Systems underlying human and nonhuman primate communication: One, two, or infinite

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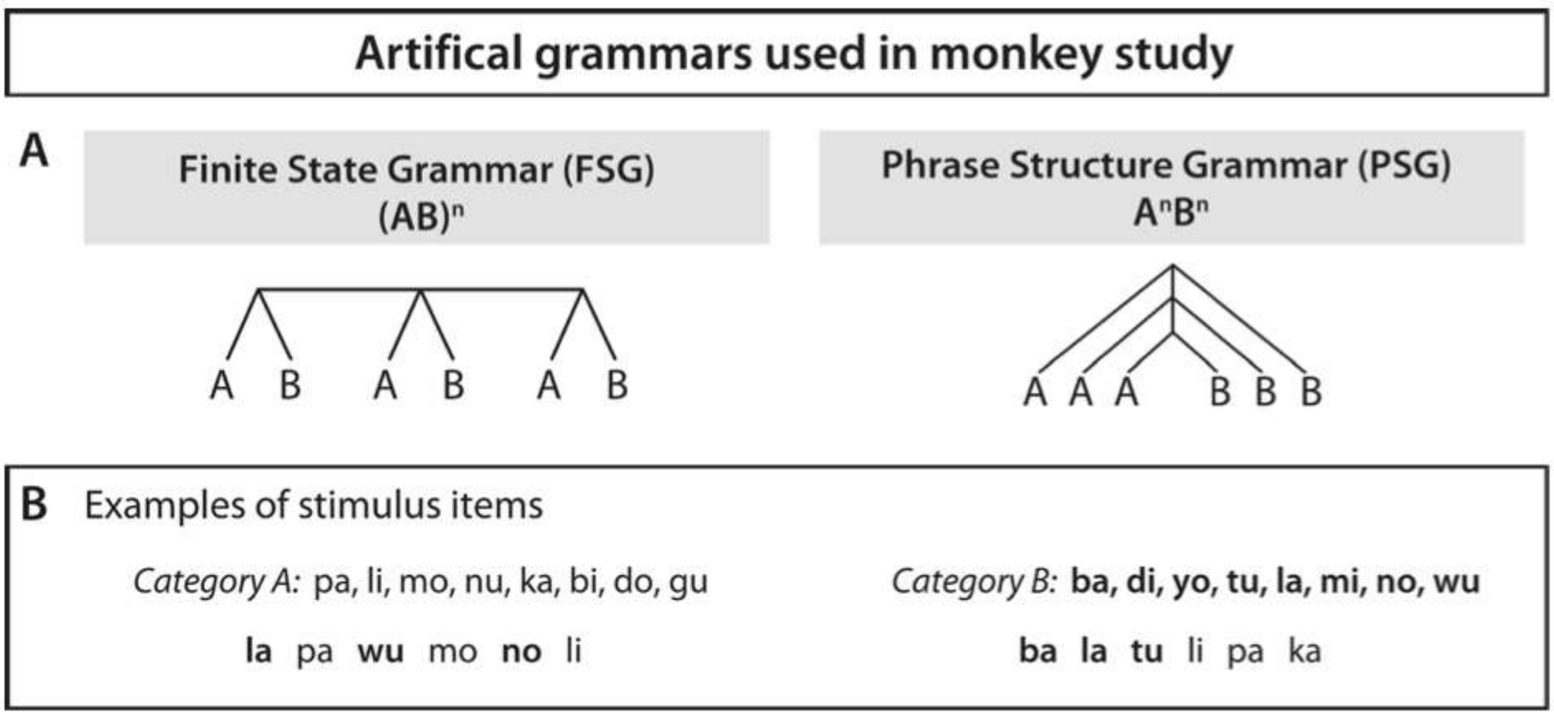
The source of infinity

- What is the source of infinity observable in human language?
- Can we learn anything from looking at the communication system of primates?

