BRIEF COMMUNICATIONS

Effects of Backward Speech and Speaker Variability in Language Discrimination by Rats

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Human infants use prosodic cues present in speech to extract language regularities, and it has been suggested that this capacity is anchored in more general mechanisms that are shared across mammals. This study explores the extent to which rats can generalize prosodic cues that have been extracted from a training corpus to new sentences and how this discrimination process is affected by the normalization of the sentences when multiple speakers are introduced. Conditions 1 and 2 show rats' abilities to use prosodic cues present in speech, allowing them to discriminate between sentences not previously heard. But this discrimination is not possible when sentences are played backward. Conditions 3 and 4 show that language discrimination by rats is also taxed by the process of speaker normalization. These findings have remarkable parallels with data from human adults, human newborns, and cotton-top tamarins. Implications for speech perception by humans are discussed.

Human infants are so sensitive to the rhythmic regularities of language that they can detect them independently of the modality (oral or manual) in which these regularities are expressed (Petitto, Holowka, Sergio, Levy, & Ostry, 2004; Petitto, Holowka, Sergio, & Ostry, 2001). It has been claimed that the early sensitivity to these prosodic (rhythmic and intonational) regularities helps the infant in the segmentation of speech (e.g., Morgan, 1994; Norris, McQueen, Cutler, Butterfield, & Kearns, 2001), the bootstrapping of syntactic aspects of language (Christophe, Nespor, Guasti, & Van Ooyen, 2003; Gleitman & Wanner, 1982), and, generally, transforming serial auditory input into organized patterns (Mehler, Dupoux, Nazzi, & Dehaene-Lambertz, 1996). If it is demonstrated that the ability to detect such regularities in speech is rooted in more general capabilities possessed by other mammals, an evolu-

tionary line could be drawn from early nonlinguistic analyses of acoustic signals to the development of syntactic structures by humans. Following this direction, the goal of this article is to study the processing of rhythmic cues present in speech from a comparative perspective, by testing the degree to which rats can generalize the cues extracted from a set of sentences to another set they have not heard before, and to explore the extent to which the rats' discrimination results are affected by the process of speaker normalization, as seen in human infants.

When a comparative approach is used to explore the phylogenetic origins of speech perception mechanisms, striking patterns emerge. Studies with birds, and how they acquire their specific songs, have provided invaluable insights into topics relevant to the development of language, such as those of the *sensitive* period (Doupe & Kuhl, 1999), the specialized neural substrates for its development (Brainard & Doupe, 2002), or the role of experience and social interaction among conspecifics (Goldstein, King, & West, 2003). Experiments with Harpy eagles, in which orienting to relevant or irrelevant stimuli was measured, have shown experience-dependent orienting asymmetries (Palleroni & Hauser, 2003) that were thought to be exclusive to humans reflecting only sensitivities to linguistic input (see Holowka & Petitto, 2002). Phoneme discrimination has been demonstrated in macaques (Kuhl, 1981), budgerians (Dooling, Best, & Brown, 1995), chinchillas (Burdick & Miller, 1975), pigeons (Hienz, Sachs, & Sinnott, 1981), gerbils (Sinnott & Mosteller, 2001), and rats (Reed, Howell, Sackin, Pizzimenti, & Rosen, 2003), to cite a few. Even in the perception of music (a system that shares formal features with language such as its hierarchical organization and its compositionality) similarities have been found between humans and other species (Hauser & McDermott, 2003; Porter & Neuringer, 1984). Research with human newborns, cotton-top tamarin monkeys, and rats has demonstrated that these species can discriminate between synthesized sentences of two languages when played forward, but not when they are played backward (Ramus, Hauser, Miller, Mor-

ris, & Mehler, 2000; Toro, Trobalon, & Sebastián-Gallés, 2003). Together, these studies reveal that the processing mechanisms shared across different species extend beyond phonemes and provide the basis for a low-level analysis of the speech input.

