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Reply to Fischer et al.

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We welcome the correspondence from Fischer and colleagues regarding our recent paper on vocal learning in chimpanzee food grunts [1]. Fischer *et al.* make two challenges to our paper's conclusions, which we address here.

First, Fischer *et al.* assert that we did not adequately control for the influence of arousal on call structure, arguing that excitement induced by a food may not depend on its preference value. They suggest initially high arousal elicited by apples decreased over time due to habituation, resulting in changes in food call structure. Conceptually, whilst we agree arousal could have additional effects, on-top of preference, with a favourite food (chosen all

the time, as Fischer *et al.*'s example), it is hard to explain in our study how any such initial excitement could have affected vocal behaviour but not translated into choosing this food more often during preference testing (BB chose apples on average 70% in both 2010 and 2013). We are not aware of any literature indicating arousal would selectively influence vocal behaviour independently of foraging behaviour. Importantly, we have now obtained the BB chimpanzees' feeding history and can confirm apples were a regular part of their diet in both Edinburgh and the Netherlands. Between 2007 and 2010, the BB chimpanzees were fed apples daily, routinely eliciting high-pitched tonal grunts (Hofmeijer, BB Senior Keeper, personal communication). We believe it is biologically implausible to propose that being regularly fed apples evoked high arousal in BB that was impervious to habituation from 2007 to 2011, yet suddenly resulted in lower arousal in 2013, despite a stable apple-feeding regime.

Fischer *et al.* also suggest that BB may have had a higher 'general' level of arousal upon their arrival, caused by their new physical and social environment, which could have resulted in heightened responses to all foods, decreasing over time. We think this is unlikely for several reasons: First, the ED chimpanzees also experienced a new social environment (11 new group members), which could have been relatively stressful for this territorial species, yet any associated change in arousal did not affect their call structure, which remained stable. Second, BB keepers recognised BB apple recordings from 2010 as typical of the high pitched grunts they routinely produced to apples at BB from 2007 to 2010 (Hofmeijer, personal communication), indicating that there were no noticeable changes in call structure associated with any increases in arousal induced by BB's new physical and social environment. Lastly, after a whole year of habituation to their new environment, in which BB arousal levels could be expected to fall, BB call structure had not converged with ED, with the two groups' calls remaining significantly different.

Arousal is commonly cited as an alternative proximate mechanism driving various aspects of animal call production. However, arousal itself is so poorly understood there are few limits to the effects researchers attribute to it, most of which are currently untestable in free-ranging, group-living animals. Given preference can be objectively measured and has previously been shown to have a significant effect on chimpanzee food call structure [2], we think preference remains the most relevant arousal-related measure to examine, and there does not seem to be a parsimonious account of how general arousal levels can explain our pattern of results.

Secondly, Fischer *et al.* question our interpretation of the data. Although Fischer *et al.* independently replicate our statistical findings, based on their revisualisation of the data, they argue: first, that the calls of the two groups were highly similar in 2010; and second, that there was only weak evidence for acoustic change. We disagree with this conclusion for the following reasons: Firstly, as chimpanzee food calls are graded signals and given individuals were heterogeneous in terms of age and sex, overlap between the groups on PC1, where frequency parameters loaded highly, was expected. The initial calls of the two groups were not completely different call types, but acoustically distinct calls within this graded call type. In keeping with the literature identifying acoustically distinct calls within graded vocal repertoires, we endorse the use of inferential rather than descriptive statistics (range; SD), to test whether, on average, call structure differs between groups or contexts. In order to assess if differences in call structure identified with inferential statistics are biologically meaningful, playback experiments are the gold standard method as they test if conspecifics can distinguish between call subtypes. Unfortunately it was not possible to complete experiments to test cross-group understanding of apple calls as intended in 2013 as calls of the two groups had converged by then. Secondly, it is difficult to estimate acoustic change in Fischer *et al.*'s Figure 1, as it is hard to visually match an individual's calls across years and hence track the

direction of individual acoustic shifts, which is central to our claim. To address this, in Figure 1, we revisualise the data to show on average how call structure of each individual from the two groups changed across years.

