HI unit, grandchildren (L, M, N, O) were helpers for their grandfather's (B) nestlings as well as for their cousins and half-sibs. Other relationships not found in nuclear families were also found, such as cousins, aunts, uncles, nieces, and nephews (units HI, BY, and UC in Fig. 1).

In 1979 the average relatedness of unit members to the nestlings in their units was low compared to that of singular-breeding species (*10*). It varied from 0.08 to 0.34 (Table 1). When parents of the nestlings concerned are excluded, the relatedness values ranged from 0 to 0.28. The values are low for several reasons. We have mentioned the presence of third-generation relatives and others more distant than the nuclear family, but perhaps the main cause is the typical presence of immigrants as breeders. In the six units, across 6 years, about 30 of 41 male breeders and 30 of 39 female breeders were immigrants. A third factor is the rarity of yearling full-sibs because of the underrepresentation of the 1978 class in 1979.

Communal birds, in addition to serving as nest helpers, also benefit their unit by calling alarm and harrassing predators. Therefore, it is appropriate to consider the relatedness of unit members exclusive of nestlings (Table 1). Again, average relatedness is low, ranging from 0.02 in the RC unit to 0.22 in the SW unit. In this case there are many more full-sib and parent-offspring relationships (see columns for relatedness = 1/2 in Table 1) than with nestlings included, but their effect on the averages is reduced by the immigrants.

The variability in average intraunit relatedness is striking (*11*). The two extremes are the SW unit, with high relatedness, and the RC unit, with low relatedness. The principal origin of these differences is the frequency of immigration: there are many immigrants in the RC unit but few in the SW unit. Conversely, many of the members of the SW unit were hatched in the same unit, reflecting the generally higher rate of reproductive success in this unit over the years.

The relatively low relatedness in social units of Mexican jays suggests that the indirect component (*12*) of inclusive fitness (*3*) might be less important in the evolution of communal breeding in jays than previously hypothesized (*4*). However, the low relatedness might be partially offset by three factors. First, individuals might choose to aid recipients that are more closely related than the average (*13*). Second, the number of related recipients in a unit is often larger than in nuclear families. In trait groups the intensity of selection for alarm-calling and territorial defense increases in direct proportion to the number of recipients carrying the gene in question (*14*). Third, reproductive success might be above average in units with higher relatedness (*13*).

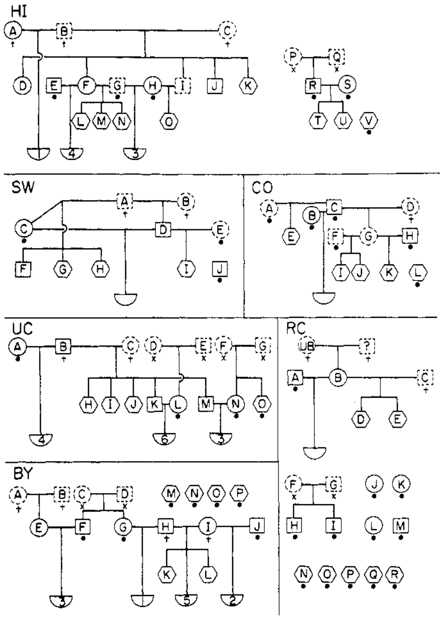

Fig. 1. Genealogies of the six social units of Mexican jays. All individuals present in May 1979 are indicated by symbols with solid lines. Selected ancestors no longer alive or in another unit are indicated by dashed symbols. Symbols: (□) male, (○) female, (○) sex unknown, (◡) nest with young, (●) immigrant, (+) present at start of study (1971), ancestry unknown, and (×) in neighboring unit.

Our estimates of relatedness do not take into account the general level of inbreeding in the population, which, in the absence of pure outbreeding, must be greater than zero. However, since we have not yet discovered any inbred offspring. we defer consideration of the effects of inbreeding. Another factor whose significance cannot yet be evaluated is the degree of relatedness between neighboring units. Some members of the BY, HI, and UC units came from the SW unit (Fig. 1) and were related to members of the SW unit in 1979.

