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Even under majority influence, great apes fail to copy novel actions

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Abstract

It remains unclear when and why the ability to copy actions evolved and also its uniqueness to humans. Thus far, a lack of valid evidence for spontaneous action copying by other apes supports the view that only humans spontaneously copy actions. However, wild apes have access to multiple demonstrators and have been demonstrated to be affected by majority influences, thus raising the possibility that ape action copying might require a majority ratio of demonstrators to observers. We tested for spontaneous ape action copying across all four non-human great ape species using a demonstrator majority. Nineteen captive mother-reared apes (across 4 species) were tested ($R_{age}=9-52$; $M_{age}=18.63$; ♀=14; ♂=5). All failed to copy the demonstrated actions, despite observing it in a majority influence condition. We conclude that culture in non-human great apes is more likely supported by variants of social learning which regulate frequencies, rather than forms, of observed behaviours.

Significance Statement

This research is presented at a time when the United Nations have recently placed an example of ape culture as a factor to be conserved through protected heritage sites. There is no question that ape cultures exist, but the nature of their culture remains in question. Our own culture often relies on the ability to copy novel actions, it has been shown that some or all of ape cultural variants do not *require* social learning, in any form, to occur in naïve populations. However, the question remains, do great apes have the capacity to copy novel actions? The answer to this question will allow us to draw phylogenetically informed conclusions about our own evolutionary past.

Introduction

The cumulative cultural evolution of human behaviour has allowed our species to populate an impressively wide range of habitats as well as manipulate our environments on an unprecedented scale. Although cumulative culture has been defined in multiple ways, most consider it to consist of changes in behavioural forms (or forms of artefacts) across time that increase in complexity or efficiency, until they are beyond the learning capacity of an individual to acquire in their lifetime (Boyd & Richerson, 1996; Tomasello, 1999). Consequentially, one important social learning mechanism argued to be necessary for cumulative culture is the ability to copy others' behavioural forms, known as 'action copying' or 'imitation' (Galef, 1992; Tennie et al., 2009); though this does not mean that other mechanisms are unimportant (Osiurak & Reynaud, 2020; Sperber, 2000). For clarity, here we define imitation/action copying *sensu* (Whiten, 1998; Whiten et al., 2004; Whiten & Vallejo, 2016): that is, assuming imitation requires that the *actions* of a demonstrator/model are copied, rather than the results (which would enter the realms of emulation). Novel action copying appears necessary for many aspects of human cumulative culture, including some aspects of 'material culture', but particularly for cultural practices that consist only of actions, e.g. dances and sign languages (Legare & Nielsen, 2015). The term 'material' refers to those cultural variants with physical results/artefacts (McGrew, 1991), and thus contrast with the aforementioned action based practices.

It is necessary to consider whether the material culture of non-human great apes (hereafter: apes) is based on action copying. The answer to such a question would provide an indication of whether the last common ancestor of extant humans and apes was also capable of action copying (Tennie et al., 2017). The first question is relevant to the ongoing, and now somewhat classical, debate about the proposed uniqueness of human culture (contrast Tomasello, 1998; Whiten & Custance, 1996). Whereas, the second question is relevant for the

more contemporary issue of determining the timeline of the emergence of cumulative culture in our lineage and the evolutionary pressures shaping it (Stout et al., 2019; contrast Tennie et al., 2017). From an evolutionary perspective, although the fossil record provides evidence of the *outcomes* of material culture (e.g., stone tools), the social behaviours resulting in these outcomes do not fossilise. Great apes, in this respect represent an important opportunity to examine the cognitive and behavioural processes underlying material culture, by acting as imperfect, but phylogenetically relevant ‘model’ for our ancestors.

Attempts have been made to identify the social learning mechanisms underlying ape material culture, this has often resulted in the conclusion that action copying is a necessarily underlies its transmission and maintenance (Boesch, 1991; Byrne, 2007; Whiten, 2000; Whiten et al., 1999; Whiten & Vallejo, 2016). This said, an increasing body of evidence indicates that many, if not all, social aspects of *non*-human material culture do not *require* imitation (Bandini & Tennie, 2017; Menzel et al., 2013; Motes-Rodrigo et al., 2019; Neadle et al., 2017; Tennie et al., 2008). The overwhelming conclusion of these studies is that individual learning (catalysed by social information; so-called “socially mediated serial reinnovations” Bandini & Tennie, 2017, p. 13) is sufficient to explain the specific forms of ape cultural behaviours (see also Tennie, Bandini, et al., 2020). Given the controversy, the question remains, are our closest living relatives capable of copying actions for material culture? But also, and perhaps more importantly, if they are, what would be the socio-ecological circumstances that would drive them to apply this specific social learning mechanism?

There exist several theoretical explanations (see a recent review Osiurak & Reynaud, 2020) that attempts to harmonise the lack of imitative capacity in apes with the observed geographical patterns in putative cultural traits (Hohmann & Fruth, 2003; Robbins et al., 2016; van Schaik et al., 2003; Whiten et al., 1999)(Hohmann & Fruth, 2003; Robbins et al.,

2016; van Schaik et al., 2003; Whiten et al., 1999). However, various scholars have questioned the idea of apes' imitative capacities and imitation's relevance to ape cultures/traditions (Galef, 2015; Kendal, 2008; McGrew, 2002; Tennie et al., 2009; Tennie, Bandini, et al., 2020). A theoretical account that dispels the idea of non-human imitation is the Zone of Latent Solutions (ZLS) hypothesis (Tennie et al., 2009; Tennie, Bandini, et al., 2020; Tennie, Hopper, et al., 2020). The ZLS predicts that, given appropriate social, ecological and nutritional settings, individual apes are able to individually develop ("reinnovate"; Bandini & Tennie, 2018) the forms required to express their material culture. One prediction of the ZLS hypothesis is therefore that ape material culture should occur even in the absence of action copying. A number of studies, from various research groups, do indeed show that some forms of non-human material culture can be individually reinnovated by apes in the absence of action copying or even any social learning (Bandini & Tennie, 2017, 2019; Huffman et al., 2010; Lonsdorf et al., 2009; Menzel et al., 2013; Meriel et al., 2020; Motes-Rodrigo et al., 2019; Neadle et al., 2017; Sherry & Galef, 1984; Visalberghi, 1987).

This said, even the ZLS hypothesis does not suggest that non-imitative forms of social learning are absent from ape culture (e.g., local enhancement or stimulus enhancement). Instead of transmitting the behavioural form ("know-how"; Bandini et al., 2020), these social learning variants – while often present – instead transmit other types of relevant knowledge: for example, 'know-where' (e.g., where to find nuts) or 'know-what' (e.g., what type of hammer to use). Whilst it is clear that social learning does occur in these instances (Eshchar et al., 2016; Luncz et al., 2012), these mechanisms cannot convey information about the 'know-how'. 'Know-how' transfer either requires language (as in modern humans; Dunbar, 1996), form teaching (Tennie, Bandini, et al., 2020; Zwirner & Thornton, 2015) or the ability

for observers to copy the behavioural form itself – i.e., an ability to copy the underlying actions (imitation; Tennie, Hopper, et al., 2020).

