


 The logo for Biology Letters, with "biology" in a light green, lowercase, sans-serif font and "letters" in a darker green, lowercase, sans-serif font below it.

**Evidence of an evolutionary precursor to human language
affixation in a nonhuman primate**

Journal:	<i>Biology Letters</i>
Manuscript ID:	draft
Article Type:	Research
Date Submitted by the Author:	
Complete List of Authors:	Endress, Ansgar; Harvard University, Psychology Department; Harvard University, Linguistics Department Cahill, Donal; Harvard University, Psychology Block, Stefanie; Harvard University, Psychology Watumull, Jeffrey; Harvard University, Psychology Hauser, Marc; Harvard U., Psychology, Organismic Evol Biol
Subject:	Behaviour < BIOLOGY, Cognition < BIOLOGY, Evolution < BIOLOGY
Categories:	Animal Behaviour
Keywords:	Animal cognition, evolution of language, language acquisition, Inflectional morphology


 The logo for ScholarOne Manuscript Central, featuring a blue square icon with a white 'S' and the text "scholarONE™ Manuscript Central" in blue.

**Evidence of an evolutionary precursor to human language affixation
in a nonhuman primate**

Ansgar D. Endress

Donal Cahill

Stefanie Block

Jeffrey Watumull

Marc D. Hauser

Harvard University, Cambridge, MA

Corresponding author: ADE, ansgar.endress@m4x.org

Key words: Animal cognition, evolution of language, morphology,
language acquisition

Summary

Human language, and grammatical competence in particular, relies on a set of computational operations that, in its entirety, is not observed in other animals. Such uniqueness leaves open the possibility that *components* of our linguistic competence are shared with other animals, having evolved for nonlinguistic functions. Here we explore this problem from a comparative perspective, asking whether cotton-top tamarin monkeys (*Saguinus oedipus*) can spontaneously (no training) acquire an affixation rule that shares important properties with our inflectional morphology (e.g., the rule that adds *-ed* to create the past tense, as in the transformation of *walk* into *walk-ed*). Using playback experiments, we show that tamarins discriminate between bisyllabic items that start with a specific “prefix” syllable and those that end with the same syllable as a “suffix.” These results suggest that some of the computational mechanisms subserving affixation in a diversity of languages are shared with other animals, relying on basic perceptual or memory primitives that evolved for nonlinguistic functions.

Introduction

While it is clear that only humans have a language faculty, it is less clear which components of this system are unique to humans, and which unique to language. In fact, although attempts to teach nonhuman animals to produce simplified languages largely failed (Savage-Rumbaugh et al., 1993; Terrace, Petitto, Sanders, & Bever, 1979), and studies of their natural communication show only weak evidence of homologous or analogous abilities (Arnold & Zuberbühler, 2006; Cheney & Seyfarth, 2005; Hauser, 1996; Liebal, Call, & Tomasello, 2004; Suzuki, Buck & Tyack, 2006), different animals show perceptual competences that may well feed into language processing in humans (Kuhl & Miller, 1975; Kluender, Diehl, & Killeen, 1987; Ramus, Hauser, Miller, Morris, & Mehler, 2000).

Here, we build on the above tradition exploring aspects of perceptual competence, asking whether animals have nonlinguistic abilities that are necessary for some forms of language-specific, grammatical computations (Hauser, Newport & Aslin, 2001; Hauser & Fitch, 2004; Gentner, Fenn, Margoliash, & Nusbaum, 2006; Murphy et al., 2008). We start from the observation that, across the world's languages, morphological transformations adding verbal material to the word-edges (i.e., prefixation and suffixation) are much more frequent than transformations adding verbal material in other positions (Greenberg, 1957). For example, the English past participle

1
2
3
4
5
6
7 is formed by adding the “*ed*” suffix to the end of a stem (as in talk-
8 *ed*), while the German past participle is formed by adding the “*ge*”
9 prefix to the beginning of a stem and either the “*en*” or the “*t*” suffix
10 to its end (as in *ge-sag-t*, ‘said’). In these and other languages, word-
11 edges appear well suited for some linguistic transformations
12
13 (McCarthy & Prince, 1993; Nespore & Vogel, 1986).
14
15
16
17

