Primates evolved spectrally complex calls
in compensation for reduction in olfactory cognition
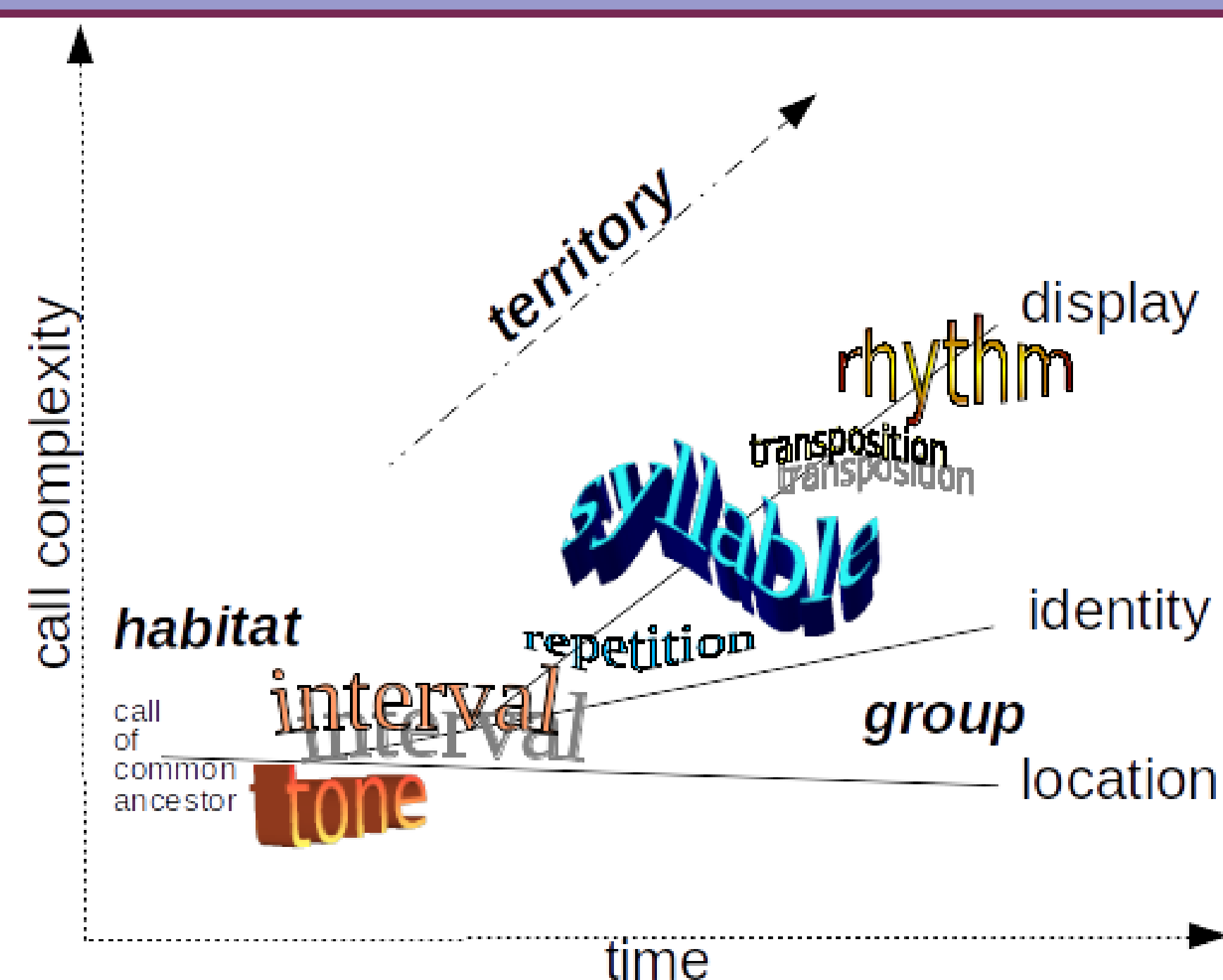
David M. Schruth, Ph.D.