However, even in the absence of action form transmission (as expressions of ‘know-how’), the transmission of other types of knowledge (e.g., ‘know-what’) has lasting effects on the distribution of behaviours within populations and may even lead to approximations of human culture (Caldwell & Millen, 2009; Reindl et al., 2017; Zwirner & Thornton, 2015). These mechanisms can therefore explain the emergence and maintenance of the rich great ape cultures we see today (Hohmann & Fruth, 2003; Robbins et al., 2016; van Schaik et al., 2003; Whiten et al., 1999) and regulate the relative frequencies of expressed ‘know-how’ in apes, but without the need to culturally transmit this ‘know-how’ itself (Bandini & Tennie, 2017; Neadle et al., 2017; Tennie et al., 2009; Tennie, Hopper, et al., 2020). This view differs from the ‘action copying hypothesis’ which claims that, in addition to these other types of knowledge, apes also transmit the ‘know-how’ itself by copying actions (Whiten, 2017; Whiten et al., 1999). Suffice to say, neither the action copying nor the ZLS hypothesis rejects the existence of ape cultures. Where these accounts differ is in whether these cultural patterns have been interpreted as direct evidence for a capacity for/reliance on action copying by adherents of the ape action copying hypothesis (Boesch, 1991; Byrne, 2007; Whiten, 2000; Whiten et al., 1999; Whiten & Vallejo, 2016) whilst the ZLS makes no such assumption.

The essence of this debate then can be reduced to the question of whether or not apes copy action forms. Given that the presence of action copying in wild ape cultures is not a necessary conclusion, further experimental studies are required to solve this debate. Several studies have claimed to have identified action copying in apes, but all of these studies incur confounds (Call, 2001; Galef, 2015; Russon & Galdikas, 1993; Tomasello et al., 1993; Whiten et al., 2005). Some conclusions derive from data collected from individuals that have

been trained/formally conditioned to copy or approximate it (Call, 2001; Tomasello et al., 1993). Such data may be useful when the task is to consider theoretically developable capacities of apes, however they lack ecological validity and relevance to wild apes, which lack this exposure. Studies that seek to understand the capacity of apes, in their natural state, should avoid a protocol that involves training the subjects; though, it should be recognised that there is a necessary trade-off between methodological rigour (to specify exactly social learning mechanisms) and ecological validity (Kendal et al., 2010). Meanwhile, other claims are based on anecdotal reports (Russon & Galdikas, 1993), which may lack the scientific rigour expected to support such a controversial claim.

One of the most common claims for imitation derives from the results of so-called “two-target” (Tennie et al., 2010) or “two-action” (Whiten & Custance, 1996) tests. These tests fail to methodologically discriminate action copying from other variants of social learning (Whiten et al., 2004). Instead of learning the behavioural forms needed to get to a reward/complete a task, these tasks allow observers to augment technical reasoning with environmental results. In this way observers could have copied ‘know-where’ knowledge (i.e., where an object moved to; e.g., Kis et al., 2015), and/or the forms that environmental changes took in the task (object movement re-enactment; Custance et al., 2001). Overall, two-target tests do not necessitate the copying of the demonstrated *actions* and therefore fail to isolate action form copying. Indeed, even when solutions of two-target tests were demonstrated, in the absence of actions, thus rendering imitation impossible, (so-called ‘ghost’ conditions), apes still show evidence of copying (Hopper et al., 2008).

Instead, to elucidate whether apes copy actions, other types of tests are required; specifically, controlled tests that are designed to address whether apes isolate action copying. The necessary tests must be those with tasks that are *only* ‘solvable’ if actions are clearly copied and other types of information (e.g., ‘know-where’, ‘know-what’, object movements)

are experimentally be rendered unsuitable/unavailable. We might refer to these as ‘action-only’ or ‘pure action’ tasks.

To date, several ape studies using action-only tasks have been conducted. However, in some of these tests, apes who have been specifically trained in action copying were included (i.e., the Do As I Do paradigm; e.g., Custance et al., 1995; Hayes & Hayes, 1952; Hribar et al., 2014). With the inclusion of such extreme levels of past human interference, the tested apes in these studies reached some statistically detectable level of action copying performance (though the level of novel action copying remained imprecise; Huber et al., 2009). But, as human training is absent in wild apes (Henrich & Tennie, 2017) these types of data must be supplemented by more ecologically-valid tests. But even when untrained apes are tested, it is important that the demonstrated actions are novel (Whiten, 1998), or at least not actions that the observer apes would attempt to use on their own, without demonstrations (Tennie et al., 2012; Tennie, Bandini, et al., 2020). This is necessary to control for potential alternative explanations (such as response facilitation; Byrne, 1994; Tomasello, 1996) and also because the claim of the action-copying hypothesis is that the underlying actions must require copying to come about (compare Whiten et al., 1999).

To our knowledge, only three ape action copying experiments (all *Pan*) have fulfilled these criteria, i.e., have tested untrained apes in action-only tests, using novel action forms for demonstrations (Clay & Tennie, 2017; Tennie et al., 2012; Tomasello et al., 1997). Of the 69 tested apes across these three studies, none showed any evidence of novel action copying. This is in stark contrast to human children (3-5 years of age), who, when tested under the same paradigm, copied the demonstrated actions reliably (Clay & Tennie, 2017): 77% of human children copied at least one of the “uncommon” demonstrated actions, compared to 0% of bonobos (aged 3-29 years). A lack of evidence in 69 untrained apes to spontaneously copy novel actions suggests that, rather than depending on action copying (as the action

copying hypothesis claims), apes must derive the specific forms of their actions individually. A conclusion consistent with the Zone of Latent Solutions hypothesis (which predicts lack of action form copying; Tennie et al., 2009; Tennie, Bandini, et al., 2020; Tennie, Hopper, et al., 2020).

