

OPEN Reply to 'Sigmoidal Acquisition **Curves are Good Indicators of Conformist Transmission'**

Alberto Acerbi¹, Edwin J. C. van Leeuwen 2^{2,3}, Daniel B. M. Haun⁴ & Claudio Tennie⁵

Accepted: 24 July 2018

Received: 13 March 2018

Published online: 18 September 2018

In the Smaldino et al. study 'Sigmoidal Acquisition Curves are Good Indicators of Conformist Transmission', our original findings regarding the conditional validity of using population-level sigmoidal acquisition curves as means to evidence individual-level conformity are contested. We acknowledge the identification of useful nuances, yet conclude that our original findings remain relevant for the study of conformist learning mechanisms.

Replying to: Smaldino, P. E., Aplin, L. M. & Farine, D. R. Sigmoidal Acquisition Curves Are Good Indicators of Conformist Transmission. Sci. Rep. 8, https://doi.org/10.1038/s41598-018-30248-5 (2018).

Smaldino, Aplin & Farine provide a thorough criticism of a series of models where we identified three scenarios producing a sigmoidal relationship between the frequency of a trait in a population and the probability to copy it (henceforth: the sigmoid), without a conformity bias at individual level^{2,3}:

- (1) When there is a preference for one cultural trait over the other (the condition "Variant Preference")².
- (2) When the (random) choice of demonstrators is limited to a subset of the population (the condition "Demonstrators subgroup")2.
- When copying probability is plotted against the cumulative frequency of behaviours in the population, rather than against the frequency of individuals showing the behaviour at each time step³.

Discussion

Regarding the scenario "Variant Preference", Smaldino et al. show that the sigmoid is produced (in part) because (i) the outputs of the simulations are averaged across all runs, and (ii) the simulations are initialised by randomly populating the individuals with one of the two variants. This is correct, but we do not believe these assumptions are problematic. First, we intended to show that experiments in which results of different runs are pooled together (as in the key empirical study considered by Smaldino et al.4) might produce the sigmoid in the absence of conformity, when a stable within-run preference for one of the two variants is present. Second, the decision to initialise randomly each individual in the population with one of the two variants was based on several empirical studies in which conformity was tested after many, if not all, individuals had obtained one or the other cultural variant (e.g.⁵⁻⁸). In a model not addressed by Smaldino et al., we additionally analysed a comparable scenario in which the sigmoid was caused by random initialisation, and we showed that similar results could be obtained when cultural variants were not randomly initialised but were diffused from a small part of the population^{3,9}.

Regarding the scenario "Demonstrators subgroup", Smaldino et al. provide a successful replication of our model. The fact that, to produce a sigmoid in absence of conformity at individual-level, the total group size and the total number of demonstrators should be relatively small is studied and reported in detail in our original contribution². Note that the scenario in which empiricists study small populations in which a small set of "leaders" may influence group dynamics (i.e., the model parameters under which the sigmoid may emerge in the absence of individual-level conformity) does not seem exceptional (e.g. 10,11). Our original finding thus means

¹Eindhoven University of Technology, School of Innovation Sciences, Eindhoven, 5600 MB, The Netherlands. ²University of St Andrews, School of Psychology & Neuroscience, Westburn Lane, St Andrews, Fife, KY16 9JP, United Kingdom. ³Max Planck Institute for Psycholinguistics, Wundtlaan 1, 6525 XD, Nijmegen, The Netherlands. ⁴University of Leipzig, Department of Early Child Development and Culture and Leipzig Research Center for Early Child Development, Jahnallee 59, Leipzig, 04109, Germany. 5 Department of Early Prehistory and Quaternary Ecology, University of Tübingen, 72074, Tübingen, Germany. Alberto Acerbi and Edwin J. C. van Leeuwen contributed equally. Correspondence and requests for materials should be addressed to A.A. (email: a.acerbi@tue.nl)

that the sigmoid cannot be taken as evidence for individual-level conformity unless the alternative mechanism of "copy-any-kind-of-subset of the population" (e.g. the dominants or experts) is ruled out. Such a discriminant analysis may not be complicated¹, but has, hitherto, been absent from many, if not all, conformity studies (e.g. ^{4,5,11,12}).

Finally, regarding the third scenario, Smaldino et al. state that (i) conforming to the majority of "instances" and "individuals" is functionally equivalent in all but the most exceptional of cases (based on^{4,13}), and (ii) the result that plotting instances as opposed to individuals can lead to an artefactual sigmoid is due to sampling from the entire history of events rather than from a subset. The first aspect refers to an open question. Here, we note that one example of converging results cannot resolve the issue¹³, and that, even in the study on which this assertion is based, there is a sub-population of birds in which following the majority of instances would lead conformists to adopt the opposing cultural variant from when they would follow the majority of individuals (see⁴, Figure 1C, control population "C2": the majority of instances points to option B, whereas the majority of individuals use option A). Regarding the second aspect - sampling from the entire history of events - we acknowledge that applying a limited time-window to the calculation of the observed distribution of traits may be sensible. At the same time, we note that, to our knowledge, there are no conformity studies other than Aplin et al.4 that apply any time-window for the calculation of observed trait distributions. In other words, our model concerns other conformity studies and Smaldino et al.'s results should be taken as a validation of our cautionary statements in this regard. Note also that the time window of ~2,000 observation events that Smaldino et al. identify as the threshold after which the sigmoid can be produced in absence of conformity is not that large, given that events in the models represent individual interactions. To put this into perspective, Smaldino et al.'s exemplary study in which a time-window (245 seconds) is applied presents evidence for the sigmoid based on more than 2,000 interactions (i.e., 367 birds observing a mean of 6 interactions, leading to a total number of 367*6=2,202 observation events). This means that the sigmoid as reported in Aplin et al.⁴ could have emerged in the absence of individual-level conformity.