It is important to note that the two languages used in Ramus et al. (2000) and Toro et al. (2003) were Dutch and Japanese. These languages belong to different rhythmic categories (Dutch is stress timed, whereas Japanese is mora timed), a notion that has been used in linguistics to denote distinct language groups. Rhythmic category correlates with the relative proportions of vocalic intervals among sentences and the average standard deviations of consonantal intervals (Ramus, Nespor, & Mehler, 1999).[1] To keep constant the prosodic regularities of the sentences used in these experiments while controlling for phonetic factors, the authors synthesized the sentences. By so doing, the original prosodic information was preserved while speaker or irrelevant phonetic cues were eliminated. But when these sentences are played backward, prosodic information is also eliminated, because phonetic cues sensitive to temporal order are distorted (VanLancker, Kreiman, & Emmorey, 1985; see also Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002, on how different neural circuitry is recruited for the perception of backward speech by human infants). So, the finding that human infants, cotton-top tamarins, and rats can discriminate forward, but not backward, sentences of Dutch and Japanese allows the conclusion that the auditory processing of these species permits them to extract the features that differentiate languages, features that are distorted in backward speech to the point that none of the three species could effectively discriminate between sentences when played this way.

Despite this coherent pattern emerging from the discrimination of synthesized sentences, natural sentences yield different results. In the Ramus et al. (2000) study, human newborns could not discriminate between natural Dutch and Japanese sentences. That is, they could not discriminate between these sentences when they were uttered by four different speakers and were not synthesized. In contrast, tamarins succeeded in discriminating these languages across speakers. The explanation given by Ramus and colleagues was that tamarins focused on the phonetic rather than on the prosodic features of the stimuli. Results for rats with the same natural sentences were intriguing because only the group trained with Dutch sentences could effectively differentiate them from the Japanese sentences, whereas the other group, trained with Japanese sentences, could not (Toro et al., 2003).

In the field of human speech perception, studies using sentences produced by different speakers have shown that newborns can readily extract the invariant prosodic features of languages that belong to the same rhythmic category (Nazzi, Bertonici, & Mehler, 1998). But sentences used in these experiments were low-pass filtered, which eliminated much of the variability across speakers (Ramus, 2002). Thus, the experiment by Ramus et al. (2000) was the first to directly test newborns' performance with such variability, finding that it did interfere with discrimination. Even though it has been demonstrated that human newborns can differentiate vowels across speakers (Kuhl, 1983), authors studying the perception of whole sentences have also found that speaker variability taxes discrimination processes in human adults (Bradlow, Nygaard, & Pisoni, 1999; Kirk, Pisoni, & Miyamoto, 1997) and newborns (Jusczyk, Pisoni, & Mullenix, 1992), presumably in the way of a more demanding memory load.

Do these difficulties in normalizing speaker variability arise from the fact that language might be a privileged stimulus for human newborns (i.e., Werker & Vouloumanos, 2000), or is it the result of giving the subject information that is irrelevant for the task? To study this issue one should be sure that the extraction of prosodic features by rats is powerful enough to generalize to new sentences, and then to test the role of speaker variability in the discrimination process. Therefore, the first aim of the present study was to explore the capacity of rats to generalize the features extracted from the sentences to new utterances that they have not heard before. The second objective was to investigate what cues rats are using for language discrimination and to draw parallels with what humans do when facing similar tasks. To study these issues, an experiment with four conditions (synthesized forward sentences, synthesized backward sentences, natural sentences, and natural sentences, single speaker), all of them identical in methodology but different in the salient features of the stimuli used, was run.

The goal of Condition 1 (synthesized forward sentences) was to study whether rats can discriminate between Dutch and Japanese sentences they have never heard before on the basis of the regularities they extract from other sentences during training. That is, whether rats are able to extract certain features from the speech signal that are different in the Dutch and Japanese sentences, and are then able to discriminate between two new sentences of these languages which belong to different rhythmic categories.

Regarding Condition 2 (synthesized backward sentences), previous experiments with human newborns (Mehler et al., 1988), cotton-top tamarin monkeys (Ramus et al., 2000), and Long-Evans rats (Toro et al., 2003) have found that subjects cannot discriminate between sentences when they are played backward. If results from Condition 1 are just the outcome from the training regime, after the same amount of training, then rats should be able to discriminate between backward sentences as well. That is, rats can be trained to discriminate between any set of complex sounds, but their results would not tell us anything about human perceptual abilities. Nevertheless, if results from Condition 1 reflect the ability to detect and use prosodic cues in acoustic stimuli that are not present in backward speech, rats should not be able to learn to discriminate this type of sentence. To test this, in Condition 2 we used synthesized sentences played backward.

