.1	99.8	122.6	80.5	60.7	90.9	113.1
[b]	33.2	5.1	64.6	29.3	33.1	19.4	62.3	7.0	23.9	2.5	23.9	26.2
[g]	35.1	24.1	7.8	40.7	26.9	21.9	2.2	7.2	16.4	27.4	13.3	23.1
[b/g]	34.1	14.6	36.2	35.0	30.0	25.6	32.2	7.1	20.2	15.0	18.6	24.7
Bird 768												
[d]	61.5	76.5	75.9	84.5	74.6	82.9						
[b]	30.8	26.0	53.4	63.8	43.5	23.4						
[g]	49.9	41.1	21.8	53.2	41.5	15.7						
[b/g]	40.3	33.7	37.6	58.5	42.5	19.6						

for higher level psychological explanations when lower level ones will do (*20*). A theory of human phonetic categorization may need to be no more (and no less) complex than that required to explain the behavior of these quail.

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9. Phonetic symbols represent these English vowel sounds:

   [i] “heat”
   [ɪ] “hit”
   [e^{y}] “hate”
   [u] “hoot”
   [ʊ] “hood”
   [o^{w}] “hope”
   [æ] “hat”
   [ɛ] “head”
   [o^{y}] “hoist”
   [a] “hot”
   [ʌ] “hut”
   [ɝ] “hurt”

10. Quail were deprived of food 5 to 10 hours before experimental sessions. Each was trained and tested in a standard pigeon operant chamber lined with sound-attenuating foam. Birds pecked a single lighted 4-cm round key 15 cm above the floor and centered between two 9-cm speakers. Stimuli were presented and reinforcement was controlled by a DEC PDP 11/34 computer. On each trial, a single syllable was presented repeatedly once per second at a peak level of 75-dB sound pressure level. The average duration of each trial was 30 seconds, varying geometrically from 10 to 76 seconds. The interval between trials was 15 seconds. Responses to stimuli beginning with [d] were reinforced on a variable interval schedule by a 2-second access to food from a hopper beneath the peck key. The average interval of reinforcement was also 30 seconds (10 to 76 seconds), so that positive stimuli were reinforced on an average of once per trial. When a positive trial was relatively long (56 or 76 seconds) and times to reinforcement were short (10 to 16 seconds), reinforcement was available more than once. Likewise, on shorter positive trials reinforcement was not available at all if time to reinforcement was longer than the trial. Such intermittent reinforcement encouraged consistent peck rates during nonreinforced test trials. Training sessions lasted about 70 to 80 minutes.
11. Asymptotic performance was defined as the largest ratio of pecks per minute to positive versus negative stimuli over a sustained period of at least 1 week. This criterion was reached for bird 716 after 4,240 trials, bird 730 after 8,176 trials, and bird 768 after 12,304 trials.
12. Statistical analyses of peck rates to novel stimuli were carried out separately for each of three birds across eight test sessions. The mean peck rate for 96 presentations of novel positive stimuli (three trials by eight sessions by one consonant [d] by four vowels) was compared with the rate for 96 presentations of novel negative stimuli (three trials by four sessions by two consonants [b,g] by four vowels). Comparisons are significant at $P < 0.001$ (two-tailed *t* tests) for each of the three birds.
13. Bird 768 began training 2 months later than birds 716 and 730 and finished testing on the first four novel vowels after those birds had completed testing on the second four novel vowels. Given the clarity of the results from birds 716 and 730, bird 768 was not tested on the second set of vowel contexts.
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Chemical Conversion of a DNA-Binding Protein into a Site-Specific Nuclease

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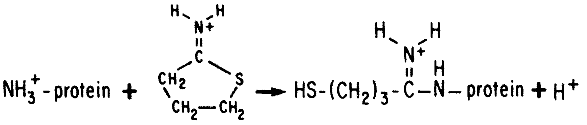
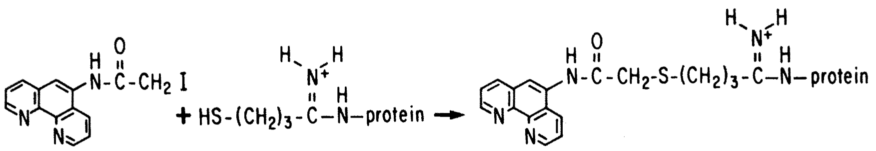
The tryptophan gene (*trp*) repressor of *Escherichia coli* has been converted into a site-specific nuclease by covalently attaching it to the 1,10-phenanthroline–copper complex. In its cuprous form, the coordination complex with hydrogen peroxide as a coreactant cleaves DNA by oxidatively attacking the deoxyribose moiety. The chemistry for the attachment of 1,10-phenanthroline to the *trp* repressor involves modification of lysyl residues with iminothiolane followed by alkylation of the resulting sulfhydryl groups with 5-iodoacetamido-1,10-phenanthroline. The modified *trp* repressor cleaves the operators of *aroH* and *trpEDCBA* upon the addition of cupric ion and thiol in a reaction dependent on the corepressor L-tryptophan. Scission was restricted to the binding site for the repressor, defined by deoxyribonuclease I footprinting. Since DNA-binding proteins have recognition sequences approximately 20 base pairs long, the nucleolytic activities derived from them could be used to isolate long DNA fragments for sequencing or chromosomal mapping.

THE TRANSFORMATION OF DNA-binding proteins into site-specific nucleases provides an approach to the construction of a new family of endonucleases with recognition sequences about three to four times as long as naturally occurring restriction enzymes. Since fewer binding sites for these semisynthetic nucleolytic agents would be present in any genome, they might be useful in chromosomal mapping and the isolation of large DNA fragments for sequencing. In this report, the chemical conversion of the *Escherichia coli trp* repressor (*1*) into a site-specific nuclease is outlined. This was achieved by



$$NH_3^+\text{-protein} + \text{iminothiolane} \rightarrow HS\text{-}(CH_2)_3\text{-}C(=NH_2^+)\text{-}NH\text{-protein} + H^+ \quad (1)$$



$$\text{5-}(ICH_2C(=O)NH)\text{-1,10-phenanthroline} + HS\text{-}(CH_2)_3\text{-}C(=NH_2^+)\text{-}NH\text{-protein} \rightarrow \text{phen-}NH\text{-}C(=O)\text{-}CH_2\text{-}S\text{-}(CH_2)_3\text{-}C(=NH_2^+)\text{-}NH\text{-protein} \quad (2)$$

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