infection of murine cells (15) and transgenic mice expressing human CD4 (16) and provides a rationale for transgenic approaches to developing animal models of HIV disease.

**REFERENCES AND NOTES**


4. H. Cho et al., Cell 85, 1135 (1996); B. J. Doranz et al., ibid., p. 1149.


8. We cloned cDNAs encoding human or murine CCR5 into the expression vector pcDNA3 (Invitrogen) after engineering the FLAG epitope into the NH2-terminus as described (13). Expression of each construct was determined by FACS with an antibody to FLAG (anti-FLAG) (Boehringer Mannheim), and relative expression for each (see below) was calculated as the percent of cells expressing human CCR5 on the cell surface normalized to the expression of hCCRF5 (defined as 100%), with standard errors of the mean. The mean fluorescence intensity of the positive cells from any single sample never varied from the average by more than 30% in a single experiment. Therefore, neither the relative number of positive cells nor the absolute expression levels within transfected cells explains the differences in cocactivity. Chimeric receptors were prepared by the overlap polymerase chain reaction (PCR) method (17). HCCR5 (H-Flag+, human CCR5 (100% relative expression); mCCR5 (21%); mHMMH, NH2-terminus of human CCR5 (amino acids (aa) 1 to 32) fused to murine CCR5 (aa 35 to 354) (77% ± 22%); mHMMH, NH2-terminus of murine CCR5 (aa 1 to 34) fused to human CCR5 (aa 33 to 352) (73% ± 17%); mHMMH, extracellular loop 1 and a portion of transmembrane domain 3 of human CCR5 (aa 86 to 118) replacing the corresponding segment of the murine receptor (aa 88 to 120) (37% ± 22%); mHMMH, extracellular loop 2 and adjacent portions of human CCR5 (aa 130 to 150) replacing the corresponding region of the murine receptor (aa 136 to 212) (81% ± 30%); mHMMH, NH2-terminal half of mCCR5 (aa 1 to 162) fused to the CD8(1)-terminal half of CCR5 (aa 161 to 352) (80% ± 39%).


11. F. Chao et al., J. Biol. Chem. 271, 19064 (1996); F. S. Montecelio et al., unpublished observations.

12. We cloned cDNAs encoding human CCR2B or chimeric into the expression vector pcMV4 (18) after engineering the FLAG epitope into the NH2-terminus as described (13). Expression of each construct (see below) was determined as described earlier. Chimeric receptors were prepared by the overlap PCR method (17). 5555, human CCR5 (100% relative expression); 5222, human CCR5 (77% ± 2%); 5222, NH2-terminus of human CCR5 (aa 1 to 32) fused to CCR5B (aa 45 to 360) (27% ± 5%); 5255, NH2-terminus of CCR2B (aa 1 to 44) fused to CCR5 (aa 33 to 352) (106% ± 17%); 2555, CCR2B (aa 1 to 136) fused to CCR5 (aa 124 to 352) (119% ± 93%).


14. J. Saito et al., unpublished observations.


20. COS-7 cells were transfected with 2 µg of plasmid DNA per well in a six-well plate as described (19). DNA samples consisted of appropriate combinations of 0.6 µg of a human CD4 expression plasmid (pCD4Neo [79]) or plasmid vector, and 1.5 µg of a chemokine receptor–expressing plasmid or plasmid vector. About 30 hours after addition of DNA, the medium in each well was replaced with 1.0 ml of medium containing HIV-1 Ba-L (−100 to 170 ng of p24 per sample; source: NIH AIDS Reagent Repository, passed on primary human macrophages). About 10 hours later, an additional 1.0 ml of medium was added to each well. After 30 hours, the cells were recovered from the dish as described (19) and analyzed with a FacScan (BectonDickinson). Staining for intracytoplasmic HIV-1 p24 was carried out with the Fix and Perm reagents (Caltag Laboratories), with a monoclonal antibody to p24 [Coultier Immunology] and goat anti-mouse fluorescein isothiocyanate (FITC)-conjugated secondary antibody (Becton Dickinson). Cells were further stained with phycoerythrin (PE)–conjugated anti-CD4 (Becton Dickinson). Appropriate controls indicated that the appearance of double-positive cells (FITC + PE) was dependent on cotransfection with both CD4 and human CCR5 expression plasmids and on the presence of HIV-1 Ba-L.