Because the specific prosodic features of a given language generalize across speakers, at some point in development, humans must detect those features while ignoring particular speaker-related information, in a way similar to which human adults and infants ignore irrelevant cues under artificial language learning conditions (i.e., Saffran, 2001). Such information might be relevant to guide the infant in bilingual environments in which specific speakers use a given language (Bosch & Sebastián-Gallés, 2001; Sebastián-Gallés & Bosch, 2002), but even in this case, general linguistic regularities must be extracted from utterances from different individuals. To test rats' abilities to detect prosodic cues present in natural speech that generalize across different speakers,

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[1] Vocalic and consonantal intervals are measured between the onset and the offset of vowels and consonants, or clusters of vowels and consonants in each sentence. For a detailed description of the measures, see Ramus et al. (1999).

in Condition 3 (natural sentences) we used sentences uttered by four different speakers of Dutch and Japanese.

Nevertheless, there are at least two factors in Condition 3 that could explain any obtained result, namely, speaker variability and phonetic cues present in natural speech. To disentangle these two factors, in Condition 4 (natural sentences, single speaker) we trained rats with natural sentences uttered by a single speaker of each language and then tested using new sentences uttered by the same speaker. Results from Condition 4, together with those of Condition 3, will assist us in drawing a clearer picture of what features rats use to discriminate sentences from different rhythmic groups.

Method

Subjects

Subjects were 16 Long-Evans rats in each condition, for a total of 64 rats. All were males of around 3 months of age. They were caged in groups of 2 or 3. They had water ad libitum and were food-deprived until they reached 85% of their free-feeding weight. Food was administered after each session. Two rats in Condition 3 and 2 rats in Condition 4 failed to finish the experiment because of low lever-pressing rates, so they were dropped from the study.

Stimulus

In Condition 1, 20 Dutch and 20 Japanese synthesized sentences were used. Sentences were synthesized with the MBROLA software (Dutoit, Pagel, Pierret, Bataille, & van der Vrecken, 1996) and were the same ones used by Ramus et al. (2000), who described the sentences' characteristics as follows: "Phoneme duration and fundamental frequency were preserved, whereas the phonetic inventory was narrowed to only one phoneme per manner of articulation: all fricatives were synthesized as /s/, vowels as /a/, liquids as /L/, plosives as /t/, nasals as /n/, and glides as /j/" (p. 349; a more detailed description of the sentences is found in Ramus & Mehler, 1999). Each sentence was about 5 s in duration, had an average of 17 syllables, and was played at 68 dB SPL measured at 10 cm from the speaker.

The same 20 Dutch and 20 Japanese synthesized sentences used in Condition 1 were used in Condition 2. The only difference was that sentences were played backward, so even though frequency information was preserved, phonetic cues sensitive to temporal order were distorted (see VanLancker, Kreiman, & Emmorey, 1985).

For Condition 3, the same 20 Dutch and 20 Japanese sentences used in Condition 1 were uttered by four different female speakers of each language. Two speakers were used for the training sessions, and two other speakers were used for the test session. The sentences were digitized at 16 kHz. Finally 20 Dutch and 20 Japanese sentences uttered by a single female speaker of each language were used in Condition 4.

Apparatus

Rats were placed in Letica L830-C Skinner boxes (Panlab S.L., Barcelona, Spain). A PC computer was used to record the lever-press responses as well as to provide reinforcement. A Pioneer Stereo Amplifier A-445 and two E.V. (S-40) speakers that were located besides the boxes were used to present the sentences.