All three, ape action-only, studies performed so far used *individual* demonstrators to perform target action forms. However, where cultural variants are “customary” or even “habitual” in the wild, it is instead a plurality of apes that will perform the relevant actions. This might occur either simultaneously or near-simultaneously (as in Figure 1 in Inoue-Nakamura & Matsuzawa, 1997) or over time (e.g., observer A might see individuals X, Y and Z all cracking nuts over the course of a longer time period – as would likely be the case for “customary” or “habitual” behaviours; Whiten et al., 1999, 2001). In this way, observers are generally outnumbered by potential demonstrators, who will demonstrate specific actions – creating a potential for a majority bias (or even for a conformity bias, see S1 for distinction). It therefore remains possible that wild apes do copy actions, but that past experiments have been unable to detect ape action copying due to not incorporating a majority bias into demonstrations. Thus far, the influence that multiple demonstrators might have on the spontaneous action copying of apes remains unstudied. This lack of data is especially problematic given that majority biases result in marked effects on both human and chimpanzee social learning (e.g., Haun et al., 2014). That is, a majority effect has already been shown for other social learning mechanisms in at least one ape species (Pan troglodytes; Watson, Botting, et al., 2018). These social learning biases are not restricted to apes, or even to primates more generally (e.g., vervet monkeys; *Chlorocebus pygerythrus*; E. Van de Waal et al., 2013). Rather, a range of species show majority biases, from fruit flies (*Drosophila melanogaster*; Danchin et al., 2018) to fish (*Pungitius pungitius*; Pike & Laland, 2010). Perhaps most importantly for current purposes, a majority bias for know-what information

has also been found in wild chimpanzee hammer material selection (Luncz & Boesch, 2014). We therefore hypothesised that majority bias might be a necessary, additional, element to elicit the so-far elusive evidence of spontaneous ape action copying.

In the current study, we addressed the majority-bias gap in the ape action-only demonstration literature, by conducting a controlled experiment, which included a majority demonstration. In this way we tested the four non-human great ape species for action copying (*Pan troglodytes*, *Pan paniscus*, *Pongo abelii* and *Gorilla gorilla gorilla*). In order to ensure a valid test of spontaneous ape action copying, we employed a novel action-only task where to ‘pass’ the task, observers were required to copy the form of demonstrated actions.). In particular, demonstrators (four humans), who were in a majority over the ape subjects, showed the subjects (N = 33, of which 19 were mother-reared) two novel actions (which do not appear in ape baselines but do appear in related tests with human children; Clay & Tennie, 2017). These actions were gestures, performed either on top of or in the proximity of a puzzle box, before opening the box to reveal a reward. Subjects were then passed a puzzle box, matched in appearance to the box used by demonstrators. We observed the subjects to ascertain whether they copied or even approximated either of the demonstrated actions. Given our usage of an action-only test method, using novel action forms, any such case would provide strong evidence for the apes’ ability to copy novel actions.

Evidence of a single, untrained ape copying novel actions in our study would provide the necessary evidence for the action copying hypothesis of ape cultures, albeit under the conditions of a majority bias. It would also suggest that previous controlled tests for ape action copying (Clay & Tennie, 2017; Tennie et al., 2012; Tomasello et al., 1997) may have failed to detect copying because these earlier tested apes lacked multiple demonstrators/demonstrations. By contrast, human children will already reliably copy actions in action-only tests (and at near ceiling rates) with just a single demonstrator (e.g., Clay et al.,

2018; Clay & Tennie, 2017). It is for this reason that we did not include a further human comparison here (it can be assumed that children continue to copy under majority demonstrations conditions). Conversely, failure of all of these untrained apes to copy novel actions – despite majority demonstrations – would be inconsistent with the assertion that ape culture *requires* action copying (Whiten et al., 1999).

263 **Methods**

264 Given the controversy of action copying in apes debate (Kendal, 2008; McGrew, 265 2002), we pre-registered our study design to the Open Science Framework (Neadle et al., 266 2018). Notably, no major methodological deviations from our registered plan were required 267 (minor deviations are described in text). Our pre-registered study was designed to follow a 268 result-dependent design: the methods included a decision tree, such that the particular 269 protocol implemented depended on whether or not evidence of action copying was identified 270 (and when). As no such evidence was found, only the first condition (i.e., “Conformist 271 Transmission” at the top of S2) was implemented. All other conditions as they would have 272 been implemented, following positive results, are described in the registration (Neadle et al., 273 2018).

274 **Design & Stimuli**

275 Ape subjects were exposed to human demonstrator(s) performing causally irrelevant 276 actions prior to opening a wooden box (demonstration box). Once the demonstrator opened 277 the demonstration box, the reward inside – a grape – was provided to the subject (Clay & 278 Tennie, 2017). Following the demonstration phase, subjects were provided with their own 279 version of the box (“test box”) which was visually identical to the demonstrator box but in 280 reality, could not be opened (see below). Subjects were then observed and recorded for a 281 *maximum* of 5 minutes while free to interact with the box. If subjects relinquished contact 282 with the test box for 30 seconds prior to three, four or five minutes of exposure time

(depending on the stage of testing, see S3) the trial ended once the next whole minute was reached. In this respect, trial duration was directly influenced by the subject performance – accounting for and accommodating potential differences in motivation across subjects and species. The logic was that, if the subject would attempt, and fail (due to the box being unopenable), to open the box in any way unlike those demonstrated (i.e., lacking the demonstrated actions), they may be more motivated to copy the observed actions, either from remembering demonstrations and/or by paying more attention to demonstrated actions in later trials. This logic therefore implemented the ‘copy if unsuccessful’ (Laland, 2004; see S4) and ‘copy when uncertain’ (Toelch et al., 2013) social learning biases.

Our study also used a ‘puzzle box’ (see Figure 1), which shared the same design a previous study on action copying with bonobos and human children (Clay & Tennie, 2017). As in this previous study, we used two variants of this box: the “demonstration” box and the “test” box. In order to remain consistent with the previous study (Clay & Tennie, 2017), the demonstration box was made from a piece of wood, cut in half, with a small depression cut into the centre of both halves (see Figure 1 left panel). The demonstration box was used by the human demonstrators and was never provided to any subjects.

Figure 1. Photographs of puzzle box. Left panel contains demonstrator's box (demonstration box), opened to reveal hidden compartment, right panel contains subject's box (test box), showing the apparent divide between the two "halves" of the box, note that this box could not be opened as the "divide" was simply a line scored into the still-solid wood.

Subjects

Subjects (N=33; main sub-sample N=19 of mother-reared apes) were all housed at the Wolfgang Köhler Primate Research Center (WKPRC), Leipzig, Germany. All species at the WKPRC were tested between 11th June and 9th July 2018. Ages were correct at time of testing (S5 for full details): bonobos ($n=6$; Male=2, Female=4; mother-reared = 3; $M_{age}=19.83$; $SD_{age}=8.28$), chimpanzees ($n=19$; Male=5, Female=14; mother-reared = 9; $M_{age}=29.42$; $SD_{age}=12.26$), western lowland gorillas ($n=2$; Male=1, Female=1; mother-reared = 2; $M_{age}=16.5$; $SD_{age}=3.54$) and Sumatran orangutans ($n=6$; Male=2, Female=4; mother-reared = 6; $M_{age}=23.16$; $SD_{age}=10.65$).