18
19 Here we ask whether a nonhuman animal – the cotton-top
20 tamarin monkey – has the requisite mechanisms for learning formally
21 similar prefixation and suffixation patterns. Our goal, therefore, is not
22 to show that animals such as tamarins *have* language, but rather, that
23 certain components of our expressed languages rely on domain-
24 general mechanisms of learning and memory that are likely to be
25 shared with other animals, including, we suggest, the capacity to
26 extract patterns of temporal ordering.
27
28
29
30
31
32
33
34
35

36 In brief, we exposed subjects to a sequence of bisyllabic items
37 conforming to a common pattern. For example, they heard a sequence
38 of “stem” syllables all preceded by the same prefix syllable.
39 Following this familiarization, they were exposed to new bisyllabic
40 items. Half were preceded by the same prefix syllable as during
41 familiarization, and half were *followed* by that syllable, and thus
42 violated the familiarization pattern. We asked whether tamarins would
43 respond more to bisyllabic items violating the familiarization pattern
44 than to items consistent with it.
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Materials and method

The detailed methods are described in Hauser et al. (2001); here, we highlight only critical differences.

Participants

We tested 14 adult tamarins (7 males; mean age 8.2 years) socially housed in a colony room. For medical reasons, one subject completed only the suffixation condition, and one only the prefixation condition.

Materials

We used naturally recorded syllables as stimuli from native speakers of American English. The affix syllable was always “shoy” uttered by a male speaker. The familiarization stems (see below) were “bi, ka, na, to, gu, lo, ri and nu”, pronounced by a female speaker, and “ba, pu, di, ki, lu, ro and mo” pronounced by a male speaker with a lower voice than that of the speaker of the affix syllable. We used a mixture of different speakers of different genders to prevent subjects from using low-level cues (such as pitch differences between vowels) for their generalizations.

The test stems were the syllables “brain, breast, wasp, snake and swan”, all pronounced by a different female speaker; we used words because speakers found it easier to read English words than phonemic transcriptions.

Syllables were recorded individually, normalized to a duration of 400ms and then RMS amplitude normalized.

Design

We first familiarized subjects to bisyllabic items conforming to either a prefixation or suffixation pattern, and then tested them on new items that either violated or were consistent with the familiarization pattern. Our dependent measure was an orienting response (see below) toward the speaker playing back a test item. Based on prior work using the same method, we predicted that tamarins would orient more to violations of the familiarization pattern than to items consistent with it.

Half of the subjects were first tested with the prefixation pattern, and 29 days later with the suffixation pattern. The other half was first tested on the suffixation pattern, and 33 days later with the prefixation pattern.

Familiarization

During the familiarization phase, subjects heard a sequence of bisyllabic items (hereafter “words”) that all conformed to a common pattern. In the prefixation condition, all words were composed of the prefix “shoy” and one of the familiarization stems mentioned above (e.g., “shoy-bi”, “shoy-mo”). In the suffixation condition, all words were composed of a familiarization stem and the suffix “shoy” (e.g., “bi-shoy”, “mo-shoy”). There was no silence between the prefix and the stem, and words were separated by silences of 2s.

The evening before being tested, monkeys not participating in a condition were brought out of the colony room. Then, the

familiarization stream was played to the remaining monkeys through speakers inside the colony room.

The 14 words were played 70 times, yielding a familiarization duration of 29.4min. Words followed each other in random order with no repetitions.

Test

The morning following this familiarization, subjects were transferred from their homecage to a test cage inside a sound-attenuated chamber. Before proceeding to the test phase, they were given a refresh familiarization of 2.1min consisting of 5 repetitions of the 14 familiarization words.

During test, subjects typically clung to the wire mesh on the front of the test cage, facing the camera. Stimuli were played through a concealed speaker. Stimuli consisted of the five test stems mentioned above. Each stem was presented twice, once with the prefix “shoy”, and once with this syllable as the suffix. Stimuli were arranged in a list alternating prefixed and suffixed stems. Half of the subjects started with a prefixed stem, and half with a suffixed stem.

