

Questions and some Replies, Whiten NIMBios Webinar 13th October

Thanks to all who asked these interesting questions below. I think its not appropriate to try to provide full answers here – instead I am offering pointers to where you can find what I have already written about the issue raised, and in some cases I add suggestions of other key sources to explore. If you still have questions after reading these, feel free to email me at a.whiten@st-andrews.ac.uk and I'll try to find time to write further.

1. Do the traditions come in "packages" or are each of them independent from the others? Is there a concept that reflects this measure?

AW: Well first let's note that there has been debate about this in the human literature, and one overriding issue is what is going to count as a 'package' – see e.g. debates about 'memetics, and Boyd, R., Borgerhoff-Mulder, M., Durham, W. H. & Richerson, P. J. 1997 Are cultural phylogenies possible? In *Human by nature: between biology and the human sciences* (eds P. Weingart, P. J. Mitchell, P. J. Richerson & S. Maasen), pp. 355 –386. Mahwah, NJ: Lawrence Erlbaum Associates.

I first discussed this issue under the heading of 'linkage of traditions through core cultural ideas' in: Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. *Phil. Trans. R. Soc. B* 366, 997-1007 (or for a summary see Whiten, A. (2017) Social learning and culture in child and chimpanzee. *Annual Review of Psychology*, 68, 129-154), quoting a field study by Thibaud Gruber et al. that concluded "wild chimpanzees rely on [their] cultural knowledge to solve an experimental honey acquisition task", implying that such existing cultural knowledge shapes how they approach and assimilate a novel problem, the kind of phenomenon that may underly the formation of linked cultural 'packages'.

2. Does in-group/out-group play any role in chimp inter-group cultural diffusion (rather than just learning opportunities)? What is your sense of the current evidence concerning whether or not non-human animal culture includes social norms, i.e. rules that are stabilized by enforcement (including crucially, third party punishment)?

AW: There is experimental evidence for cultural diffusion within and between chimpanzee communities (e.g. summarised and cited in Whiten 2017 above). In the wild, nut-cracking using natural hammers appears present only in the most westerly populations, but there it has spread to multiple communities across Liberia, Côte d'Ivoire, Guinea and Liberia.

Turning to conformity to norms, its important to distinguish between statistical/descriptive norms (like 'copy the majority') and prescriptive norms defined by what an individual 'ought' to do. There is mounting evidence for conformity to majority norms across mammals, birds, fish and insects, reviewed in: Whiten, A. (2019). Conformity and over-imitation: an integrative review of variant forms of hyper-reliance on social learning. *Advances in the Study of Behavior*, 51, 31-75. In chimpanzees this includes evidence for females dispersing to new communities adopting the new local norms they experience. A recent study of bonobos by Samuni et al. even finds different prey preferences of neighbouring

communities within their overlap zone (Whiten, A. (2020). Does culture shape bonobo hunting behavior? Commentary on Samuni et al. *eLife* 9, e62104.

Do groupmates exert any pressures to conform? Much literature suggests not, but see the following (that I missed when writing the above review in *Advances!*), the relevance of which you can judge from its title: de Waal, FBM (2014) Natural normativity: The 'is' and 'ought' of animal behaviour. *Behaviour* 151, 185-204.

3. What is your response to the argument by Hill (in Laland et al 2009, "Question of Animal Culture") that the bar for using the term "culture" needs to be set not just at social learning, but also require the existence of norms & ritual, namely (a) valued expectations of behavior whereby social groups adjust evolutionary payoffs by cultural means, and (b) symbolic performances that reinforce them? On this account, unless and until norms and symbolic performances are present, we could talk about "animal traditions" rather than "culture".

AW: For norms, see Q2 above. My principal reply to this question focuses on 'needs to be set': I'd argue that there can never be any 'correct' definition of culture (or any other entity). In my chapter in *The Question of Animal Culture* edited by K Laland and BG Galef (2009) I suggested there are two main steps in any research focused around a question like "Does species X exhibit cultural phenomenon Y (e.g. culture, imitation, etc):" Step 1 is to define Y, and there is no empirical way to decide if that definition is 'true' – 'good' definitions are simply those that are clearly defined for the community using them: Step 2 is the crucial scientific, empirical step – once the phenomenon has been defined by the researchers in Step 1, its existence can be tested for using all the scientific and statistical tools available to us. My own view is that rather than obsessing about any 'correct' definition of terms like culture, its productive (especially if we are interested in evolution from elementary, to complex) to start with a broad definition then dissect and test for subcategories or more restricted senses of the term at stake. See Whiten references for Q1 for examples.

4. Alternatively, from the POV of cultural anthropology, one would reserve "culture" for social learning which relies on symbol systems employing arbitrary signs, such as language. Arbitrary symbol systems can easily refer to phenomena not immediately present (displacement), communicate about abstractions, and be used to generate new signs and combinations of signs with relative ease (productivity). As such, they could be expected to facilitate & co-evolve with cumulative cultural evolution. What, if any, research has there been in this direction?