Procedure

Each group of 16 rats ran only one condition, so there would not be problems with overlapping stimuli or training. Rats were trained to press a lever until they reached a stable rate at a variable–ratio–10 schedule

(VR-10). After this rate was reached, rats were divided in two groups—Dutch group and Japanese group—balancing mean lever pressing. Discrimination training consisted of 20 sessions, 1 session per day. In each session, rats were placed individually in a Skinner box, and sentences were presented. Eight Dutch and 8 Japanese sentences were played in a balanced manner, for a total of 16 presentations per session. The order of sentence presentation was also balanced across training sessions. Out of the 20 sentences from each language, only 16 were presented during training, so the 4 remaining sentences were used in the test session.

Between each sentence presentation there was a 2-min interval. Following a sentence that was reinforced (Dutch sentences for the Dutch group, and Japanese sentences for the Japanese group), rats received food throughout the 2 min on a VR-10 schedule. After a sentence that was not reinforced (Dutch sentences for the Japanese group, and Japanese sentences for the Dutch group), rats did not receive food during the first minute of the 2-min interval, but only during the second minute on a VR-10 schedule. This procedure helped to avoid extinction of the response in the nonreinforced trials.

After the 20 sessions of training, a test session was run. It consisted of the presentation of eight new sentences (four Dutch and four Japanese sentences) that the rats had not heard before. There were 2 min between the presentation of each sentence during which lever-pressing responses were registered. But, in contrast to training sessions, the food dispensers were disconnected, so rats did not receive food after any sentence. As a result of the methodology used, we analyzed the data in terms of a discrimination ratio.[2] This method had already been used yielding satisfactory results with rats in discrimination experiments (Toro et al., 2003).

Results

Mean discrimination ratio values for each group in each condition during the test session can be seen in Table 1. Independent analyses of variance were run for each of the four conditions with language (Dutch or Japanese) as a within-subject variable, and group (Dutch group or Japanese group) as a between-subjects variable. Condition 1 (synthesized forward sentences), yielded no significant differences between languages ($F < 1$), or groups ($F < 1$). Nevertheless, there was an interaction between language and group, $F(1, 14) = 13.74$, $p < .005$. Further analysis revealed that for the Dutch group, responses to Dutch and Japanese sentences were significantly different, $t(7) = 2.78$, $p < .05$, as were for the Japanese group, $t(7) = -2.67$, $p < .05$. This result shows that rats can discriminate between Dutch and Japanese sentences they have never heard before on the basis of the features they have presumably extracted from these languages during training (Figure 1 shows, for comparative purposes, the data from all four conditions).

In Condition 2 (synthesized backward sentences), both groups responded in a similar manner to the test sentences, $F(1, 14) = 2.08$, $p = .17$; as well, there was no significant differences between languages ($F < 1$). There was also a nonsignificant interaction between variables ($F < 1$). None of the groups responded differentially to the test sentences, for the Dutch group ($t < 1$), and for

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[2] The discrimination ratio was calculated by dividing the mean frequency of lever pressing in the first minute (A) of the 2-min interval after each sentence by the mean responses in A plus mean responses in the second minute of this interval (C). This operation gives values between 1 and 0. Values tending to 1 indicate a higher mean response in A than in C; values tending to 0 indicate a higher mean response in C than in A (Tarpy, 2000).

Table 1
Mean Discrimination Ratio for Dutch and Japanese Groups During the Test Session in Each of the Four Conditions

Group	Forward sentences		Backward sentences		Natural sentences		Natural sentences (single speaker)	
	Dutch	Japanese	Dutch	Japanese	Dutch	Japanese	Dutch	Japanese
Dutch	0.491	0.407	0.401	0.420	0.545	0.485	0.600	0.422
Japanese	0.410	0.552	0.462	0.503	0.405	0.421	0.425	0.588

the Japanese group ($t < 1$). So, even after 20 days of training, rats could not discriminate between new Dutch and Japanese sentences played backward.

As in the previous condition, no significant differences between languages ($F < 1$), or groups, $F(1, 12) = 3.76$, $p = .08$, and no significant interaction between languages and groups ($F < 1$) was found in Condition 3 (natural sentences). Further analysis for the results in each group revealed no significant differences in the responses to the test sentences, for the Dutch group ($t < 1$) and for the Japanese group ($t < 1$). In opposition to what was found using synthesized sentences played forward, with natural sentences uttered by different speakers of each language, rats did not respond differently to the new sentences.