Outside of the testing sessions, all subjects were housed in semi-natural indoor and outdoor enclosures containing climbing structures, such as ropes and platforms; and natural features, such as vegetation, trees and streams. They received their regularly scheduled feedings, primarily consisting of vegetables, had access to enrichment devices including shaking boxes and poking bins, and water ad lib. Subjects were never food- or water-deprived for the purposes of this study. All research was conducted in the subjects' sleeping rooms. If subjects showed signs of distress the trial was terminated, and the subject was released back into the main enclosure immediately – this occurred on one occasion (see S6).

Although the apes in this sample have extensive experimental experiences, it is important to note that none of the tested subjects included here were trained to engage with this task or to copy actions. Nevertheless, we also tested one "do-as-I-do"-trained subject – a male chimpanzee aged 17 (Hribar et al., 2014). This subject did not enter our main analysis given that such trained subjects must be excluded in controlled experiments (Henrich & Tennie, 2017). All hand-reared subjects (i.e., human-reared), and those whose rearing

histories were unclear (see S5) were considered separately to mother-reared conspecifics and their results are compared to determine the role that rearing history might play in terms of attention paid or engagement with the task.

Procedure

Demonstrator Training

Prior to testing, all human demonstrators were trained (approx. 1 hour) on the demonstration procedure to ensure consistency across demonstrators. In addition, each demonstrator was provided with a video of DN modelling the action demonstration once (S7) via email, which the demonstrator could watch as many times as needed in order to match the actions. Demonstrators were required to copy both the form and speed of the actions using DN's as a template during demonstrations, which were in turn modelled after the demonstrated actions from Clay and Tennie (2017). ZC instructed and commented on the training videos prior to them being provided to demonstrators.

DN and CT observed each demonstrator's performance prior to the start of testing, to confirm that their demonstrations were proficient; videos of each demonstrator (taken after training) are included in S7. To ensure consistency across time, demonstrator action consistency checks were also performed after each week of testing. Although retraining would have been used, if a reduction in performance occurred, performance remained consistently high quality thus retraining proved unnecessary.

All demonstrators (N=2 male; N = 2 females) were human adults between the ages of 23 – 30. None of the demonstrators were zoo staff who might otherwise be familiar to the apes (see S8). In order to reduce possible order effects, subjects were randomly allocated to each possible iteration of demonstrator order. The same demonstrators were used throughout, and demonstrators remained in place throughout each trial to maintain the influence throughout the trial, akin to other studies (Haun et al., 2014).

Demonstrated Actions

This study followed the protocol of a previous, related, study (Clay & Tennie, 2017), in which a (single) demonstrator performed two actions either on or next to the demonstration box (depending on action) during demonstrations. They did so whilst standing in the keeper/researcher side of the so-called “sleeping room” of the subjects. Demonstrations were visible to the subjects through plexiglass and metal mesh. Both actions were preceded by demonstrators extending their arms forwards away from their bodies at a roughly 90° angle, whilst holding the demonstrator box, and performing the actions with their arms extended (see S7).

For the first action – “Rub” – the demonstrator rubbed the back of the right hand in a consistent, but slow, circular, clockwise, motion across the top of the demonstrator box – in contact with the box, four times (1 sec per rotation, 4 sec total). For the second action - “Rotate”- the demonstrator raised the right hand and rotated it, at the wrist, in a clockwise motion – not in contact with the demonstrator box, four times (1 sec per rotation, 4 sec total). The demonstrator then opened the demonstrator box, showed the contents of the box (a grape) to the subject and gave the grape to the subject.

Demonstrators stood in a line, facing the subject, but out of reach (see Figure 2). Once all demonstrators moved into the testing room the demonstration phase began. In the pre-registered methods, demonstrators were supposed to be present in the testing room *prior* to the subject entering (Neadle et al., 2018). As it transpired, the human area in the testing rooms was not spacious, and animal keepers preferred to have the group of demonstrators enter after the subject had entered. Thus, subjects entered first, and demonstrators after. This represents the only deviation from our registered methods.

Demonstrators performed the actions individually following a predefined order (see S9); with demonstrator order randomly assigned across trials using a random number

generator (1 to 24) relating to a pre-defined demonstrator order table, see S9. Once the individual demonstration phase was complete, all four demonstrators also additionally performed a simultaneous group demonstration of both actions.

Subject Attention

Subjects had the opportunity to observe *at least* eight full demonstrations: one per demonstrator (performed in sequence), followed by a simultaneous additional demonstration by each of the four demonstrators. Each subject was given up to five demonstrations of the Rub-Rotate action by each demonstrator, and the test box was rebaited after each successful demonstration. If the subject did not see at least one iteration of each action (i.e., Rub or Rotate) during any demonstrator's demonstration, up to four repeats were given until the subject had either seen both Rub and Rotate or five attempts were given by that demonstrator. As a result, up to 20 demonstrations would have occurred for a subject that never attended to the demonstrations (i.e., four initial demonstrations and 16 repeat demonstrations – four per demonstrator).

Figure 2. Pictorial representation of experimental set up. Subjects were unable to observe demonstrators using the re-baiting station due to the occlusion screen. The subject's test box was retrieved from behind the occlusion screen as though the demonstration box was being rebaited again. Chimpanzee image by Jose R. Cabello from Pixabay and is permitted for use under the "Pixabay licence" agreement.

Several measures were put in place to ensure that subjects witnessed the demonstrations and that the demonstrators could confirm that the subject had seen the demonstration. Once the subject indicated a ‘readiness to start the trial’ (defined as head oriented towards the demonstrator, who was holding the box, for one second or more), the demonstration began. Subjects were required to watch each action (i.e., one iteration of Rub and one of Rotate), as performed by each demonstrator, at least once (we define this as ‘attending’). In order to facilitate this, all demonstrators were permitted to call the subject’s name to gain their attention as often as required prior to and throughout the demonstration. This definition of attentiveness is in line with the concept of “peering” (Schuppli et al., 2016), adopted in wild orangutans. Each iteration of the action (4x Rubs or 4x Rotations) lasted for approx. 4 seconds, coupled with the 1 second ‘readiness’ period resulting in the 5 seconds required for peering. Our subjects were also always within the 2-5m radius required for peering, owing to the size of the testing rooms (approx. 2.5 x 2.5m – including human and animal areas).

After observing the subject during each demonstration, all demonstrators verbally reported (yes/no for each action, in demonstrator order) whether the subject observed *none*, *part of*, or the *whole* of each demonstration. If two or more of the demonstrators replied with a “no” to either of the actions (i.e., it had not been observed), the previous demonstrator repeated their demonstration (up to a maximum of five demonstrations; see above). The next demonstrator followed the same procedure, and so on, until the subject had observed the full demonstration of both actions at least four times (across all demonstrators). The number of repeat trials required to attain agreement was recorded after the study was completed, by reviewing the video footage and used as a proxy for subject attentiveness, such that higher numbers of repeat trials equate to less attentiveness to the demonstrations. This meant that a

maximum of 21 (20 single demonstrator & one group) demonstrations were possible, with a maximum of 16 repeated demonstrations (four repeats per demonstrator).

