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1 **Is there any evidence for vocal learning in chimpanzee food calls?**

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12 In their study [1] published in *Current Biology*, “Vocal Learning in the Functionally
13 Referential Food Grunts of Chimpanzees”, Watson and colleagues claim (in the highlights
14 section) that they “provide the first evidence for vocal learning in a referential call in non-
15 humans”. We challenge this conclusion, based on two counts. Firstly, we are not convinced
16 that the authors controlled for arousal (or at least they did not report such data); secondly, the
17 vocal characteristics of the two groups largely overlapped already at the beginning of the
18 study. Accordingly, we also question the authors’ claim that their finding “sheds new light on
19 the evolutionary history of human referential words“.

20

21 Firstly, Watson et al. argue that “call structure was not tied to arousal as calls changed while
22 preferences stayed stable”. Given the theoretical and empirical basis for linking vocalization
23 structure (especially aspects related to frequency) to affective states [2], we agree with the
24 authors that controlling for arousal (degree of stimulation) is critical to their conclusion. If the
25 BB individuals were simply highly aroused by apples when they moved to Edinburgh
26 compared to ED individuals, and if this arousal declined over time, any changes to BB calls
27 would be best explained by simple habituation to a stimulus (apples). Watson et al.’s

28 conclusion relies on equating arousal and preference, which is fallacious. To demonstrate how
29 different these two are, imagine a human repeatedly offered his/her favorite food in a series of
30 choice trials (the authors' measure of preference). Regardless of how stable preference for
31 this food remains, this person is surely going to be more excited to have their favorite food for
32 the first time in months than for the third time in a week. No data are presented on apple
33 feeding rates that BB individuals experienced in the Netherlands vs Edinburgh. It is thus
34 plausible that BB individuals have an established preference for apples that is maintained,
35 while the apple feeding at Edinburgh Zoo nonetheless led to a reduced state of arousal over
36 time. A higher level of arousal of BB individuals at the start of the study could also be related
37 to more excitement or higher levels of stress due to feeding in new environments and social
38 contexts. Either way, it is important to rule out changes in arousal as the simplest explanation
39 for the results, by collecting data on other aspects of behaviour (e.g., self-directed behaviors
40 [3]) and/or physiology.

41

42 Secondly, there is an issue with the interpretation of the data. Despite the significant
43 interaction reported for year and group, we observed that only 7 calls from 3 subjects (out of a
44 total of 20 calls from 7 subjects) of the BB group recorded at the beginning of the study fell
45 outside 2 SD of the mean of the ED group (see Fig. 1). In other words, the majority of calls
46 did not differ in the first place, indicating that irrespective of their provenance, most subjects
47 of both populations had always responded with the general same call type to the presentation
48 of apples. Moreover, the pattern whereby BB group individuals give calls outside the range of
49 ED individuals does not convincingly converge when looking at the data (Fig. 1) – the 7 BB
50 calls outside the ED range before group integration (2010) becomes 5 calls outside the ED
51 range following integration (2013) – weak evidence at best. Obviously two groups of humans
52 from different linguistic backgrounds would most likely have entirely different words for the
53 same things, not vocalizations that largely overlap.

54

55 More generally, even if Watson et al. can provide new data that rule out the possibility that
56 the observed changes result from habituation to the stimulus or the novel social context, there
57 are still underlying conceptual issues that call into question the authors' suggested
58 implications of their findings. Specifically, we disagree that their study "challenges long-held
59 assumptions that [...] functionally referential primate calls cannot be decoupled from the
60 arousal state experienced by the signaler and are completely fixed in their acoustic structure".
61 There are two main problems with this statement. First, it's not clear how one plausibly
62 explains the observation that, at the beginning of the study, most individuals from the two
63 groups already produced the same call type in response to the same stimulus as anything other
64 than a reaction to the stimulus that is mediated by the affective state that the stimulus elicits.
65 Second, the authors create a straw man for themselves to knock down in stating that it is
66 assumed that functionally referential calls (FRC) are "completely fixed" structurally. The core
67 of the argument against FRC being a precursor to linguistic reference is that FRC do not
68 differ fundamentally from other call types [4], and the authors acknowledge the well-
69 documented variation in non-FRC types based on variation in the social environment. Indeed,
70 such modification of fine aspects of otherwise species-specific vocalizations has been shown
71 in a number of anthropoid primates [5], as well as goats (*Capra hircus*) [6]. Further, this
72 phenomenon is not limited to social influence, but has been documented in response to
73 changes in the physical environment [7]. The most generous conclusion to draw from the
74 Watson et al. study is that it provides additional evidence of an already well-documented
75 phenomenon: some terrestrial mammals (including chimpanzees; [5]) which appear unable to
76 learn unique call types in the way that vocal learners such as songbirds, cetaceans, and
77 humans can [8], have the ability to modify their species-specific call types within a limited
78 range. Watson et al. offer no new evidence to link this modest modifiability (of what appears
79 to be largely emotionally-driven call types) to the open, highly flexible system underpinning
80 language.
81