Finally, in Condition 4 (natural sentences, single speaker), there were also no significant differences between languages ($F < 1$), or groups ($F < 1$), but a significant interaction was found between languages and groups, $F(1, 12) = 19.95$, $p < .005$. Contrary to

what was found in Condition 3, rats could discriminate between sentences spoken by a single speaker; there were significant differences in the responses to the test sentences for the Dutch group, $t(6) = 3.55$, $p < .05$, and for the Japanese group, $t(6) = -2.84$, $p < .05$. So, when the speaker variability was reduced to one, rats could discriminate natural sentences as they did with synthesized ones.

Discussion

The present study shows the extent to which, as a result of discrimination training, rats can use the prosodic cues present in human speech and suggests conclusions on the patterns of language discrimination across species on the one hand and the processes of speaker normalization on the other. Regarding patterns of language discrimination, using synthesized sentences, rats could extract the relevant prosodic cues that differentiate Dutch
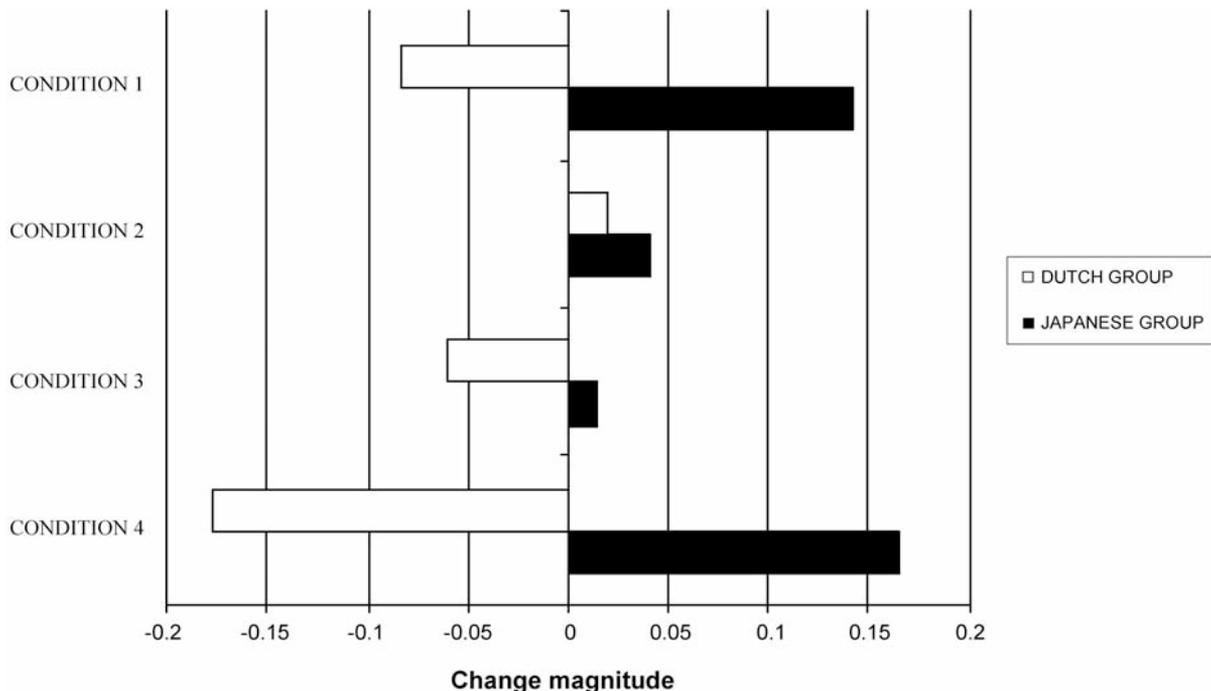

Figure 1. Change magnitude in the four conditions, which was calculated as the mean discrimination ratio value for Japanese sentences minus the mean discrimination value for Dutch sentences. Condition 1 = synthesized forward sentences; Condition 2 = synthesized backward sentences; Condition 3 = natural sentences; Condition 4 = natural sentences, single speaker.

from Japanese and generalize them to new sentences they had not heard before (Condition 1). Nevertheless, they could not do so using synthesized sentences played backward (Condition 2). These results confirm a recurrent pattern of results for language discrimination abilities in three species of mammals: humans, tamarins, and rats, by which differentiating cues present in forward speech are not detected in the same sentences when played backward. If languages have been shaped by, among other factors, constraints in the human auditory system (i.e., Saffran, 2002, 2003), the ability to bootstrap linguistic regularities from low-level cues, such as rhythm, may represent the use for linguistic purposes of an already-existing ability present in the mammalian auditory system, as has been proposed by Hauser, Chomsky, and Fitch (2002).