Task Period

Each subject was then exposed to the task. The final demonstrator took the demonstration box behind the occlusion screen and swapped it for the test box. The subject was given the test box by the demonstrator, via a secure hatch. The subject then had a maximum of five minutes to copy the actions demonstrated (see above and S3). All trials were recorded using two camcorders (Panasonic HC-V777) mounted on tripods at either end of the line of demonstrators, in addition to the demonstrator-mounted GoPro (Hero Session 5) cameras. Subjects were exposed to three trials each.

Ethics

The study was ethically approved by an internal committee of the Max Planck Institute for Evolutionary Anthropology (director, research coordinator), the Leipzig zoo (head keeper, curator, vet) and the University of Birmingham AWERB committee (reference no. UOB 31213). No medical, toxicological or neurobiological research of any kind is conducted at the WKPRC. Research was non-invasive and strictly adhered to the legal requirements of Germany. Animal husbandry and research comply with the “EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria”, the “WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums” and the “Guidelines for the Treatment of Animals in Behavioral Research and Teaching” of the Association for the Study of Animal Behavior (ASAB). IAUCUC was not necessary to conduct this research.

Participation was voluntary: internal doors were opened, and the subjects could enter voluntarily. Those that entered were released as soon as they showed any potential signs of stress – this occurred twice in the gorilla sample (see S5). Three trials were attempted with

each subject, though due to the voluntary nature of this study, sometimes fewer trials were attained (see S5). Five subjects from the WKPRC chose not to participate in all trials (two orangutans, two gorillas and one bonobo; see S5).

Subjects were tested individually in most cases as this was something they were already accustomed to, excluding cases of mothers and dependent offspring and any individuals that were uncomfortable being separated. Such cases were noted ($n_{bonobo}=2$; $n_{chimpanzee}=2$; $n_{gorilla}=1$; $n_{orangutan}=2$; though, the ‘other’ individual present was a dependent juvenile/infant in all cases except the chimpanzee cases see S5). Individual testing ensured an effective demonstrator majority to maximize the effect of majority. An effective majority in human tests has been shown to be 3:1 (Bond & Smith, 1996; Haun et al., 2013), but here we used a 4:1 ratio to also harvest potential effects of demonstrator sex majority (by always using two male and two female demonstrators). When subjects were tested in dyads an overall ratio of 4:2 was the maximum that could be achieved (still, this represented a majority).

Behavioural Coding & Analysis

Behaviours were live coded and after each trial each demonstrator independently wrote down whether they considered *any* of the subject’s actions during a trial to constitute action copying. The paper on which the live coders independently wrote their decision was then folded in half and placed into a container for later counting. A positive case of copying would have been recorded if more than half (i.e., 3 or 4) of the demonstrators had ever considered that the subject had copied at least one of the demonstrated actions.

Demonstrators were additionally instructed that *any* approximation of action copying (see Table 1 of this report and Table 2 of Needle et al., 2018) should be noted. For example, even a subject copying the Rub action with the *left* hand and for a *half rotation* and without attempting a Rotate action would be considered as having copied the Rub action for the

purpose of the result dependent design. These approximations would have been further analysed *post hoc* (see Table 2 in Neadle et al., 2018).

Table 1. Description of behaviours as provided to demonstrators several days prior to the first trial, after demonstrators had received training on the actions from DN. These instructions were later reiterated, immediately prior to first testing session.

Behaviour	Description
Rub	The subject places the back of their hand (either hand), on top of (or close above) the box and rubs it in a circular motion (regardless of direction).
Rotate	The subject raises their hand (either hand) and rotates it – for a minimum of 180° at the wrist (regardless of direction).
Rub-Rotate	The subject performs the “Rub” behaviour, and this is followed by the “Rotate” behaviour
Rotate-Rub	The subject performs the “Rotate” behaviour, and this is followed by the “Rub” behaviour
No relevant behaviour	The subject performs none of the actions described here

Using video analysis, we calculated the mean time an individual spent interacting with the test box, which we used as a proxy for *motivation to engage*. As each subject had either a three, four or five-minute trial (see S3), the total number of seconds that the subject was in contact with the test box was divided by the total trial time (in seconds), resulting in a percentage of “motivation”.

All analyses and data-based figures were produced in R (version 3.4.3(R Core Team, 2020)) and R-Studio (version 1.1.423 (RStudio Team, 2016)). The following packages were utilised for analysis/visualisation: ggplot2 (version 3.1.0), ggpubr (version 0.2.0), psych (version 1.8.10), car (version 3.0-2), cowplot (version 0.9.3), multcomp (version 1.4-8), ggsignif (version 0.4.0), pastecs (version 1.3.21) Additional, planned, analyses (Neadle et al., 2018) were not performed given the null findings.

Interrater reliability

Interrater reliability for attentiveness to the demonstration was assessed during trials. In the case that even a single potential instance of action copying was identified during live coding, a naïve second coder would have been required for *post hoc* coding. However, as no

cases of action copying were observed, a second coder was not required. There were always four independent witnesses to any given event. As a result, a four-way instantaneous interrater reliability was possible. As there were no cases in which any of the demonstrators suggested that either action had been approximated at by any of the tested apes, there was no need for further interrater reliability checks.

Results

We found no evidence of action copying, not even in approximation, in any trial by any subject (mother-reared ($N=19$), hand-reared ($n=10$) or those whose rearing history was unclear or unknown ($n=3$)). Neither was there any evidence of action copying or approximations of it in an additional chimpanzee who was previously trained the Do-As-I-Do paradigm (see S10). Findings, from all subjects, were confirmed using a four-way live coding system (see above). Coding demonstrated subjects reliably attended to the demonstrations and were motivated to interact with the test apparatus – though with inter-species variations.

As our entire matrix consisted of zero values, inferential statistics were limited. However, using a one-way Chi-Square Goodness of Fit, we determined the expected probability of copying that would harmonise our observations with expected results. We adopted an iterative approach, where expected frequencies of action copying (expressed as a percentage of ‘successful’ trials) were compared to the observed frequencies; this expected frequency was reduced until our (fully negative) data set were consistent with the theoretically expected observations at various copying percentages (see Table 2). An assumption of the Chi-square test is that the count of expected observations should not be less than 5 (Field, 2013), thus then the count falls below this the results should be treated with caution.