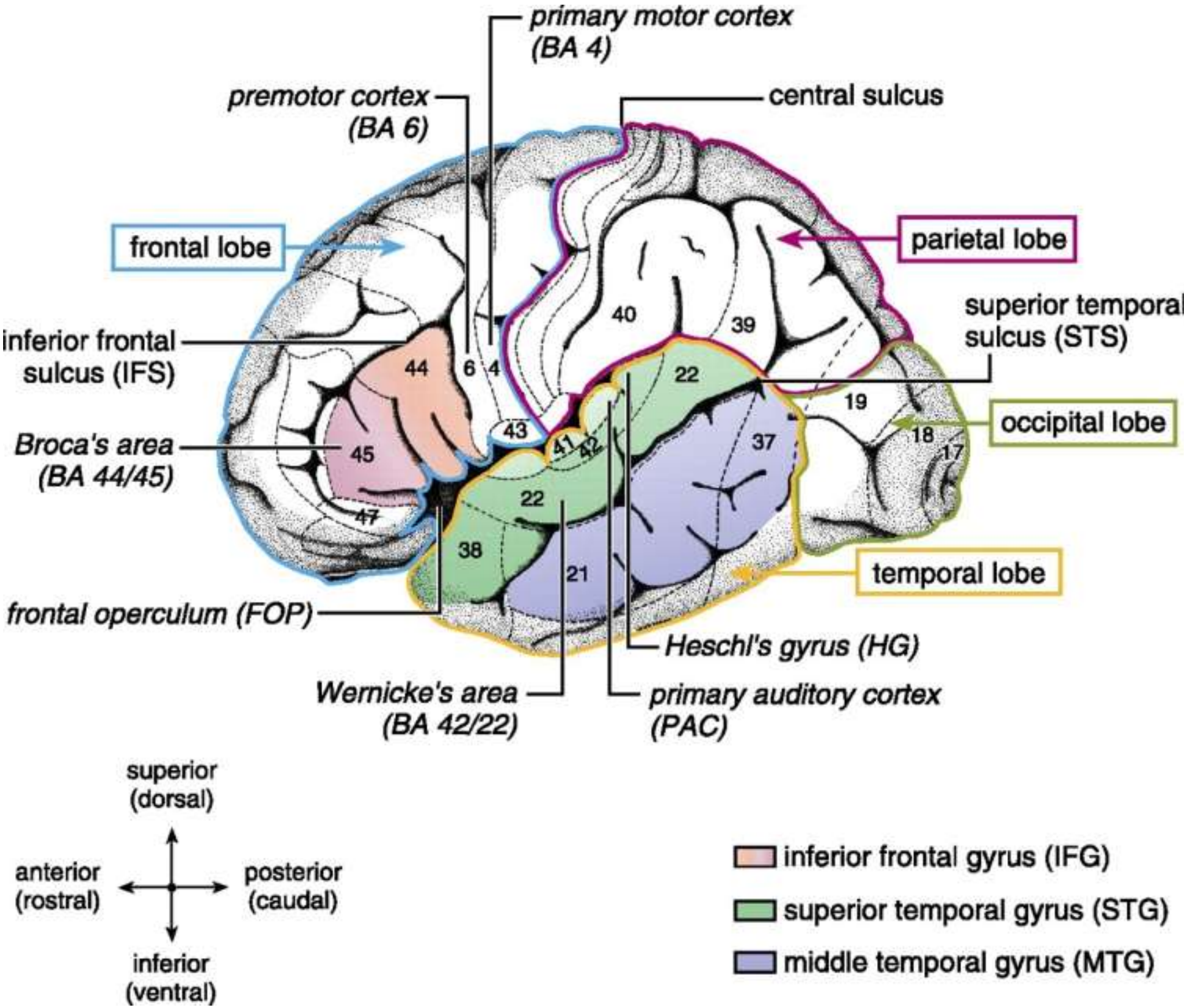
Evolution of the neural language network

Fitch & Hauser (2004) compared artificial grammar learning between human and nonhuman primates using FSG and PSG grammar types. Testing cotton-top tamarins and human adults in a behavioral grammar learning study, they found that humans were able to learn both grammar types easily, whereas the monkeys were only able to learn the FSG.



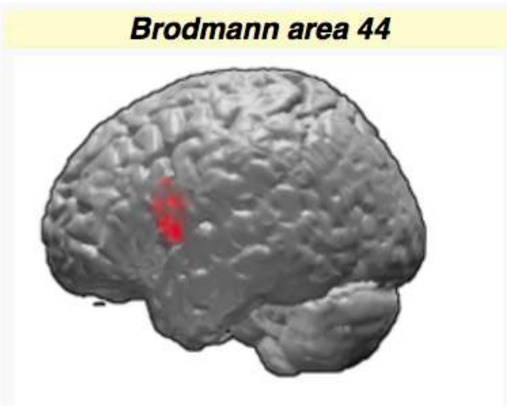
Neuroanatomical difference

A functional magnetic resonance imaging (fMRI) study in human adults using the same type of grammars was conducted (FNG vs PSG). The data revealed different activation patterns for the processing of (AB)n sequences and AnBn sequences (Friederici et al., 2006). Sequences of the PSG activated the posterior portion of Broca’s area (Brodmann area [BA 44]) and the frontal operculum, whereas sequences of the FSG only activated the frontal operculum. Because the frontal operculum is a phylogenetically older brain region (Amunts & Zilles, 2012; Sanides, 1962), the fMRI results in humans may reflect an evolutionary trait.


primary motor cortex
(BA 4)
premotor cortex
(BA 6)
central sulcus
frontal lobe
parietal lobe
inferior frontal
sulcus (IFS)
superior temporal
sulcus (STS)
44
6
4
40
39
22
19
43
45
41
42
37
18
17
occipital lobe
Broca's area
(BA 44/45)
47
22
38
21
temporal lobe
frontal operculum (FOP)
Heschl's gyrus (HG)
Wernicke's area
(BA 42/22)
primary auditory cortex
(PAC)
superior
(dorsal)
anterior
(rostral)
posterior
(caudal)
inferior
(ventral)
inferior frontal gyrus (IFG)
superior temporal gyrus (STG)
middle temporal gyrus (MTG)

Brodmann's Area 44

Brodmann area 44, or **BA44**, is part of the frontal cortex in the human brain.