Coding

We counted the orientation responses to stimuli consistent with or violating the familiarization pattern. Orientation responses were counted if, within a 2.8s window following the stimulus onset (corresponding to a 2s window following the stimulus offset), the subject performed a head rotation of at least 60° in the horizontal

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

plane, and if the subject's looking direction was not below that plane at the end of the rotation. Trials were excluded if the subject looked in the direction of the speaker at the start of the trial, jumped during the 2.8s period from the trial onset, or vocalized during the stimulus.

Trials were started at least 10s and at most 60s after the beginning of the previous trial by an experimenter blind to the trial type (consistent or violation). Trials were started when the subject looked in the direction opposite to the speaker.

All sessions were coded offline, independently and blindly by three experimenters. Average inter-observer agreement was 79.6%, Cohen's $\kappa=0.68$.

To reach a complete consensus, we reviewed all trials for which there was no uniform agreement until all experimenters could agree on the response measure; if no consensus could be reached, the corresponding trial was removed from analysis (N=2 out of 260 trials). We believe that the final consensus is much more reliable than judgments of individual experimenters; indeed, if a coder misses a criterion with probability p , all three coders miss it with probability p^3 .

On average, individual coders agreed on 85.7% of the trials with the final consensus (Cohen's $\kappa = 0.78$).

Results

For each monkey, we computed the proportion of orienting responses to violations of the familiarization pattern and to test items

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

consistent with that pattern, respectively. For the monkeys completing both conditions (N=12), we submitted these proportions to an ANOVA with the within-subject factors item-type (consistent vs. violation) and condition (prefixation vs. suffixation) and the between-subject-factor condition order. This ANOVA yielded a significant main effect of item-type, $F(1,10)=7.43$, $p=0.021$, $\eta^2_p=0.413$, but no other main effects or interactions (all p 's > .05). We thus pooled the proportions from all conditions and all subjects.

Overall, monkeys (including those participating in only one condition) oriented significantly more to violations (proportion of orientations: $\underline{M} = .519$, $\underline{SD} = .192$) than to consistent items ($\underline{M} = .370$, $\underline{SD} = .253$), $F(1,13)=5.07$, $p=.042$, $\eta^2_p=.280$ (repeated-measures ANOVA). Of the monkeys responding more to either consistent items or violations, 9 out of 11 oriented more to violations, $p = 0.033$ (one-tailed binomial test).

Discussion

Our results suggest that, in the absence of training, cotton-top tamarins learn a rule that is formally similar to affixation patterns (i.e., prefixes and suffixes) in natural language. These results cannot be explained by a simple association for two reasons. First, because the stems used during test were maximally dissimilar from those used during familiarization, subjects must have generalized the affixation rule to new stems, as opposed to recalling the position of particular stems. Second, it is highly unlikely that subjects associated the test

1
2
3
4
5
6
7 stems with the affix. As the monkeys had never heard the test stems
8 together with the affix, they could not have associated the test stems
9 with the affix through prior exposure.
10
11

12
13 Given that both humans and cotton-top tamarins can learn this
14 particular aspect of affixation patterns, one may ask how each species
15 computes these patterns. We suggest that the most plausible account
16 refers to the psychological mechanisms that are used to process
17 affixation patterns, and specifically, mechanisms that are shared in
18 different domains across human and nonhuman species. When
19 humans learn such forms during language acquisition, however, they
20 must link these domain-general mechanisms of learning and memory
21 to our distinctively linguistic phonological, syntactic and semantic
22 processes and representations; in contrast, no other animal can link
23 these forms to such representations and processes. In linguistic terms,
24 nonhuman animals may have the capacity to learn surface
25 transformations involved in affixation, but they cannot link them to
26 other aspects of linguistic structure. We conclude by making a few
27 brief remarks on this general thesis.
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43