22. We acknowledge the advice of M. Warmerdam (transfection-infection assay, E. Wolder (FACS studies), and L. Boring, H. Arii, and R. Speck (scientific interpretation). We appreciate the assistance of J. Carroll and M. Cencerro in the preparation of this manuscript. Supported in part by NIH grant HIL25773 (F.C.) and by Pitzer (M.A.G.).

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**Statistical Learning by 8-Month-Old Infants**

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Learners rely on a combination of experience-independent and experience-dependent mechanisms to extract information from the environment. Language acquisition involves both types of mechanisms, but most theorists emphasize the relative importance of experience-independent mechanisms. The present study shows that a fundamental task of language acquisition, segmentation of words from fluent speech, can be accomplished by 8-month-old infants based solely on the statistical relationships between neighboring sound segments. Moreover, this word segmentation was based on statistical learning from only 2 minutes of exposure, suggesting that infants have access to a powerful mechanism for the computation of statistical properties of the language input.

During early development, the speed and accuracy with which an organism extracts environmental information can be extremely important for its survival. Some species have evolved highly constrained neural mechanisms to ensure that environmental information is properly interpreted, even in the absence of experience with the environment (1). Other species are dependent on a period of interaction with the environment that clarifies the information to which attention should be directed and the consequences of behaviors guided by that information (2). Depending on the developmental status and the task facing a particular organism, both experience-independent and experience-dependent mechanisms may be involved in the extraction of information and the control of behavior. In the domain of language acquisition, two facts have supported the interpretation that experience-independent mechanisms are both necessary and dominant. First, highly complex forms of language production develop extremely rapidly (3). Second, the language input available to the young child is both incomplete and sparsely represented compared to the child’s eventual linguistic abilities (4). Thus, most theories of language acquisition have emphasized the critical role played by experience-independent internal structures over the role of experience-dependent factors (5).

It is undeniable that experience-dependent mechanisms are also required for the acquisition of language. Many aspects of a particular natural language must be acquired from listening experience. For example, acquiring the specific words and phonological structure of a language requires exposure to a significant corpus of language input. Moreover, long before infants begin to produce their native language, they acquire information about its sound properties (6). Nevertheless, given the daunting task of acquiring linguistic information from listening experience during early development, few theorists have entertained the hypothesis that learning plays a primary role in the acquisition of more complicated aspects of language, favoring instead experience-independent mechanisms (7).

Young humans are generally viewed as poor learners, suggesting that innate factors are primarily responsible for the acquisition of language. Here we investigate the nature of the
experience-dependent factors involved in language acquisition. In particular, we ask
whether infants are in fact better learners than has previously been assumed, thus po-
tentially reducing the extent to which experience-independent structures must be
positd. The results demonstrate that in-

fants possess powerful mechanisms suited to learning the types of structures exemplified
in linguistic systems. Experience may there-
fore play a more important role in the ac-
quition of language than existing theories
suggest.

One task faced by all language learners is
the segmentation of fluent speech into
words. This process is particularly difficult
because word boundaries in fluent speech
are marked inconsistently by discrete acous-
tic events such as pauses (8). Although it
has recently been demonstrated that 8-
month-old infants can segment words from
fluent speech and subsequently recog-
nize them when presented in isolation (9),

it is not clear what information is used by
infants to discover word boundaries. This
problem is complicated by the variable
acoustic structure of speech across different
languages, suggesting that infants must dis-
cover which, if any, acoustic cues correlated
with word boundaries are relevant to their
native language (10); there is no invariant
acoustic cue to word boundaries present in
all languages.

One important source of information
that can, in principle, define word bound-
aries in any natural language is the statisti-
cal information contained in sequences of
sounds. Over a corpus of speech there are
measurable statistical regularities that dis-
tinguish recurring sound sequences that
comprise words from the more accidental
sound sequences that occur across word
boundaries (11). Within a language, the
transitional probability from one sound to
the next will generally be highest when the

two sounds follow one another within a
word, whereas transitional probabilities
spreading a word boundary will be relatively
low (12). For example, given the sound
sequence prettybaby, the transitional prob-
ability from pre to ty is greater than the
transitional probability from ty to ba. Pre-
viously, we showed that adults and children
can use information about transitional
probabilities to discover word boundaries in
an artificial language corpus of nonsense
words presented as continuous speech, with
no acoustic cues to word boundaries (13).