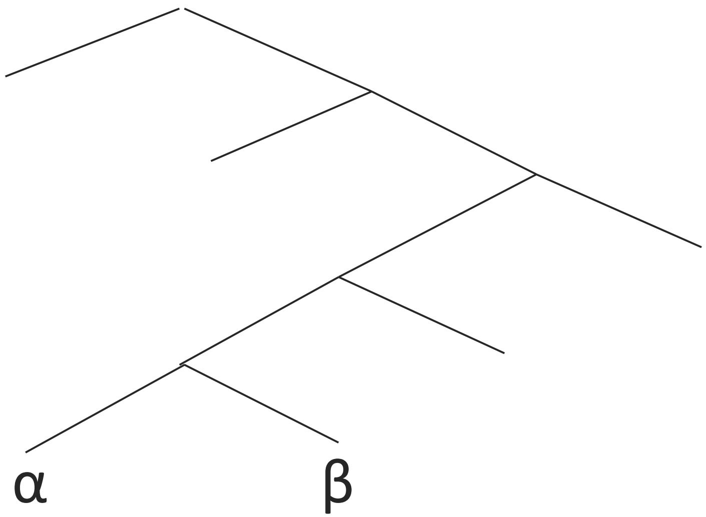
Together with left-hemisphere BA 45, the left hemisphere[1] BA 44 comprises Broca's area, a region involved in semantic tasks. Some data suggest that BA44 is more involved in motor aspect of speech. Some recent findings also suggest the implication of this region in music perception.

Frontal operculum

The frontal operculum is a phylogenetically older part of the brain compared to the Broca's area (Sanides 2019), and one of its functions is apparently to create sequences of (AB) combinations (Friederici et al. 2006).

BA 44 and hierarchical structure

The specific function of BA 44 and the frontal operculum for the computation Merge has been investigated in a series of fMRI studies (Zaccarella & Friederici, 2015a, b). It was found that <u>although the frontal operculum/anterior insula supports the binding of two elements independent of any phrase structure, BA 44 is recruited only if a hierarchical phrase structure is built</u>. <u>This indicates that BA 44 is the region in the inferior frontal gyrus that particularly subserves syntactic hierarchy building.</u>


α
β

Human and non-human primate brain circuitry

Human and nonhuman primates differ in their abilities to process complex sequences. So far, apart from humans, there is no evidence that other species can process and learn hierarchically structured sequences similar to those of natural languages (Beckers, Bolhuis, Okanoya, & Berwick, 2012; Poletiek, Fitz, & Bocanegra, 2016; Yang, 2013). A possible explanation for this behavioral difference may lie in the neural differences between humans and nonhumans with respect to language-related brain structures.

Alarm calls of monkeys

It is typically believed that alarm calls are composed of acoustically distinct, isolated utterances of alarm, such as “leopard,” “eagle,” and “snake” (Blumstein et al. 1999). They do not combine, for example, “leopard” and “eagle” to create a novel utterance.

Conveying meaning in the animal world

Vervet monkeys of Kenya

(Seyfarth, Cheney, Marler 1980 *Science*)

eagle 鷲

snake へび

leopard
レパード

bees

General issues regarding alarm calls

Based on:

"Survivor signals: The biology and psychology of animal alarm calling" 2009.
Klaus Zuberbüler

Cacophy of alarm calls for leopard

Continuous sound; difficult to divide

Evidence for mental representation with alarm calls: Diana monkeys

Arboreal guenon species that inhabits the West African rain forest belt between Gambia and Ghana.

Adults: alarm calls in response to eagles and leopards, their two main preys.

Striking

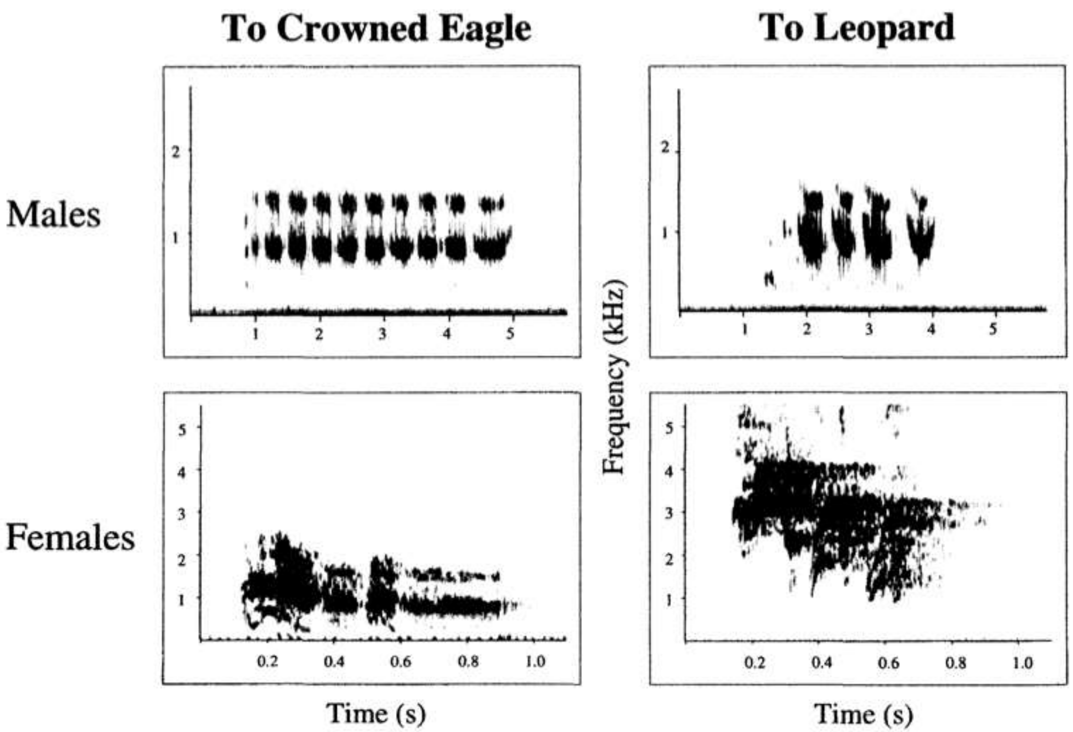


Figure 1. Alarm calls of male and female diana monkeys in response to crowned eagles and leopards.

