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Action replication ultimately supports all cultural transmission

I am thankful to Moore [1], Whiten [2], Weissing and Daras [3], Dor [4] and Croft [5] for their insightful commentaries. I am delighted that there was general agreement with the central idea that action copying plays a role in transmission. In this response I take advantage of the diversity of the remarks to clarify some of the points made in the target article.

Two of the comments expressed concern about the sharp separation between replication of actions and emergence of mental ideas in the Replication and Emergence (henceforth R&E) model presented in the target article: Whiten [2] and Weissing and Daras [3] wonder whether action replication must be content-indifferent, that is, take place independently of function, while Moore [1] argues that the developmental trajectory from action replication to emergence needs not be strictly ordered. I re-emphasize here why R&E posits that action replication is necessary to sustain human cumulative cultural lineages and that action replication must happen independently of emergence, while I agree with Moore [1] that strict ordering is not essential. A key corollary of the R&E model is that content-oriented imitation (emulation) alone cannot support human cumulative cultural evolution. This does not mean that all action copying in humans is content-indifferent replication, but it does mean that content-indifferent replication must be part of an explanation of human-typical cumulative cultural evolution. Csibra and Gergely [6] argued that pedagogy has evolved in our species as an adaptation that enables the transmission of opaque cultural traits. I use here a similar logic to argue that content-indifferent action replication is another, more basic adaptation to the same end. Let us first look at *transparent* cultural traits. Here, the causal relationship between action and outcome is readily observable. Examples include sweeping the floor, putting a coin in a slot to start a machine playing and the cultural traditions observed in chimpanzees such as ant-fishing or fanning away flies with a leafy stick [7]. Upon observing a transparent action, learners immediately understand what the outcome is, and therefore the emergence of the mental association between action and function may start during observation, at the same time as, or even before action copying. As Moore [1] points out, this does not significantly change the essence of the R&E model. In addition, when copying a transparent action, emergence does not need to be a purely individual process --it may involve vicarious, observational learning. Consequently, copying transparent actions may not be completely content-indifferent or independent of emergence, as the immediate understanding that the action will lead to the outcome may cause the learner to expect, or even to intend, that the outcome is obtained by producing the action. Things are very different for opaque cultural traits, in which the relationship between action and outcome is not readily observable, and can be extremely complex and indirect. Opaque traits are rarely, if ever, found in non-human primates; they are the hallmark of human cumulative cultural evolution [6]. I will use generosity as an example trait. There is not a unique action that clearly corresponds to this trait; instead, many actions contribute to its emergence as a concept in an individual's mind. One of those actions may be giving money to a street musician. In a population of emulators (such as chimpanzees), who focus on outcomes and do not copy actions that they perceive to causally irrelevant [8], opaque actions will not persist. Putting a coin in a hat does not *seem*, to the naive observer, to add anything of value (the musician does not stop playing if they are not given money), and it is costly. An emulator simply wanting to listen to the music would therefore omit that step. In contrast, in a population of content-indifferent action copiers such as humans, who focus on forms, opaque actions will be replicated -and performed, observed by fresh individuals, replicated again and so on over generations. In fact, if they stopped to think rationally, they may decide not to copy costly, seemingly useless actions (they would behave like emulators). Individual learners may or may not go on to develop a full understanding of

the function or causality of actions, but they will replicate them nevertheless. As actions are transmitted unchanged, the corresponding mental constructs are also transmitted, but they may change depending on the circumstances --two children raised in families who always give money to street musicians may replicate the same action, but this action may contribute to the emergence of generosity with solidarity in one case and generosity with contempt in the other if the contexts are different enough. While the associated emergent ideas do not form a true cultural lineage, the actions do. This is why R&E posits that action replication, independent of the emergence of mental entities, is necessary to sustain human cumulative cultural lineages.