The results of these analyses can be seen in Table 2. A starting rate of copying of 0.77 (77%) was chosen as Clay and Tennie (2017) identified this value in children, using this task. The results show that our figures are inconsistent with an expected copying probability of

greater than 10%. Whilst it is *theoretically* possible to attempt to determine the exact point where values fall below the accepted threshold of $p=.05$, the assumptions of Chi-Square do not allow for these figures to be interpreted meaningfully, therefore a range of values must be accepted. This implies that, in order to account for our results, the copying hypothesis would need to be caveated, specifying an expected copying probability of between 5% and 10%. Larger samples and, with these, larger expected frequencies, are required to establish where in this range the true value lies. These expected frequencies are generated using the, smaller, mother-reared only subset and therefore represent a more conservative estimate of the expected probability (due to smaller expected frequencies greater specificity is not possible). See S10 for these analyses repeated with the full sample, including hand-reared/unknown subjects.

Table 2. Iterative reduction of expected probabilities compared to observed probability (0%) of copying. Frequencies are rounded to the nearest whole number. † = these values drop below the accepted level of $n=5$.

Expected probability	χ^2	df	p
0.77	42	1	<0.001
0.7	39	1	<0.001
0.6	33	1	<0.001
0.5	28	1	<0.001
0.4	22	1	<0.001
0.3	17	1	<0.001
0.2	11	1	<0.001
0.1	6	1	<0.05
0.05 [†]	3	1	.08

Each species also contained an individual/s that required no repeat demonstrations for at least one of their trials ($N_{\text{bonobo}} = 2$, $N_{\text{chimpanzee}} = 4$, $N_{\text{gorilla}} = 1$, $N_{\text{orangutan}} = 3$). There are clear species differences (Figure 3A) in number of demonstrations required, however as there was never an instance of copying these differences clearly did not influence the outcome ($Mdn_{\text{bonobo}}=6.50$, $IQR_{\text{bonobo}}=5.25$; $Mdn_{\text{chimpanzee}}=5.00$, $IQR_{\text{chimpanzee}}=5.00$; $Mdn_{\text{gorilla}}=3.00$, $IQR_{\text{gorilla}}=3.75$; $Mdn_{\text{orangutan}}=1.50$, $IQR_{\text{orangutan}}=4.25$). These differences are characterised by a substantial degree of inter-species variance, indicating an element of intra-species idiosyncrasy.

There are no clear differences in number of repeat demonstrations as a function of either sex or rearing history (see Figure 3B & C).

Figure 3. Box plots depicting attention paid to demonstrators (via number of repeat demonstrations), as a function of species (A), sex (B) or rearing history (C). Central horizontal bar represents median value, upper and lower hinges correspond to 75th and 25th percentiles, upper and lower whiskers extend to largest or smallest value, data beyond 1.5 times IQR are displayed as • and plotted individually.

Most subjects ($N=21$; $N_{\text{bonobo}} = 6$, $N_{\text{chimpanzee}} = 9$, $N_{\text{orangutan}} = 6$) showed high motivation to interact with the test box after demonstrations (defined as $>50\%$ interaction time during trial); though, no gorillas interacted to this extent. Across all species, subjects spent an average of 39.45% of trial time ($SD=34.61$) in contact with the test box. Species differed in the percentage of time spent interacting with the box ($Mdn_{\text{bonobo}}=83.00$, $IQR_{\text{bonobo}}=40.67$; $Mdn_{\text{chimpanzee}}=15.00$, $IQR_{\text{chimpanzee}}=44.44$; $Mdn_{\text{gorilla}}=8.89$, $IQR_{\text{gorilla}}=8.47$; $Mdn_{\text{orangutan}}=58$,

554 $IQR_{\text{orangutan}}=34.67$; Figure 4A). As above, if there had been copying identified in one species
 555 then these inter-species differences would have been more relevant – as it was there was never
 556 an instance of copying identified and these figures should simply be taken as descriptive.
 557 Again, these differences are typified by very large intra-species variance, in all but the gorilla
 558 sample which consistently showed very little interaction with the box. There were again no
 559 clear differences in the percentage of interaction time as a function of sex or rearing history
 560 (Figure 4B & C).

561

562

Figure 4. Box plots depicting percentage of trial interaction as a function of species (A), sex (B) or rearing history (D). Central horizontal bar represents median value, upper and lower hinges correspond to 75th and 25th percentiles, upper and lower whiskers extend to largest or smallest value, data beyond 1.5 times IQR are displayed as • and plotted individually

Discussion

Examining the responses of a total of 33 captive great ape subjects, across four species and with a variety of rearing backgrounds, revealed no evidence (or approximations) of spontaneous action copying – despite majority demonstrations. None of these 33 untrained subjects (19 mother-reared; 14 hand-reared or unknown history), copied a single demonstrated action. Although there were species differences in attention and engagement with the task, this variability did not translate to species differences in copying behaviour.

This study included methodological elements that aimed to measure and ensure that subjects were attending to the demonstrations, thus ensuring that our sample had a ‘fair chance’ of copying. Firstly, demonstrations did not commence until the subject had oriented their head towards the demonstrator (for at least one second). Secondly, once each demonstration was completed, a four-way reliability system was used, the results of this showed that there was never an instance where all the possible repeat demonstrations had to be provided. In this way, we created measures akin to so-called “peering” in wild apes, which likewise measures close observation behaviour (within 2-5 meters – depending on the behaviour, in wild orangutans Schuppli et al., 2016). In our study, given the proximity of demonstrators to subjects (less than 2.5m apart at all times) and the timings required by the readiness to start period and an observation of a full demonstration cycle (at least 5 seconds) our measures have concurrent validity with relates research (5+ seconds watching and within 2m+ or 5m+, depending on context; 77). We observed some inter-species variation in attentiveness to demonstrators, but subjects of all species proved generally motivated to attend to demonstrations – as, again, none of our subjects ever required the maximum

possible number of demonstrations. Thus, lack of observation, or lack motivation to observe, cannot explain our negative findings.

Our sample (Penndorf & Aplin, 2020), method (Drea & Wallen, 1999) and treatment (Haun et al., 2012) were all selected to promote action copying in our subjects. Regarding captivity, it has been shown that captive animals are generally more successful in both asocial and social learning tasks as compared to wild conspecifics (Penndorf & Aplin, 2020). Therefore, our captive sample should be considered as more likely to copy actions than wild conspecifics, yet even then, they did not copy actions. Regarding individual testing, it has been suggested that individual testing neutralises the potential confounding effect of rank differences in primate social learning (Drea & Wallen, 1999). Therefore, by testing our subjects individually, we essentially controlled for social rank during the demonstrations, rendering all of our subjects equally likely to copy, regardless of rank. Regarding majority bias, it has been suggested that chimpanzees, but perhaps not orangutans, are subject to majority influence (Haun et al., 2012) and it has been claimed that this can influence learning (through unspecified social learning mechanisms; Watson, Lambeth, et al., 2018). These biases have been noted to be present not only in apes, but in primates more generally and in various other animal species (Watson, Botting, et al., 2018). Here, we employed such a majority ratio of demonstrators to observers (Luncz & Boesch, 2014). Given that previous attempts at identifying ‘pure’ action copying in apes have only utilised single demonstrator conditions, our study therefore attempted, for the first time, to utilise majority biases to increase the likelihood of action copying to the point of them occurring, however, even under this majority bias no ape action copying occurred.