[Video leopard]

Study

Taï National Park, Côte d'Ivoire, June 1994 – June 1997

Group of 20 individuals, 1 fully adult male, several adult females with their offspring. 30 different groups probably studied.

Four different vocalizations used as playback:

(a) 15s of grows of an African leopard

(b) 15s of shrieks of a crowned eagle;

(c) series of male diana monkey alarm calls in response to leopard;

(d) series of male diana monkey alarm calls in response to eagle.

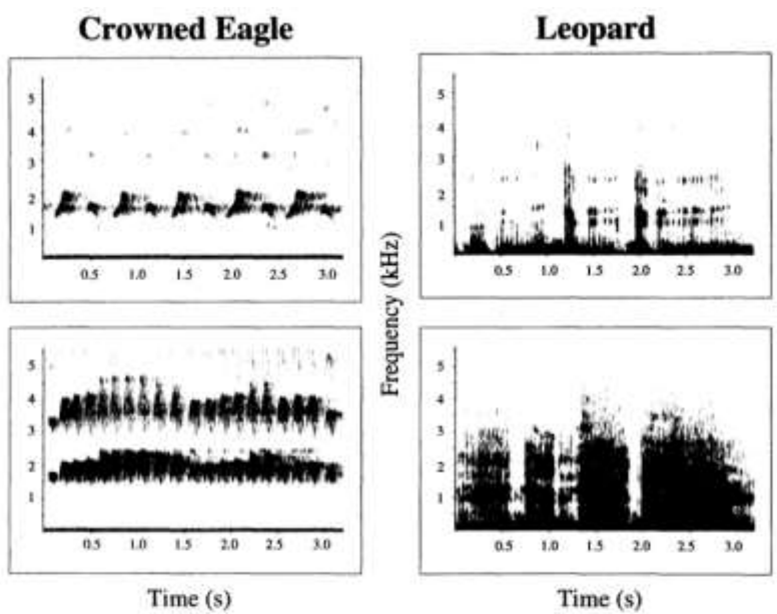


Figure 2. Representative exemplars of the predator vocalizations used as experimental playback stimuli.

Alarm calls played in series of five calls (in some cases three for the eagle call, which is longer).

Prior study:

- Presentation of acoustic predator models provides reliable way of stimulating predator presence.
- Acoustic responses to real leopards and to playbacks were identical. Same for eagles.

Experimental design: prime – probe pairings

Playback of prime, followed 5 minutes later by probe. 5 min. because that the interval after which behavior returns to baseline.

Baseline: prime and probe were alike:
Eagle shrieks, eagle shrieks

Test condition: only the semantic features were alike:
Male's eagle alarm call, eagle shrieks

Control condition: both the acoustic and semantic feature were different:
Male's leopard alarm calls, eagle shrieks