We asked whether 8-month-old in-

fants can extract information about word bound-
aries solely on the basis of the sequential
statistics of concatenated speech. We used
the familiarization-preference procedure de-
veloped by Jusczyk and Aslin (9). In this

procedure, infants are exposed to auditory
material that serves as a potential learning
experience. They are subsequently present-
ated with two types of test stimuli: (i) items
that were contained within the familiariza-
tion material and (ii) items that are highly
similar but (by some critical criterion) were
not contained within the familiarization
material. During a series of test trials that
immediately follows familiarization, infants
control the duration of each test trial by
their sustained visual fixation on a blinking
light (14). If infants have extracted the
crucial information about the familiariza-
tion items, they may show differential du-
urations of fixation (listening) during the
two types of test trials (15). We used this
procedure to determine whether infants can
acquire the statistical properties of sound
sequences from brief exposures.

In our first experiment, 24 8-month-old
infants from an American-English language
environment were familiarized with 2 min
of a continuous speech stream consisting of
four-three syllable nonsense words (hereaf-

ter, “words”) repeated in random order
(16). The speech stream was generated by a
speech synthesizer in a monotone female
voice at a rate of 270 syllables per minute
(180 words in total). The synthesizer pro-

vided no acoustic information about word
boundaries, resulting in a continuous stream
of coarticulated consonant-vowel syllables,
with no pauses, stress differences, or any
other acoustic or prosodic cues to word
boundaries. A sample of the speech stream
is the orthographic string bidakapatugolakab-
bidaku. . . . The only cues to word bound-
aries were the transitional probabilities be-

tween syllable pairs, which were higher
within words (1.0 in all cases, for example,

bida) than between words (0.33 in all cases,
for example, kapa).

To assess learning, each infant was pre-
sented with repetitions of one of four three-

syllable strings on each test trial. Two of
these three-syllable strings were “words”
from the artificial language presented dur-

ing familiarization, and two were three-syl-

lable “nonwords” that contained the same
syllables heard during familiarization but
not in the order in which they appeared as
words (17).

The infants showed a significant test-
trial discrimination between word and non-

word stimuli (18), with longer listening
times for nonwords (Table 1). This novelty
preference, or dishabitation effect, indi-
cates that 8-month-olds recognized the dif-
terence between the novel and the familiar
orderings of the three-syllable strings. Thus,
8-month-old infants are capable of extract-
ing serial-order information after only 2
min of listening experience.

Of course, simple serial-order informa-
tion is an insufficient cue to word bound-
aries. The learner must also be able to ex-
tract the relative frequencies of co-occurrence
of sound pairs, where relatively low tran-
sitional probabilities signal word
boundaries. Our next experiment examined
whether 8-month-olds could perform the
more difficult statistical computations re-
quired to distinguish words (that is, recur-
rent syllable sequences) from syllable strings
spanning word boundaries (that is, syllable
sequences occurring more rarely). To take

an English example, prettybaby, we wanted to
see if infants can distinguish a word-

internal syllable pair like pretty from a word-

external syllable pair like ty#ba.

Another 24 8-month-old infants from
an American-English language environ-
ment were familiarized with 2 min of a
continuous speech stream consisting of
three-syllable nonsense words similar in
structure to the artificial language used in
our first experiment (19). This time, how-
over, the test items for each infant consisted
of two words and two “part-words.” The
part-words were created by joining the final
syllable of a word to the first two syllables of
another word. Thus, the part-words con-
tained three-syllable sequences that the in-

fants had heard during familiarization but
statistically, over the corpus, did not corre-

spond to words (20). These part-words
could only be judged as novel if the in-

fants had learned the words with sufficient
speci-

ficity and completeness that sequences
crossing a word boundary were relatively
unfamiliar.

Despite the difficulty of this word versus
part-word discrimination, infants showed a
significant test-trial discrimination between
the word and part-word stimuli (21), with
longer listening times for part-words (Table
1). Thus, 2 min of exposure to concatenated
speech organized into “words” was suffi-

Table 1. Mean time spent listening to the familiar and novel stimuli for experiment 1 (words versus nonwords) and experiment 2 (words versus part-words) and significance tests comparing the listening
times.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Mean listening times (s)</th>
<th>Matched-pairs t test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Familiar items</td>
<td>Novel items</td>
</tr>
<tr>
<td>1</td>
<td>7.97 (SE = 0.41)</td>
<td>8.85 (SE = 0.45)</td>
</tr>
<tr>
<td>2</td>
<td>6.77 (SE = 0.44)</td>
<td>7.60 (SE = 0.42)</td>
</tr>
</tbody>
</table>
cient for 8-month-old infants to extract information about the sequential statistics of syllables. Moreover, this novelty preference cannot be attributed to a total lack of experience with the three-syllable sequences forming part-words, as was the case with the nonwords in the first experiment. Rather, infants succeeded in learning and remembering particular groupings of three-syllable strings—those strings containing higher transitional probabilities surrounded by lower transitional probabilities.