Introduction

Most vertebrate animals are adept at passing air over constricted nasal or throat passages to produce acoustic vibrations in order to communicate position and identity to conspecifics.

More complex, and perhaps music-like, patterning in the form of displays might also possibly function as honest signals of underlying cognition.

Arboreal primates and birds, as well as aquatic mammals—including dolphins, whales, seals, penguins—make such calls.

Increasingly researchers are honing in on specific aspects (e.g. tone, rhythm, transposition, repetition) of these calls to determine when how and why they have emerged.

Figfdure 1. A possible evolutionary progression of ecological pressures (bold-italics) on increasingly complex features (styled font) of vocalizations over time from a common ancestor. Possible modern day functions (normal font) are listed on the right hand side.

Yet poorly understood, still, is how specific features of each of these animals' neural circuits are involved in the processing of each of these features

Hypothesis

I hypothesized that animals should possess similarly high volume, encephalization, or utilization of brain structures (e.g. archicortex, mid-brain, and hind brain) for pattern matching of melodic content considering similarities in higher dimensional modes of locomotion.

Methods

Spectrogram Collection:
- 58 extant primate species
- over 50 sources scanned from 300 leads from the primary literature
- 1297 spectrograms ← 829 vocalizations

Spectrogram Scoring:
- Five (experiment blind) volunteers
- Training on feature definitions based on text descriptions of human acoustic structural universals and bird-call spectrographic visual examples
- Blindly scored for six features: 2 temporal, 3 spectral, & syllable count

Brain Component Volumes
- I calculated such brain component volumetric percentages of a small sample of non-human primates to investigate possible connections with spatial capacities (p=42 parts; n=48 species; Matano et al., 1985).

Musical Complexity Measures:
- Syllable count: number of unique spectral shapes
- **SCI**: euclidean measure of song complexity w/ focus on repetition & length
- **ARDI**: measure of the expected number of reappearing syllables

Analysis:
- Brain component fractions were regressed upon these three different measures of call complexity using standard, musical, and tarsier absent weighting schemes.

Figures 2-4: Each column represents brain components while rows correspond to vocal complexity metrics. Colored points correspond to musical species: green=*titi*, *tamarin*, and *marmoset* monkeys; purple=*galagos*, blue=*indri*, orange=*gibbon*, red=*tarsier*. The green regression line excludes *T. spectrum* where as the red weights musical species (colored) as double, and black treats all points as equal. Corresponding p-values for these regression lines appear in the upper corner of each plot.