Test for habituation

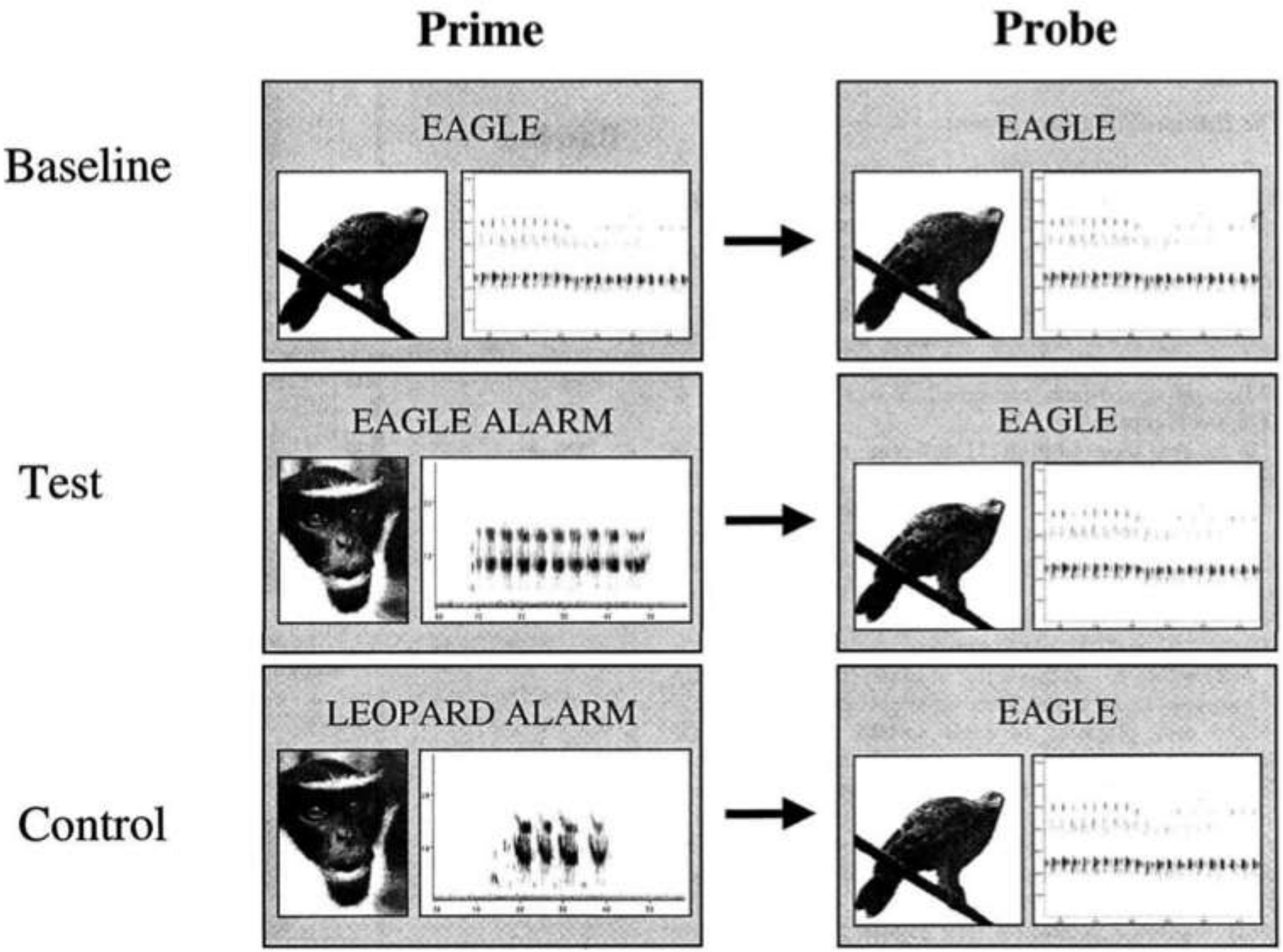


Figure 3. Example of experimental design for one set of playback experiments. Diana monkey groups were tested on two stimuli separated by 5 min of silence. Stimulus pairs differed in similarity of the acoustic and conceptual features across conditions as follows: (a) baseline condition—both the acoustic and the conceptual features remain the same; (b) test condition—the acoustic features change but the conceptual features remain the same; (c) control condition—both the acoustic and the conceptual features change.

Predictions:

Baseline: habituation

Strong reaction to the prime, weak reaction to the probe

Test: habituation

Strong reaction to the prime, weak reaction to the probe

Control: nonhabituation

Strong reaction to both prime and probe

To avoid unwanted dependencies in the data, each group was tested only once.

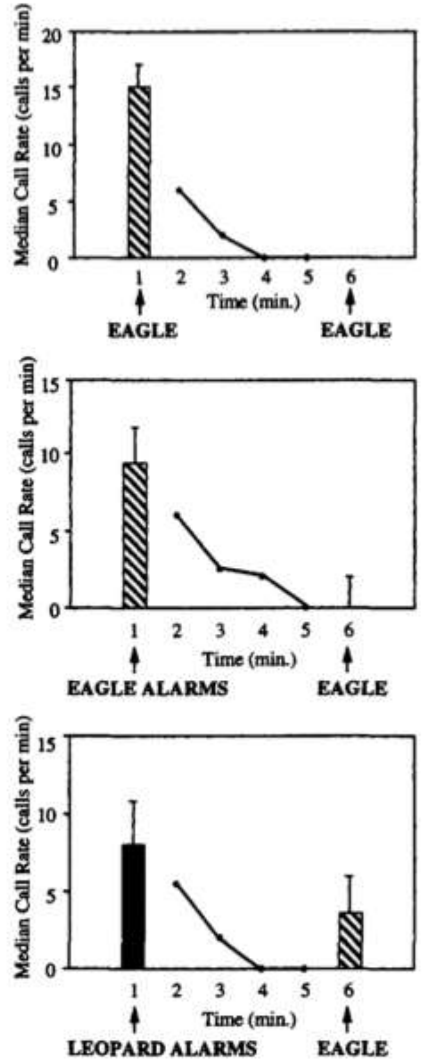
89 playback trials, 31 could not be used (experimenter detected, predation event, moved away)

Results were as predicted, crucially for female diana monkeys.