The infants’ performance in these studies is particularly impressive given the impoverished nature of the familiarization speech stream, which contained no pauses, intonational patterns, or any other cues that, in normal speech, probabilistically supplement the sequential inferences inherent in the structure of words. Equally impressive is the fact that 8-month-old infants in both experiments were able to extract information about sequential statistics from only 2 min of listening experience. Although experience with speech in the real world is unlikely to be as concentrated as it was in these studies, infants in more natural settings presumably benefit from other types of cues correlated with statistical information.

Our results raise the intriguing possibility that infants possess experience-dependent mechanisms that may be powerful enough to support not only word segmentation but also the acquisition of other aspects of language. It remains unclear whether the statistical learning we observed is indicative of a mechanism specific to language acquisition or of a general learning mechanism applicable to a broad range of distributional analyses of environmental input (22). Regardless, the existence of computational abilities that extract structure so rapidly suggests that it is premature to assert a priori how much of the striking knowledge base of human infants is primarily a result of experience-independent mechanisms. In particular, some aspects of early development may turn out to be best characterized as resulting from innately biased statistical learning mechanisms rather than innate knowledge. If this is the case, then the massive amount of experience gathered by infants during the first postnatal year may play a far greater role in development than has previously been recognized.

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3. These milestones have been well-documented both in English [for example, R. Brown, A First Language (Harvard Univ. Press, Cambridge, MA, 1973)] and cross-linguistically [for example, E. Lievenburg, Biological Foundations of Language (Wiley, New York, 1967); D. Stobin, ed., vol. 3 of The Crosslinguistic Study of Language Acquisition (Erlbaum, Hillsdale, NJ, 1987)].

4. The “argument from the poverty of the stimulus” remains widely accepted [for example, Chomsky, Aspects of the Theory of Syntax (MIT Press, Cambridge, MA, 1965); S. Cohen, Brain Sci. 14, 597 (1991)].


12. The transitional probability of frequency of XY


16. The three syllable words pabiku, tibudo, and dagola include at least two transitional probabilities that the syllables in the nonwords were all zero relative to the exposure corpus, as these syllable pairs had never occurred during familiarization. In control condition B, the first two strings were nonwords and the last two strings were words. This between-subjects counterbalanced design ensured that any observed preferences for words or non-words across both conditions would not be artifacts of any general preferences for certain syllable strings. Each of the four test strings were presented (repeated with a 550-ms interval between test strings) on three different trials, resulting in a total of 12 test trials per infant.

17. There were no significant differences between the infants in condition A and condition C (B(22) = 0.31). The data from the two groups were thus combined for the other analyses.

18. Condition A words: pabiku, tibudo, dagola, and danpoki; Condition B words: tudaro, pigola, bikutu, and danpoko.

19. Test stimuli: pabiku, tibudo, tudaro, and pigola. In condition A, the first two strings were words and the second two strings were part-words. For example, the part-word pigola spanned the word boundary between danpokigolata and thus was heard during exposure. In condition B, the first two strings were part-words and the second two strings were words. Thus, there were three syllable sequences that the infants had heard during the course of the exposure period. The difficulty of this test discrimination can be seen by comparing the transitional probabilities between the syllables in the words (1.0 between syllables 1 and 2 and between syllables 2 and 3) to the transitional probabilities between the syllables in the part-words (0.33 between syllables 1 and 2 and 1.0 between syllables 2 and 3).

20. There were no significant differences between the infants in condition A and condition B (B(22) = 0.49). The data from the two groups were thus combined for the other analyses.

21. For example, this same general mechanism could be used to find an object, such as a human face, in the environment.

22. We thank J. Gallipeau, J. Hooker, P. Jusczyk, A. Jusczyk, T. Mintz, K. Ruppert, and J. Sawusch for their help with various aspects of this research, and P. Jusczyk, S. Polak, M. Spivey-Knowlton, and M. Tanenhaus for their comments on a previous draft. Supported by an NSF predoctoral fellowship (J.R.S.), NSF grant SBR9421064 (R.N.A.), and NIH grant DC00167 (E.L.N.). The parents of all participants were informed consent.

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