AW: Following reply to Q3 above – well, one can specify language or symbol systems as necessary to one's definition of culture if one wants to, but that rather rules out non-verbal animals from the start, and I can't see how that helps us to gain any understanding of the evolutionary foundations of culture we can discern from comparative studies.

5. Would the horizontal spread of cultural traditions occur so readily in the wild, where chimps do a lot of their foraging separately, than in research facilities? Do you think most chimp culture is spread vertically - from mothers to offspring?

AW: See: - Whiten, A. & van de Waal, E. (2018). The pervasive role of social learning in primate lifetime development. *Behav. Ecol. Sociobiol.* 72, 80, where we distinguish three main phases. In the first, much initial learning is from the mother, who is the infant's principal caretaker in the case of great apes for several years. In

phase 2 as the social network expands, there is learning from others, both horizontal and oblique. In phase 3, when one or the other sex typically disperses to other groups around sexual maturity, there may be further learning from the new group about local resources etc. See also reply to Q2 above.

6. I'm curious what you think of the "zone of latent solutions" hypothesis, that animals often have the prerequisite behavioral topographies in their behavioral repertoire, and that social transmission facilitates the use of these repertoires in a new situation? i.e., the behavior isn't being directly transmitted socially, but it's something else about social groups that lets behaviors spread?

AW: The ZLS concept had its initial outing in a paper by C Tennie et al. in *Phil Trans B* in 2009. The editors invited contributions from the Tomasello group (that was Tennie et al.) and my group to discuss some of the differences emerging in our research on social learning and culture in human and non-human primates. In our paper we provided a critique of the ZLS concept as proposed then, on p in: -

Whiten, A., McGuigan, N., Hopper, L. M. & Marshall-Pescini, S. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society 'B'*, 364, 2417-2428. I have the new ZLS paper to hand but not read it yet! Intriguing that it's co-authored with two of my own sometime co-authors, one as above. So I will aim to write more on this later.

7. Given the evidence of culture in primates as well as Neanderthals, what do you think of the argument that our species really took off through a major transition in cooperation? In this account, our form of cumulative cultural evolution is contingent upon new "sociological" arrangements (i.e. Boehm's "reverse dominance" hypotheses). *Survival of the Friendliest* by Brian Hare and Vanessa Woods also points to self-domestication as the key distinguishing force between us and other hominum species.

AW: In - Whiten, A. & Erdal, D. (2012) The human socio-cognitive niche and its evolutionary origins. *Phil. Trans. R. Soc. B*, 367, 2119-2129 – we propose that, contra the earlier formulation of a 'cognitive niche', a mixture of evidence from human hunter-gathers and primates suggest five principal socio-cognitive 'pillars' in the transition: cooperation, sharing, egalitarianism, language and culture.

8. The main difference between human and non-human culture seems to be the cumulative nature of the first. What could be the reason for that? Or is there cumulative culture among non-human animals as well?

AW: See: - Whiten, A. (2019). Cultural evolution in animals. *Ann. Rev. Ecol. Evol. Syst.*, 50, 27-48 – in which I review the observational and experimental evidence for cultural evolution, and cumulative culture, in birds and mammals.

(this also cites a review of cultural evolution in birds by Lucy Aplin). I recommend you also watch the lecture on this topic by Nicolas Claidiere in our 'Animal Cultures' module.

What explains the massive gulf between our own cumulative cultures and anything seen in non-human animals? The dominant view, expressed at book length

by authors such as Tomasello, Henrich and Laland, is that the key is our high fidelity forms of social learning and teaching. For a recent opposing argument focused on individual cognitive capacities see the recent BBS paper, with peer commentary, by F Osuriak and Reynaud, 'The elephant in the room'. I think we should not lose sight of the possibility that there may not be great net benefits to be had by chimpanzees or other animals through significant cumulative material culture.

9. One issue here seems to be how culture is defined. Is it only social learning and the transmission of behavior, or is there something else involved, more even than cumulative culture, that perhaps depends on things like the psychological capacities of individuals (such as the recognition of self as both a distinct identity and simultaneously a member of a social group)?

AW: Social learning is essential for tradition and culture - Yet social learning may lead to neither – it may be merely transient in its effects, such as in the case of exploiting ephemeral resources. So social learning and culture are not the same thing. For more on definitions, see reply to Q3 above.

There is an interesting finding on the question of self-recognition. It was possible to test the imitative capacities of chimpanzees and an orangutan because they could learn to play the game of “Do this” (‘Do as I do’ – see references in Whiten 2017 in *Ann Rev Psychol*). However, several attempts to do the same with monkeys have failed. It seems that only great apes appreciate ‘what it is for them to imitate’ – and this does correlate with their ability to recognise themselves in a mirror, which monkeys seem not to grasp.

10. What is your sense of the current evidence concerning whether or not non-human animal culture includes social norms, i.e. rules that are stabilized by enforcement (including crucially, third party punishment)?