Baseline
N = 11

Test
N =10

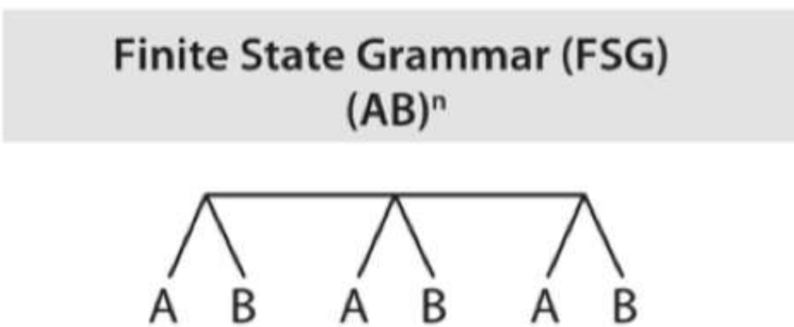
Control
N = 9

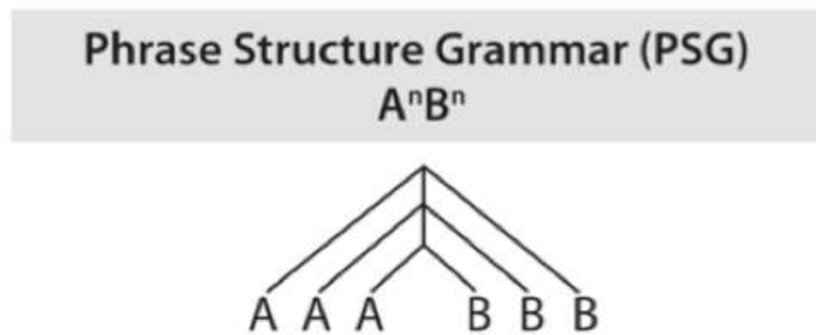


Old World Monkeys

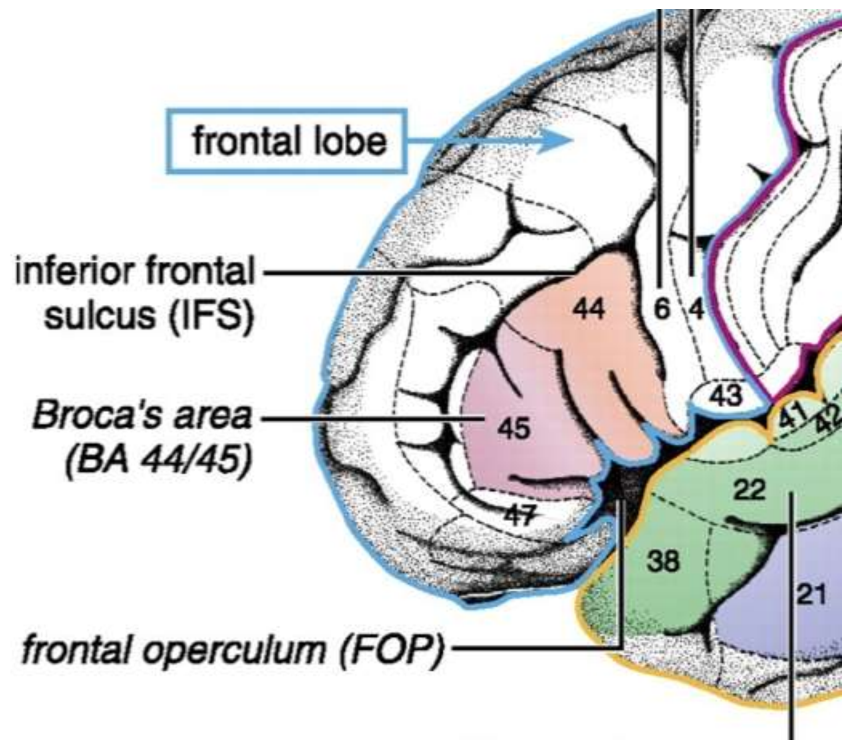
Old World monkeys such as the Diana monkeys, Campbell's monkeys, and De Brazza's monkeys have what appear to be a combinatorial system in which they can put together two independent items.

What we will show, based on the analysis of the reported data, is that these monkeys indeed have a way to create a two-term expression. This is consistent with Fitch and Hauser's finding that tamarins can learn AB sequences.





Assuming this AB sequence to be associated with the frontal operculum, this is also consistent with the observation that the frontal operculum supports the combining of two elements in sequence, rather than building a hierarchical structure



System of Two: Putty-nosed monkey

Putty-nosed monkeys (Arnold and Zuberbühler 2012)

pyow (=P) and hack=(H);

Pyows function as general alert calls, whereas hacks are usually related to aerial predators.

PPPHHH (can only be used for non-risk-related situations)

PHHHHH

PPPPHH

*PHP…

“phonologically complex,
but lexically simple” (Schlenker 2016)