Results
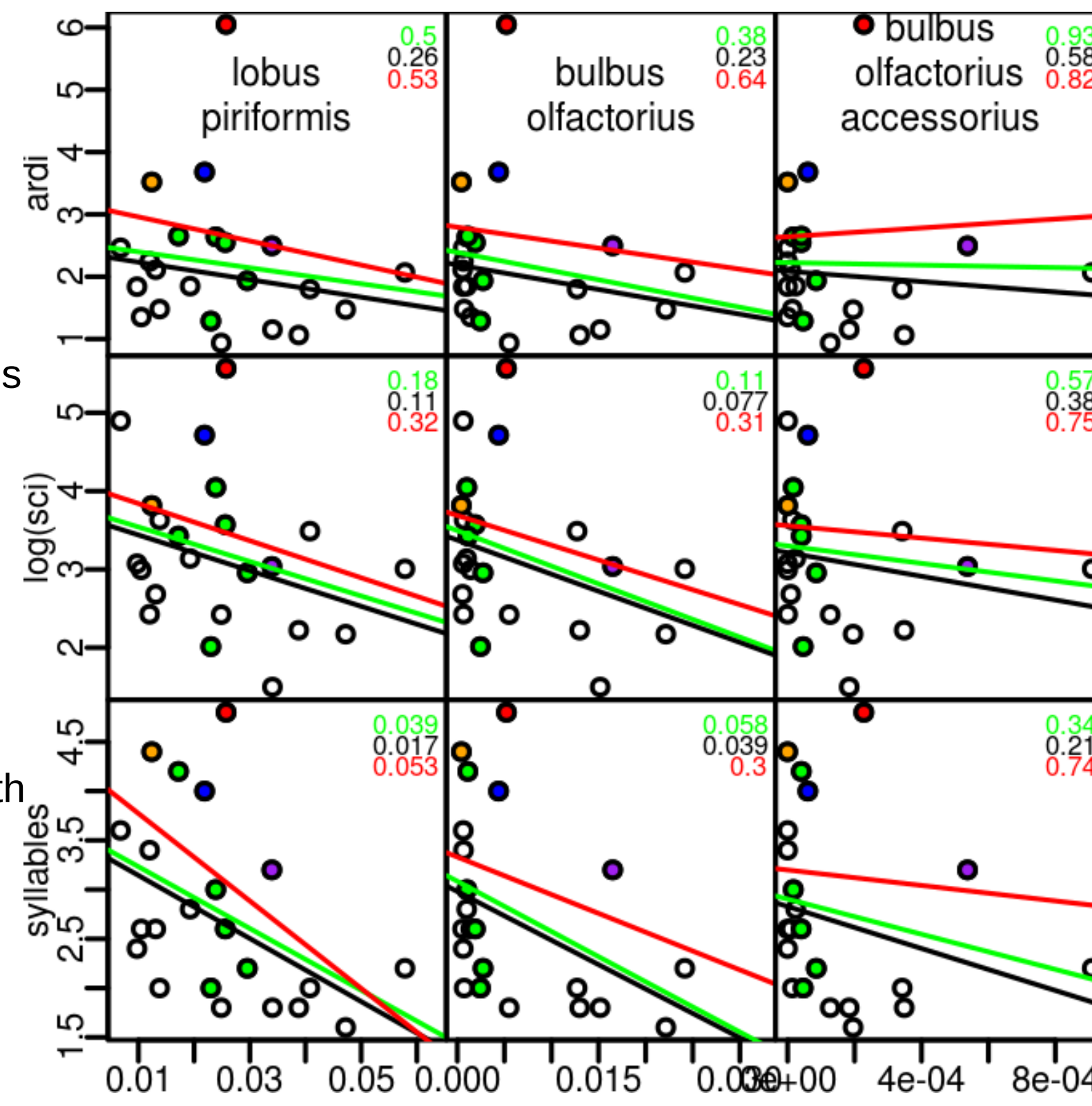
Figure 2. Olfaction relevant brain volume fractions (x-axes) versus vocal complexity indexes. All brain components involved in olfaction were negatively correlated with vocal complexity.
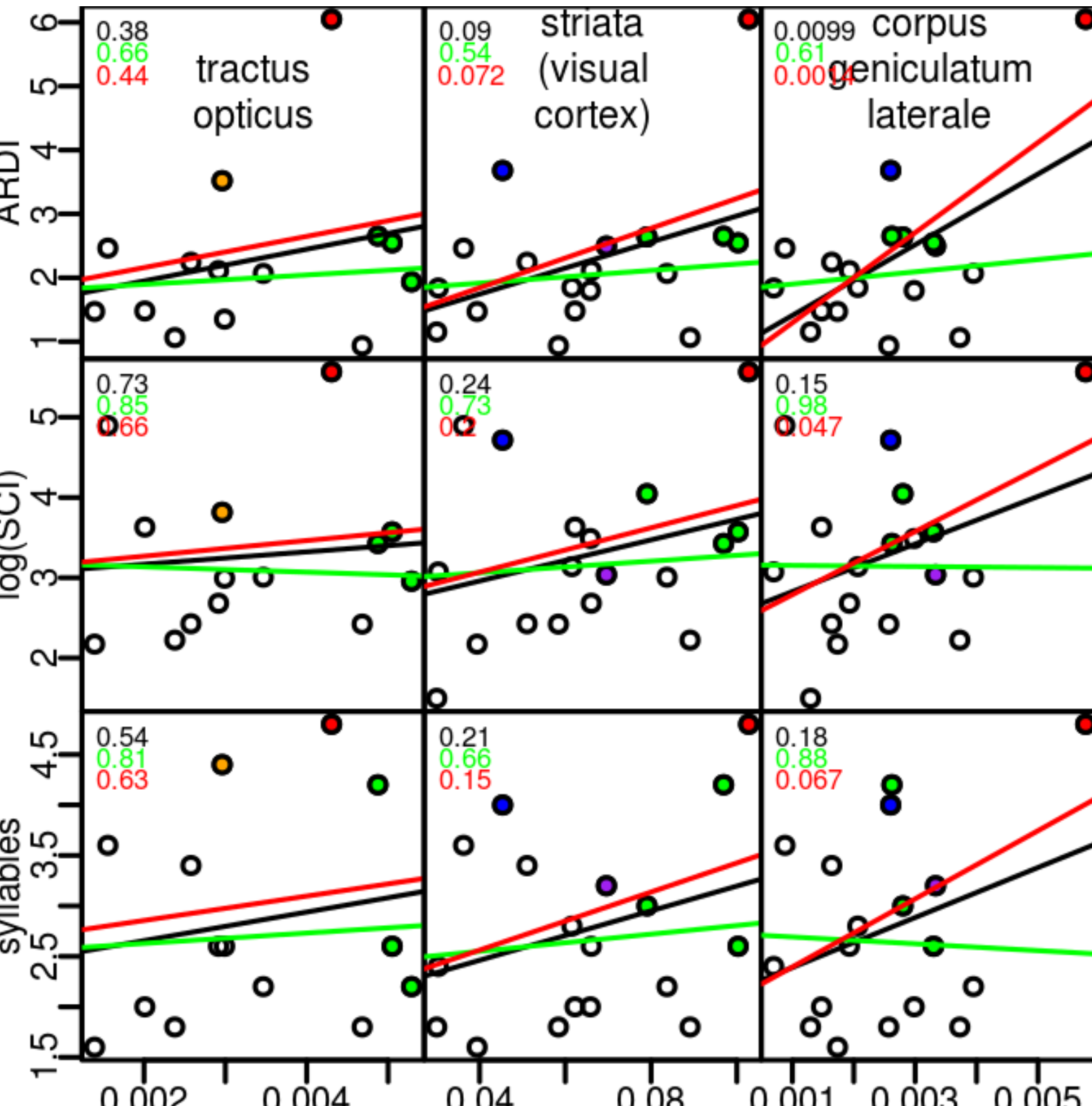
Figure 3. Vision relevant brain volume fractions (x-axes) versus vocal