Concerning speaker variability, results from Condition 3 must be considered together with those from Condition 4. As mentioned in the introduction, the failure to distinguish between natural sentences uttered by different speakers can be accounted for with two possibilities. The explanation can be found either in natural speech per se or in speaker variability. Results showed that rats could discriminate natural sentences when uttered by a single speaker and not when uttered by different ones. So, differential responding in Condition 4 demonstrated that speaker changes, not special features present in natural speech, were responsible for the failure to discriminate between sentences in Condition 3. That is, the variation created by different speakers made the discrimination task more difficult for the rats.

These results point to the same conclusion as those with human adults and newborns (Bradlow et al., 1999; Jusczyk et al., 1992; Kirk et al., 1997; Ramus, 2002; Ramus et al., 2000) in which speaker variability increased the difficulty of the discrimination process, suggesting that it is the presentation of irrelevant information for the task that is responsible for the costs of speaker normalization (even though the present experiment includes several training sessions, whereas most studies with human participants do not). If these costs were specific to the linguistic nature of the stimuli, and their special status for humans, one would not expect to find them in rats. Given that rats' performance did not differ from chance levels when confronted with speaker variability, it is very likely that this cost reflects a nonspecific normalization process. This cost resembles what has already been shown in the animal learning literature, using different procedures, in which an irrelevant stimulus can interfere in the differentiation among several stimuli (i.e., Pearce & Redhead, 1993; Redhead & Pearce, 1998). It is nevertheless puzzling that adult tamarin monkeys have succeeded in discriminating languages across different speakers (Ramus et al., 2000), whereas human newborns and rats have not. Tamarin monkeys use serial combinations of chirps and whistles for interspecific communication that encode, among other things, important information about the caller (e.g., Ghazanfar & Hauser, 2001). It could be the case that, in the adult tamarin, the experience producing and decoding theses calls would help in the normalization process needed in the experimental condition with natural speakers. It remains unknown whether tamarin newborns could also discriminate languages across different speakers. Besides this, it is worth noting that both human newborns (Kuhl, 1983) and chinchillas (Burdick & Miller, 1975) can compensate for speaker changes in a vowel discrimination task, which highlights differences between the processing of single vowels and complete sentences, and leaves open the question for even more similarities across species in the processing of these types of stimuli.

In summary, rats' abilities to extract prosodic cues from sentences of two different languages are greater than previously thought, for they can generalize those features to new sentences, while maintaining on the recurrent pattern of not being able to use any cue when sentences are played backward. When faced with the problem of different speakers, rats also have more difficulty in effectively discriminating among sentences. This difficulty is found as well in human infants, but eventually, they overcome it in order to acquire lexical and syntactic aspects of the language, and combine them with phonotactic, segmental, and semantic information (Mehler, Dupoux, Nazzi & Dehaene-Lambertz, 1996). This process will allow human infants to acquire the rich and comprehensible communication system that only humans possess. Even though much more research is required to understand the extent to which other animals are also capable of such an effective combination, and while acknowledging that the similarity in results does not guarantee identity in the underlying processes (see Trout, 2001), the rats' failure to discriminate backward speech, and the costs of the normalization process, suggest the possibility that these effects might reflect general auditory constraints that shape aspects of language acquisition.

References

Bosch, L., & Sebastián-Gallés, N. (2001). Evidence of early language discrimination abilities in infants from bilingual environments. *Infancy, 2,* 29–49.

Bradlow, A., Nygaard, L., & Pisoni, D. (1999). Effects of talker, rate, and amplitude variation on recognition memory for spoken words. *Perception and Psychophysics, 6,* 206–219.