Dual-compartment frame

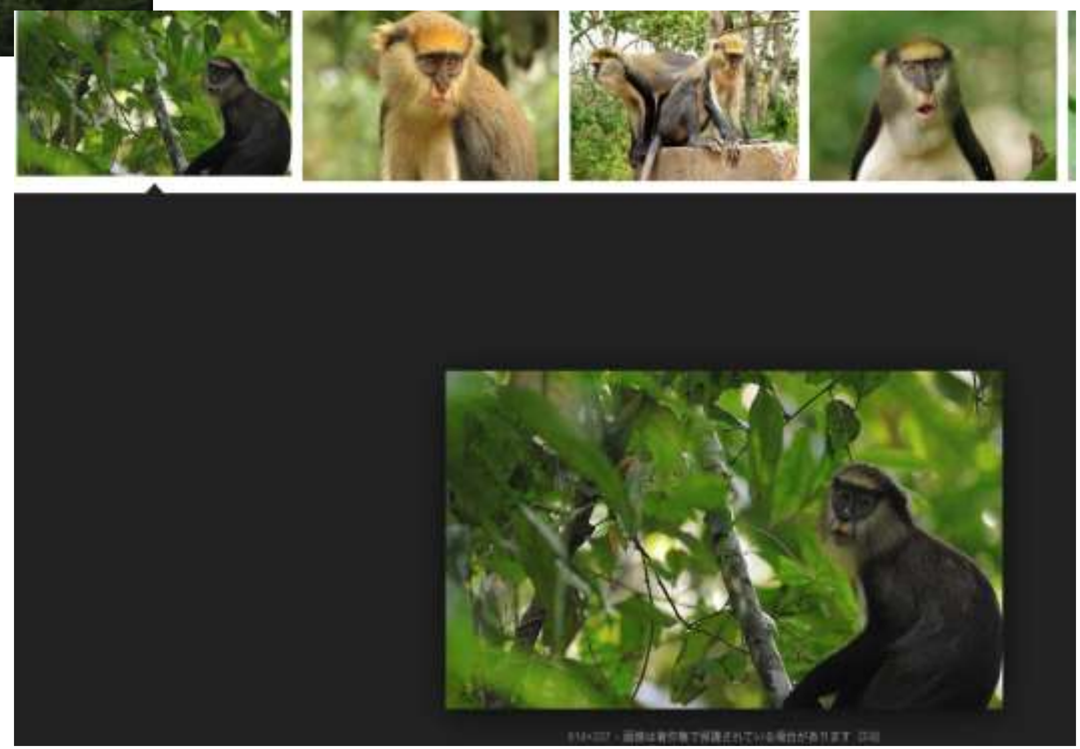
pyow^n	*hack*^{n}
1	2

See Progovac (2015)

Campbell's monkeys

Ouattara et al. (2009)

The adult males of six wild Campbell's monkey groups in the Tai Forest



Affixation in the alarm calls of free-ranging adult Campbell's monkeys (Cercopithecus campbelli campbelli)

Male alarm calls are composed of an acoustically variable stem, which can be followed by an acoustically invariable suffix.

Suffixation functions to <u>broaden the calls' meaning</u> by:

(i) transforming a highly specific eagle alarm to a general arboreal disturbance call;

or

(ii) by transforming a highly specific leopard alarm call to a general alert call.

Stems and an affix

The adult males consistently produced six different loud alarm call types:

(a) boom
(b) krak
(c) hok
(d) wak-oo
(e) krak-oo
(f) hok-oo

All were perceptually distinct to a human observer.

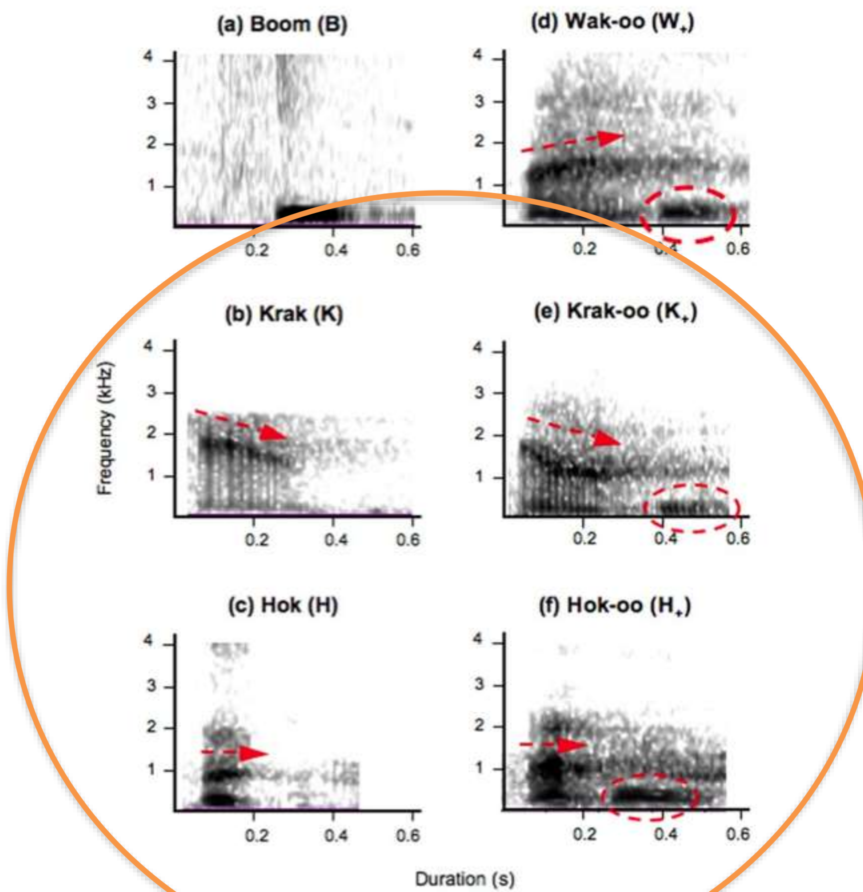


Figure 1. Spectrographic illustrations of the different loud call types produced by male Campbell's monkeys in different contexts. (a) 'boom call', a low-pitched loud call produced by the vocal sac with no frequency modulation, (b) 'krak' call [K], a single loud tonal utterance of ø = 0.176s duration, with a decreasing main frequency band starting at about 2.2 kHz; (c) 'hok' call [H], a single loud tonal utterance of ø = 0.070s with no frequency modulation starting at about 1.0 kHz); (d) 'wak-oo' call [W+], a suffixed loud tonal utterances of 0.330s consisting of a call stem with an increasing main frequency band rising from about 1.0 to 1.3 kHz, followed by a compulsory 'oo' suffix (e) 'krak-oo' call [K+], a 'krak' call followed by the 'oo' suffix; (f) 'hok-oo' [H+], a 'hok' call followed by the 'oo' suffix.
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“Meaning” of Campbell alarm calls

krak : exclusively given after detecting a leopard, suggesting that it functioned as a leopard alarm call

krak-oo : given to almost any disturbance, suggesting it functioned as a general alert call.

hok : almost exclusively associated with the presence of a crowned eagle (either a real eagle attack or in response to another monkey’s eagle alarm calls)

hok-oo : given to a range of disturbances within the canopy, including the presence of an eagle or a neighboring group.