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References and Notes

1. R. Fox, *Biosocial Anthropology* (Wiley, New York, 1975); N. A. Chagnon and W. Irons, *Evolutionary Biology and Human Social Behavior* (Wadsworth, North Scituate, Mass., 1979).
2. J. L. Brown, *Annu. Rev. Ecol. Syst.* **9**, 123 (1978).
3. W. D. Hamilton, *J. Theor. Biol.* **7**, 152 (1964).
4. J. L. Brown, *Am. Zool.* **14**, 63 (1974).
5. _____, *Condor* **65**, 126 (1963).
6. _____, *Anim. Behav.* **18**, 366 (1970); *ibid.* **20**, 395 (1972).
7. E. O. Wilson, *Sociobiology: The New Synthesis* (Harvard Univ. Press, Cambridge, Mass., 1975).
8. The mother of a brood of nestlings is the only individual to incubate eggs and brood the young at her nest. Identification of the father is slightly less certain. Typically the nest is begun by the male, who is later joined by a mate. Normally, only these two birds build (*5*). During the period of building, and especially for several days before laying, the two consort together and the male drives other males away. Paternity is established by observing which male builds and consorts with the female at a given nest. Copulations are rarely observed. Only once have two females been seen at a nest, and sexual sharing of a female by two or more males in the same year is rare.
9. J. L. Brown, *Wilson Bull.* **81**, 293 (1969).
10. Relatedness was calculated from the pedigrees in Fig. 1 by the method described by C. C. Li [*Population Genetics* (Univ. of Chicago Press, Chicago, 1955), pp. 178-1798].
11. A *G*-test for heterogeneity [R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969), p. 776] showed significant variability among units in the proportion of related and unrelated members, $P < .001$.
12. J. L. Brown and E. R. Brown, in *Natural Selection and Social Behavior*., R. D. Alexander and D. W. Tinkle, Eds. (Chiron, New York, in press).
13. Preliminary evidence suggests that this might be true.
14. D. S. Wilson, *Proc. Natl. Acad. Sci. U.S.A.* **772**, 143 (1975).
15. We thank the Southwestern Research Station of the American Museum of Natural History for use of land and facilities; E. F. Bagwell and M. C. Pugsley for permission to make observations on their property; and D. Lewis, W. Koenig, C. Barkan, and S. Strahl for their comments. Supported by NIMH grants MH16345 and MH33498.

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Hemispheric Specialization for Language Processes

Although ". . . in studies of dichotic listening, the superior performance of the right ear has been explained as a reflection of the left cerebral hemisphere's subserving linguistic abilities" (*1*, p. 1380), shifts in the *degree* of right ear superiority, with variations in the acoustic structure of competing syllables, cannot be safely interpreted as reflecting shifts in the *degree* of left hemisphere engagement. This limitation exists because an ear advantage in dichotic listening is not a simple index of hemispheric specialization.

Two conditions are necessary for an ear advantage: (i) hemispheric specialization, and (ii) some degree of ipsilateral loss. Ipsilateral loss has been attributed either to suppression of the ipsilateral signal because of the greater number of contralateral fibers (*2*) or to attentional mechanisms associated with spatial orientation toward the side contralateral to the activated hemisphere (*3*).

Either or both of these mechanisms are compatible with repeated demonstrations that the magnitude of the right ear advantage (REA) for dichotically presented speech signals may be significantly increased by embedding both signals in noise (*4*), by reducing their duration (*5*), by selective filtering (*6*), by reducing the spectral distance between competing signals (*5*), by increasing the relative intensity of the right ear signal (*6, 7*), by delaying the onset of the right ear signal relative to that of the left (*8*), and by variously manipulating the acoustic structure of synthetic syllables (*9*). Thus, the manipulation of transition duration by Schwartz and Tallal was simply one of a class of acoustic manipulations that seem to affect the relative discriminability of contralateral and ipsilateral representations in the left hemisphere. Uncertainty as to whether variations in REA should be attributed to variations in degree of lateralization, degree of ipsilateral loss, or both, is one reason the early promise of dichotic listening as a means of unraveling the processes of speech perception has not been fulfilled (*10*).

Finally, relatively slow changes in spectral structure—as in diphthongs, semivowels, liquids, and fricative transitions—are no less ". . . critical for the processing of fluent speech . . ." than the ". . . rapidly changing acoustic events . . ." (*1*, p. 1381) of stop consonant transitions. It would be odd, indeed, if the neural structures for processing speech had been reared on a capacity for handling a class of events that accounts for perhaps no more than one-fifth of a typical utterance (*11*).