While agreeing that action copying has a place in cultural transmission, two of the commentaries suggest that the kind of action replication and emergence described in the target article only captures early cultural transmission [3] or pre-linguistic, mimetic cultural evolution [4]. It is also pointed out [3] that replication and emergence's role is small compared to that of social-cognitive functions like language, intention reading and pedagogy. They emphasize that language in particular canalizes the emergence of mental states, facilitating for example learning complex skill learning, and transmitting mental states directly without replication, via emergence. Undoubtedly, language is an extremely powerful mechanism of cultural transmission, but we cannot forget that language is also itself culturally transmitted through replication and emergence. Phonemes in the native language are copied very faithfully [9] in a content-indifferent way (necessarily so, as phonemes have no meaning). Observed word-forms and phrases are produced before their meaning emerges in the speaker's mind, and it is only through interactive usage that meaning emerges in learners' minds [10]. The appearance of language in humans represented a major cultural evolutionary transition --just like the advent of eukariotic cells or sexual reproduction were biological evolutionary transitions [11]-- and as such it changed the way in which information is transmitted. However, language did not *replace* action replication; it evolved culturally in a system that relied on action replication --just like eukariotes and sexual reproduction did not replace genetic transmission; rather, it emerged in a system that relied on genetic transmission. Consequently, it makes little sense to say that language, and not replication and emergence, supports cultural transmission, or that language can transmit mental ideas 'directly', bypassing action replication. Language enables forms of communication that have transformed culture, but, importantly, not all cultural transmission needs language (rituals, skills, dance, language itself are illustrative examples; and studies on the necessity and usefulness of language for technology are inconclusive [12,13]). Culture, or at least some domains of culture, therefore, can exist in the absence of language. Language is therefore not necessary for human cumulative culture, in the same way that sexual reproduction and the eukariotic nucleus are not necessary for life (even if they open up very interesting evolutionary avenues in culture and in life, respectively). The above argumentation can be applied to factors other than language that also facilitate, augment or radically transform action-replication-based cultural transmission such as pedagogy [6], intention-reading [14], goal-directed behaviour [15] or an extended childhood [16]. These factors are in fact increasingly viewed as the outcomes of culture-gene co-evolution (e.g. [17]). All of this reinforces the point made in the target article that the R&E model does not explain *all* the processes that occur in cultural transmission (such as those catalyzed by language, pedagogy and other social cognitive factors). But it does account for the low-level processes of action copying and fully understanding the actions' function that are present in *all* cultural transmission (not only at early or pre-linguistic stages) to new individuals.

Dor [4] and Croft [5] also frame their criticism around language. Dor [4] is unsatisfied with one consequence of emergence as characterized in the R&E model, namely that it does not achieve the complete convergence of mental ideas, in particular linguistic

meanings, between individuals. He argues, in opposition to this, that language actually achieves the replication of mental culture. The R&E model is clear in this respect. Only public, observable information can be replicated by humans. We do not possess a mechanism capable of replicating mental content 'directly', that is, in a way that does not violate the criteria of information transfer and causality. Croft [5] takes issue with the distinction between inheritance and usage, which is central to the R&E model. In Croft's view [18], every time a word, sound, grammatical construction is produced (whether during learning or usage), it is replicated. He contrasts this with the R&E position, whereby inheritance is replication, but usage is emergent. I do not see a conflict of substance, but one of focus. While Croft's aim is to highlight that usage, the goal-oriented production of actions by experts, is replicative [18], the aim of the R&E model is to highlight that inheritance, the inter-individual process that underlies cultural transmission to new individuals, is replicative. The R&E model does not deny that usage involves replication. But the kind of replication that takes place in usage is only relevant to cultural inheritance if the expert is observed by a learner. This can be illustrated with reference to replication in sexually reproducing organisms: genetic material is constantly being replicated within an organism, each time a cell divides. This happens in all cells, including the gametes (although the replication mechanisms are different in somatic cells and gametes, DNA is replicated in both cases). But there is something evolutionarily significant about replication in the gametes that is missing from somatic cells: it may give rise to a new individual organism. Croft's work [18] focuses on how selection operates during usage in context, and for this he does not need to be overly concerned with the different role of learners and experts. The R&E model focuses on how culture is transmitted to new individuals, and it places a large explanatory load on the distinction between production by learners during inheritance and production by experts during usage. Incidentally, Croft understands that in the R&E model "usage is emergent" [5]. To clarify, in R&E, usage involves both replication and emergence: actions are replicated (in the intra-individual sense explained above) *and*, over multiple instances of replication, the function, or meaning, or value of the actions emerge in the mind of the learner (who is now in the process of beginning an expert).

To conclude, evolutionary theories differ greatly in the importance they give to replicators, the environment or phenotypes. As pointed out by Weissing and Daras [3], replicators only play a marginal role in modern evolutionary frameworks. However, no framework excludes replicators from explanations of evolution. *No matter how small its role*, without DNA, life as we know it, lineages of descent with modification of traits and organisms would not be sustained. Action replication is proposed as a very basic, low-level mechanism of cultural transmission. Like biological replicators, replicated actions do not explain all of culture at all levels. Nevertheless, the target article posits, against those denying a role to replication in cultural transmission, that action replication is an indispensable element of cultural transmission - ultimately, at the lowest possible level, it underlies all of culture.

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