AW: This question was embedded in Q2 above.

11. Can we have a word why 'peering' as discussed in Schuppli & van Schaik 2019 is insufficient for social learning on your view?

AW: I am largely compelled by the controversial proposals made by these authors – see - Whiten, A. (2019). Social learning: Peering deeper into ape culture. *Curr. Biol.* (invited Dispatch on Schuppli & van Schaik) 29. R845-847. I think they fit with Whiten and van de Waal (see reply to Q5 above). However I think we can imagine situations in which a youngster peers at some event out of curiosity but does not necessarily socially learn something from it. I know from e-discussions with Caroline Schuppli that she has good answers to this concern but I can't relay them all here.

12. Given that culture is exceptionally advantageous in response to rapid environmental change, should we expect an explosion [explosion?] of animal cultures with the spread of anthropogenic climate change?

AW: Yes – evolution can be slow, including cultural evolution, but I suggested anthropogenic change might allow us to see changes, in analogy to the peppered

moth story, in - Whiten, A. (2017) A second inheritance system: The extension of biology through culture. *Royal Society Interface Focus* 7, 20160142. For a recent review on this see - T. Gruber *et al.*, Cultural change in animals: a flexible behavioural adaptation to human disturbance. *Palgrave Commun.* 5, 1–9 (2019).

13. The concept of transmission seems to be used in two ways, to describe radiation, and to describe "heredity" in cultural evolution (animals and humans). But transmission of a cultural innovation doesn't seem to explain the creation of the innovation in the first place. How do you see the innovations occurring in the first place?

AW: Yes, agreed. I would say the field has had a major focus on social learning rather than innovation, probably in part because of the theories noted above that here lies the principal human/non-human difference, and partly because social learning also happens to be the more tractable phenomenon to identify. In a classical social learning experiment we achieve the 'innovation' step by training a model to do X, then compare the performance of animals who see the model do X, or don't. So innovation is crying out for more study but that is very difficult. In studies of chimpanzees, Japanese monkeys and humpback whales, for example, where new innovations are noted and their subsequent spread recorded, the innovation has already occurred when first seen. See for example an amazing field effort by Susan Perry *et al.* (2017) Older sociable capuchins invent more social behaviors, but younger monkeys innovate more in other contexts. *PNAS* 114, 7806-7813. The 'magic moment' of an innovation is difficult to observe and record. I'm not aware we have much idea of how the brain innovates.

14. What do you think is the most basic mechanism for social learning? Mirror neurons and pattern habituation?

AW: There are several alternative taxonomies of types of social learning in the literature, e.g. see Whiten *et al.* 2009 cited above for Q6 – and see the lecture by Alex Thornton in our online module on Animal Cultures. The simplest forms are often taken to be stimulus enhancement, where the actions of one individual simply draws attention to an object such as a food item, and local enhancement where attention is similarly drawn to a location. These would seem to require only the associative learning capacities widespread in animals, except that here its not one's own actions that are 'associated', but those of others.

15. Andy, you jump from endothermic vertebrates 'down' to fishes. But what about reptiles (and even dinosaurs) and their role in the evolution of culture, since social learning has been demonstrated in several species of nonavian reptiles?

AW: Yes indeed. To illustrate the recent productivity of research on animal social learning, Jeff Galef and I tabulate over 100 papers published just in 2012-2014 and these included reports of social learning in reptiles (skink) as well as crustacea (crabs), molluscs (cuttlefish, octopus) as well as insects (Galef, B. G., Jr., & Whiten, A. (2017). The comparative psychology of social learning. In J. Call (Ed.), G. Burghardt, I. Pepperberg, C. Snowdon, & T. Zentall (Assoc. Eds.), *APA Handbook of Comparative Psychology*. pp. 411-440. Washington, DC: American Psychological Association.

So if we had a time machine I would be surprised if we went back to watch dinosaurs and there was no social learning!

16. How could model-based social learning affect the formation or maintenance of traditions?

AW: I take it this is a question about what are sometimes called social learning strategies or transmission biases, in this case where the biases concern properties of the model learned from? There is a recent comprehensive review on this and other adaptive biases - R. Kendal *et al.*, Social learning strategies: bridge-building between disciplines. *Tr. Ecol. Evol.* **22**, 651-655 (2018). Such biases can refine social learning to be most effective – e.g. E. B. Ottoni, B. D. de Resende, P. Izar, Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Animal Cognition*, **8**, 215-219 (2005). Patricia Izar will talk later in the NIMBios webinar series.

17. Two days ago, Tennie et al. published 'The zone of latent solutions [ZLS] and its relevance to understanding ape cultures.' Since the ZLS is becoming increasingly prominent in the literature and gains followers, what would you say will be its role in future research in the field?

AW: see reply to Q6.

18. Should we take "social learning" to be a basic/single psychological mechanism, or would it be fruitful to distinguish between different forms of social learning?

AW: see reply to Q13, 14..