44 As noted in the introduction, morphological affixation patterns
45 tend to place verbal material either at the beginning or the end of
46 words, and thus at the word-edges (Greenberg, 1957). From a
47 computational perspective, however, edges are just the sequential
48 positions that can be encoded particularly well (since all positions are
49 encoded relative to the sequence-edges; see Henson, 1998), a
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7 conclusion that seems to hold for other primates, including
8 chimpanzees (Endress, Carden, Vesace & Hauser, under review) and
9 potentially rhesus monkeys (Orlov, Yakovlev, Hochstein, & Zohary,
10 2000; Terrace, Son, & Brannon, 2003). Hence, in line with previous
11 proposals (Endress et al., 2005; Endress, Nespors & Mehler, in press),
12 we suggest that the language faculty uses similar positional
13 mechanisms to compute affixation patterns, and though these
14 mechanisms are uniquely used in humans to create and understand
15 words, the mechanisms themselves are not specific to humans or
16 language. For example, when infants acquire the morphological
17 distinction for marking the past tense, they may simply recognize, like
18 other primates, that this distinction entails placing the “ed” morpheme
19 in the right edge of words, although they (and other animals) can use
20 similar positional mechanisms in a variety of nonlinguistic domains.
21 Unlike other primates, however, infants can use such evolutionarily
22 ancient abilities for purposes that are specifically linguistic and
23 (presumably) unique to humans.
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41

42 References

- 43
44 Arnold, K., & Zuberbühler, K. 2006 Language evolution: semantic
45 combinations in primate calls. Nature, 441, 303.
46
47
48 Cheney, D.L., & Seyfarth, R.M. 2005 Constraints and preadaptations
49 in the earliest stages of language evolution. Linguistic Review,
50 22, 135-159.
51
52
53
54
55
56
57
58
59
60

- 1
2
3
4
5
6
7 Endress, A. D., Scholl, B. J., & Mehler, J. 2005 The role of salience in
8 the extraction of algebraic rules. Journal of Experimental
9 Psychology: General, 134, 406-19.
10
11 Endress, A.D., Nespors, M. & Mehler, J. in press Perceptual and
12 memory constraints on language acquisition. Trends in
13 Cognitive Sciences.
14
15 Fitch, W. T., & Hauser, M. D. 2004 Computational constraints on
16 syntactic processing in a nonhuman primate. Science, 303, 377-
17 80.
18
19 Gentner, T. Q., Fenn, K. M., Margoliash, D., & Nusbaum, H. C. 2006
20 Recursive syntactic pattern learning by songbirds. Nature, 440,
21 1204-7.
22
23 Greenberg, J. 1957 Essays in linguistics. Chicago: University of
24 Chicago Press.
25
26 Hauser, M. D. 1996 The Evolution of communication. Cambridge,
27 MA: MIT Press.
28
29 Hauser, M. D., Newport, E. L., & Aslin, R. N. 2001 Segmentation of
30 the speech stream in a non-human primate: Statistical learning
31 in cotton-top tamarins. Cognition, 78, B53-64.
32
33 Henson, R. 1998 Short-term memory for serial order: The Start-End
34 Model. Cognitive Psychology, 36, 73-137.
35
36 Kluender, K. R., Diehl, R., & Killeen, P. 1987 Japanese quail can
37 learn phonetic categories. Science, 237, 1195-7.
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