Brainard, M., & Doupe, A. (2002, May 16). What songbirds teach us about learning. *Nature, 417,* 351–358.

Burdick, C., & Miller, J. (1975). Speech perception by the chinchilla: Discrimination of sustained /a/ and /i/. *Journal of the Acoustical Society of America, 58,* 415–427.

Christophe, A., Nespor, M., Guasti, M., & Van Ooyen, B. (2003). Prosodic structure and syntactic acquisition: The case of the head-direction parameter. *Developmental Science, 6,* 211–220.

Dehaene-Lambertz, G., Dehaene, S., & Hertz-Pannier, L. (2002, December 6). The functional neuroanatomy of speech perception in infants. *Science, 298,* 2013–2015.

Dooling, R., Best, C., & Brown, S. (1995). Discrimination of synthetic full-formant and sinewave /ra-la/ continua by budgerians (*Melopsittacus undulatus*) and zebra finches (*Taeniopygia guttata*). *Journal of the Acoustical Society of America, 97,* 1839–1846.

Doupe, A., & Kuhl, P. (1999). Birdsong and human speech: Common themes and mechanisms. *Annual Review of Neuroscience, 22,* 567–631.

Dutoit, T., Pagel, V., Pierret, N., Bataille, F., & van der Vrecken, O. (1996). The MBROLA project: Towards a set of high-quality speech synthesizers free of use for non-commercial purposes. *Proceedings of the International Conference on Spoken Language Processing (ICSLP), 3,* 1393–1396.

Ghazanfar, A., & Hauser, M. (2001). The auditory behaviour of primates: A neuroethological perspective. *Current Opinion in Neurobiology, 11,* 712–720.

Gleitman, L., & Wanner, E. (1982). The state of the state of the art. In Wanner, E., & Gleitman, L. (Eds.). *Language acquisition: The state of the art* (pp. 3–48). Cambridge, England: Cambridge University Press.

Goldstein, M., King, A., & West, M. (2003). Social interaction shapes babbling: Testing parallels between birdsong and speech. *Proceedings of the National Academy of Sciences, USA, 100,* 8030–8035.

Hauser, M., Chomsky, N., & Fitch, T. (2002, November 22). The faculty of language: What is it, who has it, and how did it evolve? *Science, 298,* 1569–1579.

Hauser, M., & McDermott, J. (2003). The evolution of the music faculty: A comparative perspective. *Nature Neuroscience, 6,* 663–668.

Hienz, R., Sachs, M., & Sinnott, J. (1981). Discrimination of steady-state vowels by blackbirds and pigeons. *Journal of the Acoustical Society of America, 70,* 699–706.

Holowka, S., & Petitto, L. (2002, August 30). Left hemisphere cerebral specialization for babies while babbling. *Science, 297,* 1515.

Jusczyk, P., Pisoni, D., & Mullenix, J. (1992). Some consequences of stimulus variability on speech processing by 2-month-old infants. *Cognition, 43,* 253–291.

Kirk, K., Pisoni, D., & Miyamoto, C. (1997). Effects of stimulus variability on speech perception in listeners with hearing impairment. *Journal of Speech, Language and Hearing Research, 40,* 1395–1405.

Kuhl, P. (1981). Discrimination of speech by non-human animals: Basic auditory sensitivities conductive to the perception of speech-sound categories. *Journal of the Acoustical Society of America, 70,* 340–348.

Kuhl, P. (1983). Perception of auditory equivalence classes for speech in early infancy. *Infant Behavior and Development, 6,* 263–285.

Mehler, J., Dupoux, E., Nazzi, T., & Dehaene-Lambertz, G. (1996). Coping with linguistic diversity: The infant's viewpoint. In J. L. Morgan & K. Demuth (Eds.), *Signal to Syntax: Bootstrapping from speech to grammar in early acquisition* (pp. 101–116). Mahwah, NJ: Erlbaum.

Mehler, J., Jusczyk, P. W., Lambertz, G., Halsted, N., Bertoncini, J., & Amiel-Tison, C. (1988). A precursor of language acquisition in young infants. *Cognition, 29,* 143–178.