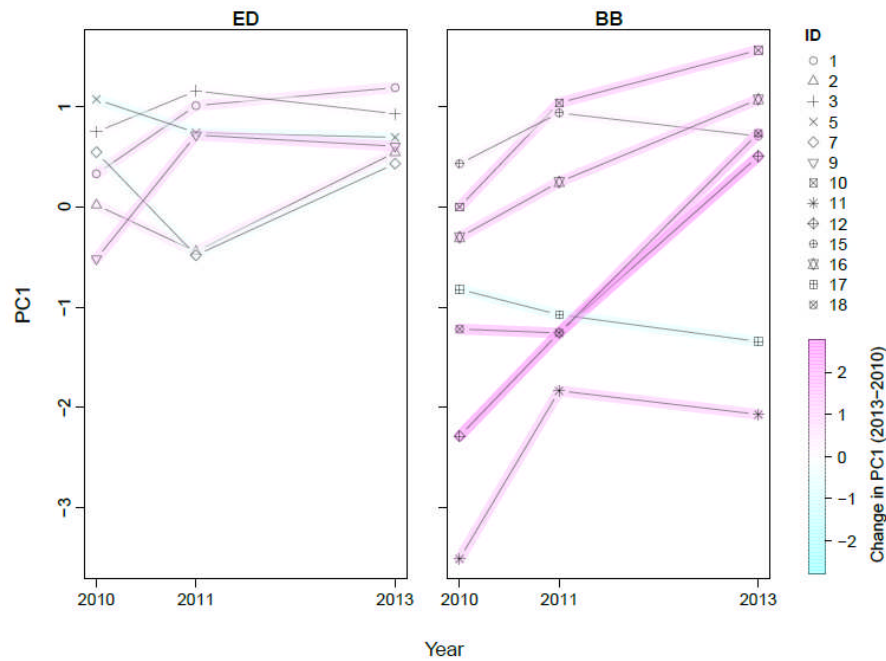


Figure 1: Change in PC1 values between 2010 and 2013 for ED and BB groups.

Each line represents an individual and colour indicates the degree of PC1 change (calculated by subtracting mean PC1/individual in 2010 from mean PC1/individual in 2013).

Finally, to test the robustness of our original result, we employed more conservative, non-parametric tests suited to dealing with small sample sizes. When averaging the PC1 values for every individual in each year, we found a significant between-group difference in acoustic structure in 2010, and not in 2013 (Exact Mann-Whitney U test, $N = 6$ versus 7 ; 2010: $U = 5$, $p = 0.02$; 2013: $U = 20$, $p = 0.95$). We also found a significant within-group change in the structure of BB food calls between 2010 and 2013 (Exact Wilcoxon Signed-Rank test: $N = 7$, $Z = -2.0$, $p = 0.047$), but not for the ED group (2010 versus 2013: $N = 6$, $Z = -1.36$, $p = 0.22$). Contrary to Fischer *et al.*'s critique, together these tests confirm: first, that

BB and ED call structures were significantly different in 2010; and second, that BB calls changed significantly over time.

Where we concur with Fischer *et al.* is that there is unexplained variation regarding how much each individual changed their calls over time. This requires further analysis, but one promising variable for future study is an individual's degree of social integration, which may influence their motivation to converge calls. Preliminary analyses showed a positive relationship between the BB individuals' degree of integration with the ED group and the magnitude of change in call structure ($R^2 = 0.4$; see Figure S1 in the Supplemental Information).

Finally, Fischer *et al.* challenge our interpretation of these findings as demonstrating the decoupling of call structure and affective state, as well as the implications this has for understanding language evolution. In 2010 the two groups had different preferences and therefore, we assume, different affective responses to apples. Following Fischer *et al.*'s argument that both groups produced the same call type in 2010, this would already show a decoupling of affective state and call structure. In contrast we argue our data, if analysed using inferential statistics, show that the two groups produced *differently* structured calls in line with their *different* preferences for apples in 2010. We agree, alone, these data support previous research linking the structure of these calls to affective state [2]. The critical finding is that these calls then changed in structure independently of food preferences.

Fischer *et al.* argue that we build a straw-man when suggesting that our findings overturn traditional assumptions that functionally referential calls (FRC) are 'completely fixed' in their acoustic structure. We welcome the chance to clarify that we were referring to the assumption that referential signals are structurally fixed *in relation to* arousal states. We believe this assumption is clearly presented in Wheeler and Fischer [3], who argue "...there

is a strong link between specific internal states and the corresponding vocalisations” (p.197) and “...the production of even highly context-specific vocalizations is hardwired...” (p.199). Given our study indicates FRC structure is modifiable through social learning, independent of preference for the referent, we maintain it represents a significant advance in understanding of FRC production. We do not claim that the observed modification in call structure is directly analogous to human word learning. Nevertheless, establishing that there is flexibility to alter call structure in this system supports FRCs as potentially important evolutionary *precursors* to socially learnt referential words that are so central to human communication.