82 In sum, there is no conclusive evidence that chimpanzees alter their vocalizations in response
83 to auditory experience. Further, the purported evidence for limited vocal modification is like
84 that already seen in other call-types and in other taxa, leaving no new evidence that the so-
85 called “functionally referential signals” of chimpanzees or other taxa warrant special
86 consideration for understanding language evolution. If any such limited modification should
87 be considered vocal learning, we would ultimately need a new term to distinguish this from
88 the true matching of vocal output to a template, seen in true vocal learners such as songbirds,
89 dolphins, and humans. For future studies, we recommend critical inspection of the data to
90 ensure biologically-meaningful conclusions rather than relying solely on statistical
91 significance [9], a more careful consideration of plausible simpler explanations, and a greater
92 effort to distinguish the effects of affect from auditory experience.

93

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97

98 FIGURE LEGEND

99

100 Fig. 1. Individual values for the principal component for each individual and year. Light grey:
101 Edinburgh subjects; Dark grey: BB subjects. Dotted lines indicate minimum and maximum
102 values for the Edinburgh subjects. Details on the statistical analysis (calculation of the
103 principal component) can be found in the Supplementary Experimental Procedures.

104

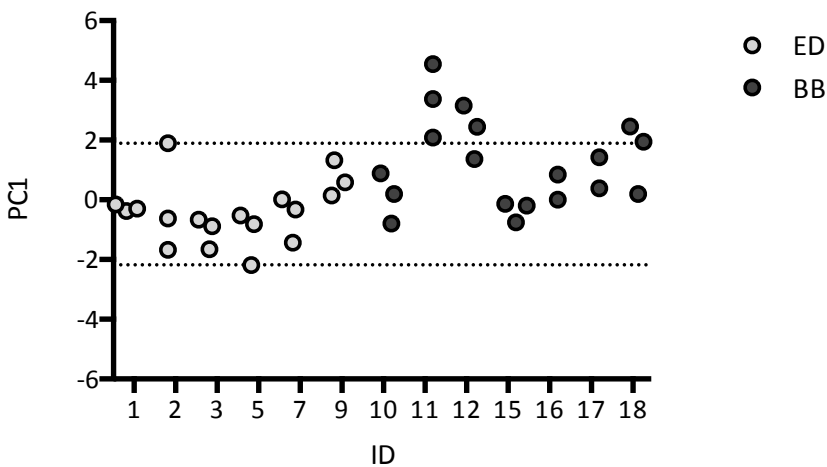
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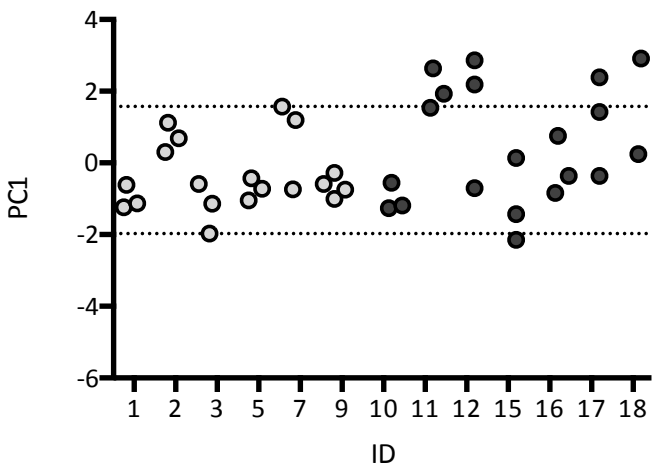
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- 129
- 130

Figure

2010



2011



2013