Morgan, J. (1994). Converging measures of speech segmentation in preverbal infants. *Infant Behavior and Development, 17,* 389–403.

Nazzi, T., Bertonici, J., & Mehler, J. (1998). Language discrimination by newborns: Toward an understanding of the role of rhythm. *Journal of Experimental Psychology: Human Perception and Performance, 24,* 756–766.

Norris, D., McQueen, J., Cutler, A., Butterfield, S., & Kearns, R. (2001). Language-universal constraints on speech segmentation. *Language and Cognitive Processes, 16,* 637–660.

Palleroni, A., & Hauser, M. (2003, February 21). Experience-dependent plasticity for auditory processing in a raptor. *Science, 299,* 1195.

Pearce, J., & Redhead, E. (1993). The influence of an irrelevant stimulus on two discriminations. *Journal of Experimental Psychology: Animal Behavior Processes, 19,* 180–190.

Petitto, L., Holowka, S., Sergio, L., Levy, B., & Ostry, D. (2004). Baby hands that move to the rhythm of language: Hearing babies acquiring sign languages babble silently on the hands. *Cognition, 93,* 1–73.

Petitto, L., Holowka, S., Sergio, L., & Ostry, D. (2001, September 6). Language rhythms in baby hand movements. *Nature, 413,* 35–36.

Porter, D., & Neuringer, A. (1984). Music discriminations by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 10,* 138–148.

Ramus, F. (2002). Language discrimination by newborns: Teasing apart phonotactic, rhythmic, and intonational cues. *Annual Review of Language Acquisition, 2,* 85–115.

Ramus, F., Hauser, M., Miller, C., Morris, D., Mehler, J. (2000, April 14). Language discrimination by human newborns and by cotton-top tamarin monkeys. *Science, 288,* 349–351.

Ramus, F., & Mehler, J. (1999). Language identification with suprasegmental cues: A study based on speech resynthesis. *Journal of the Acoustical Society of America, 105,* 512–521.

Ramus, F., Nespor, M., & Mehler, J. (1999). Correlates of linguistic rhythm in the speech signal. *Cognition, 73,* 265–292.

Redhead, E., & Pearce, J. (1998). Some factors that determine the influence of a stimulus that is irrelevant to a discrimination. *Journal of Experimental Psychology: Animal Behavior Processes, 24,* 123–135.

Reed, P., Howell, P., Sackin, S., Pizzimenti, L., & Rosen, S. (2003). Speech perception in rats: Use of duration and rise time cues in labeling of affricative/fricative sounds. *Journal of the Experimental Analysis of Behavior, 80,* 205–215.

Saffran, J. (2001). The use of predictive dependencies in language learning. *Journal of Memory and Language, 44,* 493–515.

Saffran, J. (2002). Constraints on statistical language learning. *Journal of Memory and Language, 47,* 172–196.

Saffran, J. (2003). Statistical language learning: Mechanisms and constraints. *Current Directions in Psychological Science, 12,* 110–114.

Sebastián-Gallés, N., & Bosch, L. (2002). The building of phonotactic knowledge in bilinguals: The role of early exposure. *Journal of Experimental Psychology: Human Perception and Performance, 28,* 974–989.

Sinnott, J., & Mosteller, K. (2001). A comparative assessment of the speech sound discrimination in the Mongolian gerbil. *Journal of the Acoustical Society of America, 110,* 1729–1732.

Tarpy, R. M. (2000). *Contemporary learning theory and research.* New York: McGraw Hill.

Toro, J. M., Trobalon, J., & Sebastián-Gallés, N. (2003). The use of prosodic cues in language discrimination tasks by rats. *Animal Cognition, 6,* 131–136.

Trout, J. D. (2001). The biological basis of speech: What to infer from talking to the animals. *Psychological Review, 108,* 523–549.

VanLancker, D., Kreiman, J., & Emmorey, K. (1985). Familiar voice recognition: Patterns and parameters. Pt. I. Recognition of backward voices. *Journal of Phonetics, 13,* 19–38.

Werker, J., & Vouloumanos, A. (2000, April 14). Who's got rhythm? *Science, 288,* 280–281.