On *hok* and *hok-oo*

On a few occasions, *hok* and *hok-oo* calls were produced in response to a flying squirrel, whose silhouette somewhat resembles a flying eagle, but never to any other large bird.

While producing *hok-oo* calls, males adopted a threat posture, combined with flashing their eyelids, and they sometimes conducted a short dash towards the disturbance.

Adding an *oo* unit to *hok*, thus, indicated that the male was aggressively motivated -- in response to a general disturbance within the canopy, e.g., a perched eagle or a conspecific opponent.

Field experiments

To investigate the predator warning function more directly, a series of field experiments were performed that simulated the presence of the different predators, using both visual and acoustic models.

Research question for us

Ouattara et al. (2009) (and Schlenker 2016) simply assume that *-oo* is affixed to *krak (krak-oo*) and *hok- (hok-oo*). But an equally plausible view is that *krak-oo* and *hok-oo* are single lexical items and the shape and meaning similarities are coincidental.

NOTE: *wak-oo* (similar in usage to *hok-oo*). **wak-*

To test to see if the Campbell's monkeys actually detect the "root" in *krak-oo*, we looked closely at the data presented by Ouattara et al. (2009).

Campbell’s Monkey data (Outtara et al. 2009)

Experiments with four conditions

	krak-oo	krak	hok-oo	hok
Eagle$_{visual}$	91		37	151
Eagle$_{acoustic}$	62		7 (3/7)	9 (2/9)
Leopard$_{visual}$	4 (1/7)	273		
Leopard$_{acoustic}$	67	42 (4/7)		

Campbell's Monkey data (Outtara et al. 2009)

VISUAL PRESENTATION OF THE PREY

	krak-oo	krak	hok-oo	hok
Eagle_{visual}	91		37	151
Leopard_{visual}		273		

Informativity Principle

When one call is strictly more informative than another, the most informative one is used whenever possible

(Schlenker 2016: 18)

Revision:

When two alarm calls contain reference to the same predator, the more informative one is used whenever possible.

Hok, hok-oo

When presented with an eagle model:

hok (151), krak-oo (91)

But what about hok-oo (31)? Contradicts the revised Informativity Principle?

hok-oo appears to have additional function beyond hok: ‘[w]hile producing "hok-oo” calls, males adopted a threat posture, combined with flashing their eyelids, and they sometimes conducted a short dash towards the disturbance’ (Outtara 2009: 3)."

Recap: Campbell's Monkey data (Outtara et al. 2009)

ACOUSTIC PRESENTATION

	krak-oo	krak	hok-oo	hok
$\text{Eagle}_{acoustic}$	62			
$\text{Leopard}_{acoustic}$	67			

The asymmetry in the use of *krak-oo* for leopard vs. eagle suggests that <u>Campbell's monkeys are aware that *krak* in *krak-oo* carries the meaning of "leopard" despite the fact that *krak-oo* is a general alarm call.</u>

This still does not answer the question, do the monkeys have an operation of affixation, a form of Merge, or do they learn *krak-oo* as a single expression?

De Brazza's monkeys

Bouchet et al. (2012) studied 23 De Brazza monkeys in captivity that included three juvenile males, three juvenile females, five adult males, and 12 adult females, all captive-born. The inclusion of the juvenile monkeys allowed for developmental study of calls, which becomes important for our study.

Bouchet et al. (2012) report that the monkeys produced ten distinct call types; we will focus on three of them, *On, I, and OnI*.

On calls occurred with gazes directed to the adult male by adult females as well as both sexes of juveniles. The adult male made this call when gazing at zoo-keepers, the research observer, or neighboring groups.

I calls were uttered by juveniles when approaching the adult male to establish physical contact.

OnI calls were made by adult females and juveniles of both sexes when approaching a male but with ambivalence about whether to approach or escape.

Distribution of De Brazza's monkey calls

Females		Males	
Juveniles	Adults	Juveniles	Adults
On	*On*	*On*	*On*
I		*I*	
OnI	*OnI*	*OnI*	

Conclusion

- Primates have the ability to form two-item expressions, but never more than two;
- The formation of the two-item expression does not involve an operation such as Merge, thus it is a simple regular grammar;
- The frontal operculum supports the combining of two elements in sequence, rather than building a hierarchical structure (Zaccarella et al. 2015);
- Monkeys have well-developed frontal operculum (Sanides 2019);
- Human language is infinite, and this comes from the combinatorial operation of Merge, which is located in the Broca's area (Friederici et al. 2006, etc.), which is phylogenetically newer than the FOP.