Conclusion

Taken together, Smaldino *et al.* provide nuance to our original results without dismissing the conclusion of our studies^{2,3}: the sigmoid cannot be taken as evidence for individual-level conformity unless certain conditions are fulfilled. We have shown that these conditions are often violated in conformity research and encourage follow-up work on the equifinality of (sigmoidal) population-level signatures^{14,15}, in particular with respect to the nature of inference: population-level patterns may be best used to exclude, instead of evidence, individual-level processes^{16,17}.

References

- Smaldino, P. E., Aplin, L. M. & Farine, D. R. Do Sigmoidal Acquisition Curves Indicate Conformity? Sci. Rep. 8, https://doi. org/10.1038/s41598-018-30248-5 (2018).
- 2. Acerbi, A., van Leeuwen, E. J. C., Haun, D. B. M. & Tennie, C. Conformity cannot be identified based on population-level signatures. Sci. Rep. 6, 36068 (2016).
- 3. van Leeuwen, E. J. C., Acerbi, A., Kendal, R. L., Tennie, C. & Haun, D. B. M. A reappreciation of 'conformity'. *Anim. Behav.* 122, e5–e10 (2016).
- $4. \ \, Aplin, L. \, M. \, \textit{et al.} \, Experimentally induced innovations lead to persistent culture via conformity in wild birds. \, \textbf{518}, 538-541 \, (2015).$
- 5. Whiten, A., Horner, V. & de Waal, F. B. M. Conformity to cultural norms of tool use in chimpanzees. *Nature* 437, 737–740 (2005).
 6. Dindo, M., Whiten, A. & de Waal, F. B. M. In-Group Conformity Sustains Different Foraging Traditions in Capuchin Monkeys
- 6. Dindo, M., Whiten, A. & de Waal, F. B. M. In-Group Conformity Sustains Different Foraging Traditions in Capuchin Monkeys (Cebus apella). *PLoS One* 4, (2009).
- 7. Perry, S. Conformism in the food processing techniques of white-faced capuchin monkeys (Cebus capucinus). *Anim. Cogn.* 12, 705–716 (2009).
- 8. Wrangham, R. W. et al. Distribution of a Chimpanzee Social Custom Is Explained by Matrilineal Relationship Rather Than Conformity. Curr. Biol. 26, 3033–3037 (2016).
- 9. Acerbi, A. & van Leeuwen, E. J. C. Bugs and features. A reply to Smaldino et al. (2017). arXiv 1708, 07772 (2017).
- Kendal, R. L. et al. Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. Evol. Hum. Behav. 36, 65–72 (2015).
- 11. Battesti, M., Moreno, C., Joly, D. & Mery, F. Biased social transmission in Drosophila oviposition choice. *Behav. Ecol. Sociobiol.* **69**, 83–87 (2014).
- 12. van de Waal, E., Borgeaud, C. & Whiten, A. Potent Social Learning and Conformity Shape a Wild Primate's Foraging Decisions. *Science* (80-.). 340, 483–485 (2013).
- 13. Aplin, L. M. *et al.* Counting conformity: evaluating the units of information in frequency-dependent social learning. *Anim. Behav.* **110**, e5–e8 (2015).
- 14. Eriksson, K., Cownden, D. & Strimling, P. Social learning may lead to population level conformity without individual level frequency bias. Sci. Rep. 7, 17341 (2017).
- 15. Barrett, B. J. Equifinality in empirical studies of cultural transmission. *Behav. Processes* https://doi.org/10.1016/J.BEPROC.2018.01.011 (2018)
- 16. Kandler, A., Wilder, B. & Fortunato, L. Inferring individual-level processes from population-level patterns in cultural evolution. R. Soc. Open Sci. 4, 170949 (2017).
- 17. Kandler, A. & Powell, A. Generative inference for cultural evolution. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 373, 20170056 (2018).

Acknowledgements

The Netherlands Organisation for Scientific Research (NWO VIDI-grant 016.144312) supports the research of Alberto Acerbi. EJCvL is supported in the capacity of postdoctoral fellow by the Research Foundation Flanders (FWO). The research of Claudio Tennie is supported by a grant from the UK Economic and Social Research Council (ES/K008625/1).

Author Contributions

A.A. and E.J.C.v.L. wrote the paper, all authors discussed and commented on the manuscript.

Additional Information

Competing Interests: The authors declare no competing interests.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit https://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2018