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References

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Supplemental Information

Supplemental Figures

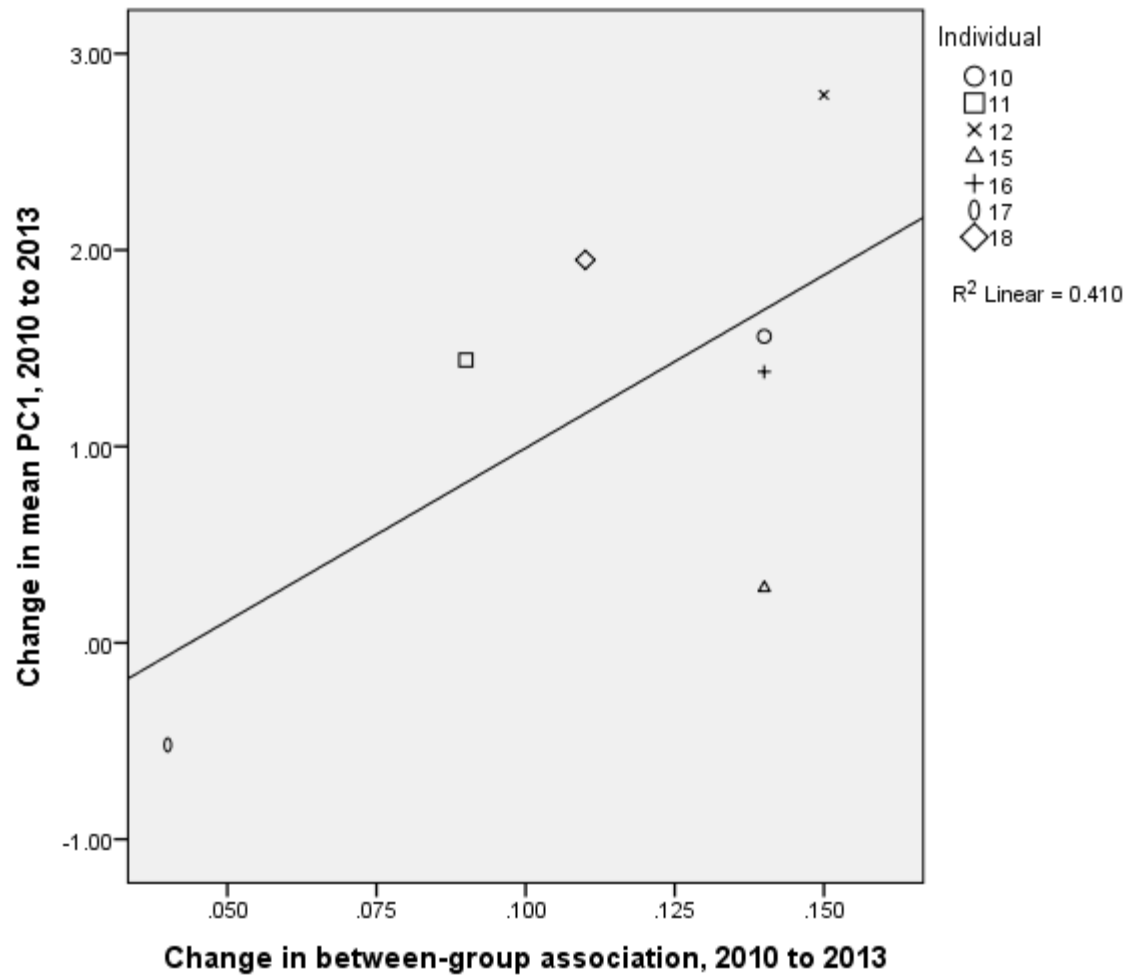


Figure S1. Scatterplot showing for each BB individual (N = 7) the relationship between the difference in mean PC1 between 2010 and 2013 (measure of acoustic change) and the change in between-group association for the same period. Between-group association was calculated from the dyadic composite association measures used in our Social Network Analysis [1], which comprised of rates of being in the same party and being nearest neighbours. In each year, for each BB individual we calculated a mean association value from all his/her dyadic association scores with each ED individual.