Furthermore, the entire underlying paradigm of overimitation/copy-when-unsuccessful (Clay & Tennie, 2017; Laland, 2004), which we applied here, was designed to improve the chances of identifying ape action copying. Specifically, regarding overimitation,

the actions that were performed were likely novel to subjects (as the keepers confirmed to us). These novel actions had been selected to be causally irrelevant (required in testing for overimitation; Lyons et al., 2007) and they are known to lead to action copying in another species - humans (Clay et al., 2018; Clay & Tennie, 2017). Regarding our use of the copy-when-unsuccessful learning bias (Laland, 2004), we provided subjects with a test box that could not be opened, thereby reliably creating a situation for each subject in which it should seem (especially across trials) as if the demonstrated actions were necessary before the box would open. This was designed to create a situation in which the failure to open the box should have resulted in higher motivation to copy the demonstrated actions (also and especially across trials). This was done to tap into a potentially existent ape ‘copy-when-unsuccessful-bias’ (Laland, 2004), especially in the event that apes failed to copy immediately in the first trial before even attempting to open the box. Note that our results were not dependent on the presence of a copy-when-unsuccessful-bias in apes (which may be absent) – we merely implemented this manipulation (i.e., an impossible box) as an additional motivation and as an additional chance of apes to copy actions. In summary, we thoroughly designed our study to maximise the chances of identifying action copying in apes. Our data are therefore the outcome of a ‘best-case scenario’ that we designed. Yet, even in this best-case scenario, not a single ape copied actions.

To date, all attempts at ‘action-only’ ape social learning studies in captivity have failed to detect action copying (Clay & Tennie, 2017; Tennie et al., 2012; Tomasello et al., 1997; and this study). Extrapolating these findings to wild apes, these results do not support the claim that ape culture could rely on action copying (see claims by Gruber et al., 2015; Horner & Whiten, 2005; Whiten et al., 1999, 2009; Whiten & Custance, 1996). That is, the absence of action copying in apes in tests clearly does not support the ‘ape action copying hypothesis’. Instead, these results are consistent with the notion that wild ape behaviour –

while often cultural in a minimal sense, i.e., in the relative frequency of behavioural forms (Neadle et al., 2017) – does instead have to rely on individual learning to develop these behavioural forms. The know-how (Bandini et al., 2020) of producing these behavioural forms is therefore unlikely to be contingent on action copying. This is not to say that no other variants of social learning play a role in regulating the frequency of wild ape behavioural forms. On the contrary, many studies have now shown that captive apes are able to socially learn non-action aspects from humans and conspecifics (Tennie, Bandini, et al., 2020; Tennie, Hopper, et al., 2020). In this way, apes have been shown, for example, to learn socially *what* they should engage with (know-what), and also where (know-where) - i.e., to engage in social learning mechanisms that do not require action copying skills. The repeated and continuing application of these non-copying social learning processes clearly has population-wide consequences. It results in socially mediated serial reinnovations of the resulting behavioural forms, or action patterns, in affected individuals (Bandini & Tennie, 2017; Tennie et al., 2009; Tennie, Bandini, et al., 2020; Tennie, Hopper, et al., 2020). Over time, this creates (and maintains) the ape cultures that have been described, i.e., specific mixes of behavioural forms at the population level that often differ between populations (Acerbi et al., 2012). In contrast, humans appear to be unique among great apes in their propensity to spontaneously copy the behavioural form itself – including novel and abstract actions – supporting the long-held claim that this skill is a fundamental component of human cumulative culture (Tomasello, 1999). This is true especially of human culture that is purely action-based (such as rituals and dances; Tennie et al., 2012).

The demonstrated actions we used in our current study were novel to subjects by our choice, they were therefore not within the existing repertoire of the subjects (Clay & Tennie, 2017). The copying of such novel actions is well demonstrated in studies of human action copying (Clay et al., 2018; Clay & Tennie, 2017). Although the use of novel actions may

makes the task more ‘difficult’ for apes (Byrne, 2009), this is by design. Novel actions must be used as target actions in such studies, to ensure that action matching is not merely a carry-over product of prior social or individual learning where mere triggering can release a similar behaviour in others (Tennie, Bandini, et al., 2020; Tennie & Hedwig, 2009). The use of novel actions thus ensures a valid test of whether the animals require that the action is indeed copied for it to occur (culture-dependency; Reindl et al., 2017). Given that absence of novel action copying in our best-case-scenario, majority demonstration study, in conjunction with all earlier failures of apes to spontaneously copy novel actions (Clay & Tennie, 2017; Tennie et al., 2012; Tomasello et al., 1997), there exists a reliably empirical distinction between ape and human action copying capacity/propensity. This difference matches the proposed distinction between human and non-human ape cultures, i.e., between the kinds of cultures that different social learning mechanisms can produce (Boyd & Richerson, 1996; Tennie et al., 2009; Tennie, Bandini, et al., 2020; Tomasello, 1998).

Our findings and conclusions might be surprising to some readers. This is likely because the now-vast animal social learning literature includes several claims for animals copying actions. These claims exist in a range of species, from lizards (Kis et al., 2015) to monkeys (Voelkl & Huber, 2000) to chimpanzees (Whiten et al., 2009). However, these results do not stand in contrast to our findings. This is because these claims, when they are about non-human great apes, invariably used methodologies that are logically unable to pinpoint novel action copying. Most typically, these claims derived from applications of so-called two-target tasks. A typical two-target task might require a bolt (or lever, or door) to either be pressed or be pushed (Bugnyar & Huber, 1997). But these tasks are confounded, as they are proven theoretically and empirically to be solvable in the absence of action copying (Heyes et al., 1994; Tennie et al., 2006) – for example, chimpanzees solve these tasks even when *no* actions were ever demonstrated (Hopper et al., 2008). Sometimes, more

manipulations are used than just two-target defences. For example, in a widely cited study by Horner and Whiten (2005), chimpanzees were said to have been required to copy ‘causally irrelevant actions’ in solving such a puzzle box. Specifically, this study used a puzzle box designs in which a whole line of “defences” existed, such as moving doors, bolt-removal and stick insertion affordances. The authors concluded with evidence of chimpanzee action copying, based on a match of some observers in their approach to what they were demonstrated. However, this conclusion does not follow, as all of the defences merely required the application of action patterns that were within individual reach of the tested chimpanzees (Tennie, Hopper, et al., 2020). The defences on the puzzle box resembled those commonly used in ape enrichment and also in other studies (e.g., Whiten et al., 2003) that simulated extractive foraging techniques (hence have been called “artificial fruits”; e.g., Whiten et al., 1996). A recent review (Tennie, Hopper, et al., 2020) showed that in all these cases, and across all two-target studies and derivatives, there is empirical evidence that all these defences could be overcome by ape subjects on their own - regardless of demonstrations. Thus, it does not matter whether a bolt had to be moved to the left or to the right, as both directional movements are perfectly producible by naïve apes in the entire absence of demonstrations. Overall, then, none of these earlier action copying claims in apes – including the one by Horner and Whiten (2005), tested for novel action copying (or even action copying more generally). The positive findings in these studies remain in stark, and telling, contrast to the negative findings in ape studies that instead tested for novel action copying.