- 1
2
3
4
5
6
7 Kuhl, P. K., & Miller, J. D. 1975 Speech perception by the chinchilla:
8
9 voiced-voiceless distinction in alveolar plosive consonants.
10
11 Science, 190, 69-72.
12
- 13 Liebal, K., Call, J. & Tomasello, M. 2004 The use of gesture
14
15 sequences in chimpanzees. American Journal of Primatology,
16
17 64, 377-396.
18
- 19 McCarthy, J. J., & Prince, A. 1993 Generalized alignment. In G. Booij
20
21 & J. van Marle (Eds.), Yearbook of morphology 1993 (pp. 79-
22
23 153) Boston, MA: Kluwer.
24
- 25 Murphy, R.A., Mondragon, E. & Murphy, V.A. 2008 Rule learning by
26
27 rats. Science, 319, 1849-1851.
28
- 29 Nespor, M., & Vogel, I. 1986 Prosodic phonology. Foris: Dordrecht.
30
- 31 Orlov, T., Yakovlev, V., Hochstein, S., & Zohary, E. 2000 Macaque
32
33 monkeys categorize images by their ordinal number. Nature,
34
35 404, 77-80.
36
- 37 Ramus, F., Hauser, M. D., Miller, C., Morris, D., & Mehler, J. 2000
38
39 Language discrimination by human newborns and by cotton-top
40
41 tamarin monkeys. Science, 288, 349-51.
42
43
- 44 Savage-Rumbaugh, E.S., Murphy, J., Sevcik, R.A., Brakke, K.E.,
45
46 Williams, S.L. & Rumbaugh, D.M. 1993 Language
47
48 comprehension in ape and child. Monographs of the Society for
49
50 Research in Child Devevelopment, 58, 1-222.
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7 Suzuki, R., Buck, J.R., & Tyack, P.L. 2006 Information entropy of
8 humpback whale songs. Journal of the Acoustical Society of
9 America, 119, 1849–1866.

10
11
12
13 Terrace, H. S., Petitto, L., Sanders, R., & Bever, T. 1979 Can an ape
14 create a sentence? Science, 206, 891-902.

15
16
17 Terrace, H. S., Son, L. K., & Brannon, E. M. (2003). Serial expertise
18 of rhesus macaques. Psychological Science, 14, 66-73.
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

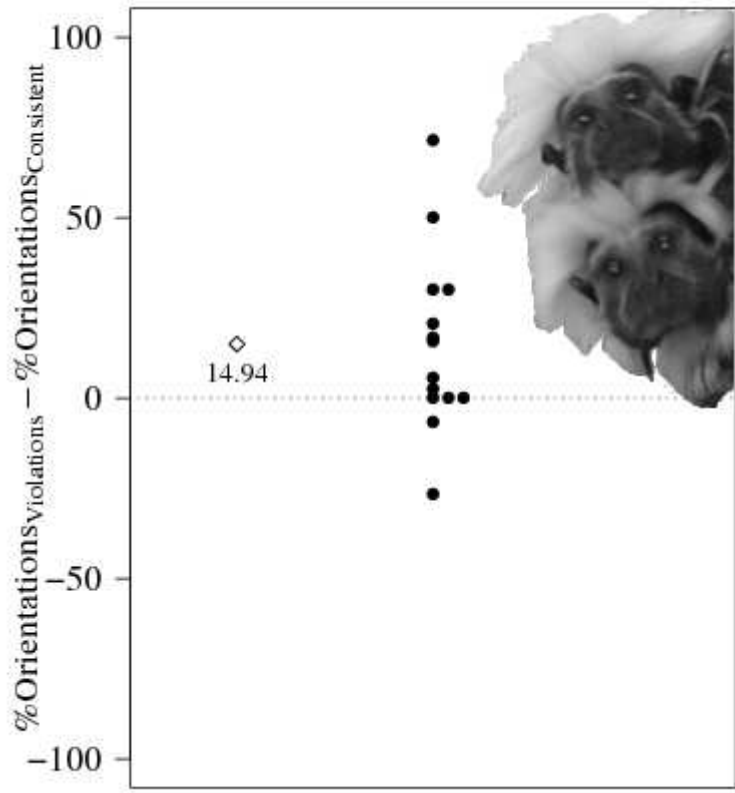
Author Notes

Author Contributions: AE and MH designed the research, analyzed data, wrote paper; AE, DC, SB and JW performed research. Funding for this work was provided by MBB grants to M. Hauser and A. Endress as well as gifts from J. Epstein and S. Shuman and a McDonnell foundation grant to MH. We thank A. Caramazza and S. Pinker for helpful comments on earlier versions of this manuscript.

Figure Captions

Figure 1: Dots represent differences between the proportions of orientations to violations and consistent items, respectively, for individual monkeys, the diamond sample average, and the dotted line the chance level of 0. Most monkeys oriented more towards violations than to consistent test items.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



Only