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References

1. J. Schwartz and P. Tallal, *Science* **207**, 1380 (1980).
2. D. Kimura, *Cortex* **3**, 163 (1967).
3. M. Kinsbourne, in *Attention and Performance*, S. Kornblum, Ed. (Academic Press, New York, 1973), vol. 4.
4. M. S. Weiss and A. S. House, *J. Acoust. Soc. Am.* **53**, 51 (1973).
5. J. Godfrey, *Brain Lang.* **1**, 323 (1974).
6. J. K. Cullen, C. L. Thompson, L. F. Hughes, C. I. Berlin, D. S. Samson, *Brain Lang.* **1**, 307 (1974).
7. S. Brady-Wood and D. Shankweiler, *Haskins Laboratory Status Report 34* (1973), p. 119.
8. M. Studdert-Kennedy, D. Shankweiler, S. Schulman, *J. Acoust. Soc. Am.* **48**, 599 (1970).
9. B. Repp, *J. Exp. Psychol. Hum. Percept. Perform.* **3**, 37 (1977).
10. D. Shankweiler and M. Studdert-Kennedy, *Q. J. Exp. Psychol.* **19**, 59 (1967); M. Studdert-Kennedy and D. Shankweiler, *J. Acoust. Soc. Am.* **48**, 579 (1970).
11. P. B. Denes, *J. Acoust. Soc. Am.* **35**, 892 (1963).

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The claim that ear advantage in dichotic listening may not be solely an index of hemispheric specialization, but also may reflect degree of ipsilateral suppression, is a reasonable concern that would bear on the interpretation of all dichotic studies.

However, Studdert-Kennedy *et al.* have themselves concluded that "inhibition of the ipsilateral signal under dichotic stimulation occurs not in the pathway to the cerebral hemispheres, but after central auditory analysis, either at the auditory-phonetic interfacing or during phonetic analysis" (*1*, p. 465). Thus, rather than limit the promise of dichotic listening as a means of unraveling the processes of speech perception, careful investigation of conditions influencing both ipsilateral suppression and hemispheric specialization have enhanced our understanding of the neural mechanisms involved in speech perception. The results of our study (*2*), which demonstrated that the rate of acoustic change, rather than the linguistic nature of the stimuli, may underlie the right ear advantage (REA) for speech perception is only one of many examples of how the dichotic listening paradigm has been used to enhance our understanding of the central mechanisms involved in speech perception.

An entire body of literature supports the claim that stimuli incorporating rapidly changing spectra are more critical for the processing of speech (are more highly encoded and perceived more categorically and produce larger REA's) than those characterized by relatively slow changes in spectral structure (*3, 4*). Liberman *et al.* stated that "the second formant transition is a major cue for all the consonants except, perhaps, the fricatives /s/ and /š/, and is probably the single most important carrier of linguistic information in the speech signal" (*4*, p. 434). It is precisely for this reason that we chose to manipulate (extend) this particular acoustic cue in our study (*2*). Furthermore, recent studies demonstrate why the analysis of rapidly changing spectral patterns may play such an important role in speech perception. While the first function of transitions is to carry phonemic information, and the second is to carry it by parallel transmission, a third and critical function is to bind together phonemic segments so that, at rapid transmission rates, the temporal order of speech may be preserved (*5*). Thus, these functions, rather than account for only one-fifth of an utterance, as suggested by Studdert-Kennedy and Shankweiler, would play a critical role in the segmentation and sequencing of the entire speech stream.

Finally, there is considerable neurophysiological evidence from animal studies that there exist special neural mechanisms for processing ecologically salient, albeit rare, events (*6*). Thus, frequency of occurrence does not seem to be either a necessary or sufficient explanation for the evolutionary development of neural structures.

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References

1. M. Studdert-Kennedy, D. Shankweiler, D. Pisoni, *Cognit. Psychol.* **3**, 155 (1972).
2. J. Schwartz and P. Tallal, *Science* **207**, 1380 (1980).
3. For review, see A. Liberman *et al.* (*4*) and J. E. Cutting, *Percept. Psychophys.* **16**, 601 (1974).
4. A. Liberman, F. Cooper, D. Shankweiler, M. Studdert-Kennedy, *Psychol. Rev.* **74**, 431 (1967).
5. M. Dorman, J. Cutting, L. Raphael, *J. Exp. Psychol. Hum. Percept. Perform.* **104**, 121, (1975); R. Cole and B. Scott, *Can. J. Psychol.* **27**, 441 (1973).
6. For review, see J. D. Newman, in *Dahlem Workshop on Recognition of Complex Acoustic Signals*, T. Bullock, Ed. (Abakon Verlagsgesellschaft, Berlin, 1976).

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