complexity indexes. All parts have positive associations with all vocal complexity measures. Only the *geniculate nucleus* has a clearly significant and positive relationship (with musicality).
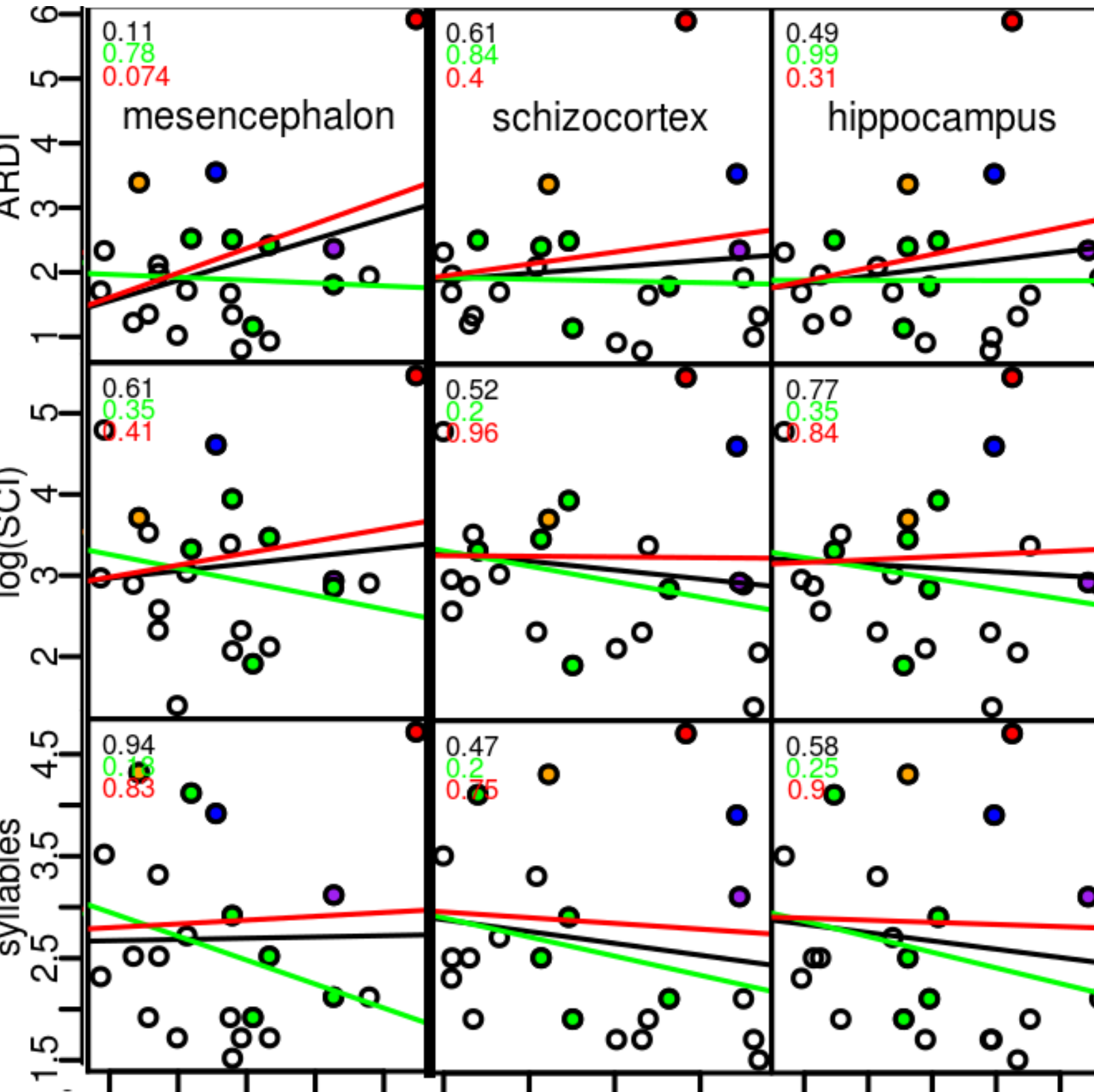
Figure 4. Motor and spatial relevant brain volume fractions (x-axes) versus vocal complexity indexes. The *schizocortex* and *hippocampus* have marginally positive relationships with ARDI suggesting musicality could facilitate spatial orientating. Note the extreme brain fraction values for *tarsier*, *indri*, and *galago* in the *schizocortex*. The medulla oblongata (esp. *mesencephalon*) as well as the *thalamus* had marginally positive relationships with ARDI

Discussion

Indicators of motor control
The obvious motor-control areas associated with ARDI are the *mesencephalon* (midbrain) and the thalamus (upper *diencephalon*). The midbrain sends sensory-motor signals to higher cortical areas while the *thalamus* relays movement, motor planning, and sensory (e.g. vision and hearing) information. Support for cranial motor control is evidenced by higher vocal complexity association with lower-brain areas of *nucleus basalis* and *vestibularis medialis*. The former is known to release the motor-neuron activator acetylcholine, whereas the later is involved in fine control over head, neck, and eye movements. See figure 4.

Co-opting of spatial areas
The *schizocortex* and hippocampus could be implicated in processing of musical sequences (Fig 4). These areas are appropriately located—between the midbrain, hindbrain, and temporal lobe, with strong adjacency to lower, archicortical, layers of cerebrum—to serve in a navigational capacity for olfaction.

Trade-off with sense of smell
The primary finding of this investigation of diminished olfactory and piriform areas (Fig 2) is unsurprising. Because complex auditory and visual processing primarily localize to the temporal and occipital regions of the cerebral cortex, the conversely decreased correspondence in brain parts for reduced olfaction was expected.

Visual-spatial signals
The LGN receives neural impulses from retinal ganglion cells. It also has strong connectivity with the visual striata. Thus a bigger LGN could indicate exceptional ability to process visual information and a need for split-second spatio-temporal circuitry, perhaps for rapid locomotor reflexes. The LGN serves to determine spatial dimensions of raw visual input both retina which is also used as feedback for visual focus on objects of interest in the external environment. Thus, the LGN could serve in locating conspecifics who might be separated in arboreal, visually occluded, environs where transposition-rich musical calls would propagate most efficiently.

Trade-off for sense of vision
Other vision associated areas, such as the visual striata, were also moderately correlated with vocal complexity measures. It is possible that nocturnal and leaping near stem-primates re-purposed the *striata* (Fig 3), a cortical area normally used for processing optical inputs, for visualizing auditory input instead. The similar phenomena of mental representation of exogenous spectral contiguities to internal spatial cortical maps has been proclaimed *auditory scene analysis* [ASA]. However, much of ASA is typically concerned with tracking of continuous streams of auditory sensory input rather than matching of discrete acoustic gestures and mapping of these gestures into ecologically relevant spatial coordinates, as I propose here.

Paralimbic Intrinsic Acoustic Neighborhood Orientation
Little work on ASA specifically addresses spatial aptitude aspects of cognition (in the signal sender) and instead focuses on distillation of contiguous shapes across topographically equivalent representations of cognition (in the signal receiver). I suggest a finding these neural representations (of *both* the signaler and receiver), specifically those interconnected to the paralimbic system. This sub-cortical system, located on the medial side of the temporal lobe, includes the *piriform*, *parahippocampal*, and *entorhinal* cortices. These ancient structures overlap with the lowest three layers of the temporal lobe, *hippocampus*, and the olfactory structures of the *piriform*. While the *piriform cortex* is primarily concerned with sense of smell, the other two, along with the adjacent *hippocampus*, are important in facilitating spatio-temporal navigation as well as memory encoding and retrieval. Interestingly, the *schizocortex*—containing the presubiculum, parasubiculum, (involved in directing of head position and used in spatial navigation), and the enthorhinal cortex—also shares contiguity with these other spatial orientating neural areas. A renewed and expanded reconsideration of ASA, in both how and why the auditory scene is connected to specific cognitive systems, is contended. I propose that an ecologically relevant capacity for orientation within an organism's acoustic neighborhood [PIANO]—one comprised of uniquely (and perhaps musically) identifiable auditory stimulii—could plausibly run conterminously with the paralimbic system.

Emotive state, attention, and predation
Other less concerted parts—including the *pineale* (sleep/wake), *amygdala* (arousal/fear), and *hebernularis* (motivation/addiction)—exhibited strong associations with musical calling suggesting that states of emotive-arousal (no figure) were important early co-evolutionary factors shaping complex calling in primates. A complete evolutionary depiction should also account for related predation risk.

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