While apes did not copy actions in two-target tasks, it is not the case that they ignored other aspects of demonstrations. While apes could solve these tasks on their own – as they had no need to learn anything novel and copying-dependent – they nevertheless often showed a proclivity to match aspects of demonstrations, such as *where* a bolt moves to, *where* to

insert a stick, or *what* object(s) to interact with. Future studies that aim to detect ape action copying must therefore continue to control for these and other confounding types of knowledge (e.g., ‘know-where’, ‘know-what’; Bandini et al., 2020) before claims can be made regarding the transmission of actions (behavioural know-*how*). Furthermore, again, even after these confounds are controlled for, when it comes to action copying, the demonstrated actions must be novel and copying-dependent. These actions should not, therefore, appear in baselines. They should not be anything that apes do in the absence of demonstrations – at least when the goal of the study is to determine whether apes, like humans, are able to copy something that they could not do on their own.

If the ape action copying hypothesis is to be upheld, then apes should prove able to copy *novel* actions, as this would then necessarily be the mechanism by which naïve individuals, of a new generation, must learn the actions of the existing generation (Boyd & Richerson, 1996; Tomasello, 1998, 1999). But then the apes in our study should have copied the demonstrated actions – yet this copying never occurred. That is, the prediction of the ape action copying hypothesis, that apes should prove able to copy novel actions, has once again failed to be identified, which remains consistent with previous tests (Clay & Tennie, 2017; Tennie et al., 2012; Tomasello et al., 1997). In stark contrast to the case of apes (Tennie et al., 2012; Tomasello et al., 1997; this study), human children have been shown to copy at least one of these demonstrated novel actions – even at near ceiling levels – and even when a majority demonstration was lacking (in 77% of trials; Clay & Tennie, 2017). Therefore, regardless of whether this ape/human difference in novel action copying is perceived to be one of absolute ability (Tennie et al., 2009; Tennie, Bandini, et al., 2020) or one of degree, it is clear that an important species difference exists in novel action copying. This difference is so large that, based on all evidence to date, we must conclude that action copying cannot

feasibly be the cornerstone of ape culture that it has been claimed to be (e.g., Whiten et al., 1999).

Our results suggest that the hypothesis that action copying is often the basis of ape culture (e.g., Whiten et al., 1999) should be rejected. Even considering the notion that action copying might merely be rare in wild apes, their number could only be very few. Given all the data available, support for this hypothesis must depend now on the presentation of positive evidence - namely that these behaviours must not occur in baselines, or through non-copying social learning variants (Bandini et al., 2020), and that their occurrence fully depends on access to action demonstrations.

The conclusion that ape cultures cannot feasibly be reliant on action copying is consistent with accumulating findings that wild ape behaviours indeed do not *require* action copying to be expressed. The action forms of various wild behaviours have been shown to reappear spontaneously in naïve, untrained, mother-reared apes without any need to observe these actions (Tennie et al., 2009; Tennie, Hopper, et al., 2020). Such copying-independent action forms have been shown to include gestures (Byrne et al., 2017) and foraging techniques, including tool-use (Bandini & Tennie, 2017; Motes-Rodrigo et al., 2019; Neadle et al., 2017; Tennie et al., 2008). Given that various ape ‘cultural’ behaviours *can* be explained through individual learning alone, and the likelihood that ape action copying is rare to absent, it seems highly unlikely that wild ape cultures are reliant on copying or that they could be reliant on such learning. Instead, the highest likelihood is that ape culture can be explained by the effects of “socially mediated serial reinnovations” (Bandini & Tennie, 2017). That is, wild ape culture is explicable through an interplay between social and asocial learning (Galef, 2015) in the absence of form copying (Tennie, Bandini, et al., 2020; Tennie, Hopper, et al., 2020). Specifically, whilst the frequency of the (re)innovation of affected behaviours appears to be regulated by non-copying social learning variants (e.g., local or

stimulus enhancement; or know-where and know-what etc.), the behavioural *form* is more parsimoniously be explained through individual reinnovation (Tennie et al., 2009; Tennie, Hopper, et al., 2020). Again, the very fact that form-naïve apes proved perfectly capable of producing these forms supports this theory.

It might seem a potential limitation of our study that human demonstrators were used, as opposed to conspecifics (Whiten, 2017). But whilst the use of human demonstrators for apes is considered as less effective than conspecifics (Hopper et al., 2015), the overwhelming pattern in previous social learning studies is that apes attend well to human demonstrators (Horner & Whiten, 2005; e.g., Whiten, 1998); the apes in our study were no exception (see our peering/attention data). Indeed, two earlier ape tests of pure novel action copying in which *conspecific* demonstrators were used also showed similar negative results (Tennie et al., 2012; Tomasello et al., 1997). Even so, future studies might consider replicating our methodology using trained conspecifics as demonstrators; and these studies should then contain multiple demonstrators, as we did here (in a majority influence paradigm; sensu Asch, 1956).

It might further be objected that perhaps apes may only copy their mothers, within a ‘master-apprentice’ model (Matsuzawa et al., 2008). At first, this hypothesis would seem to explain the negative results of all ape ‘pure’ action copying studies thus far. However, in the earliest of the ‘pure’ action copying studies (Tomasello et al., 1997) the two demonstrators were mothers, and indeed performed their action demonstrations in the presence of their offspring. One daughter often failed to attend to her mother’s demonstrations. The juvenile daughter of the other subject observed her mother’s demonstrations 99 times (indeed, the most observations of all test subjects) and yet she failed to copy her mother’s novel actions. Empirically, therefore, even the notion that it requires mother demonstrations for apes to copy actions fails. But there are strong additional reasons to doubt any such “Uniparental cultural

transmission” hypotheses – as these could not give rise to and neither could they maintain the ape cultures we see in the wild (Enquist et al., 2010). Other mechanisms must be at work (and given all data, this can only be socially mediated reinnovation, see above). This is the unequivocal outcome of cultural transmission modelling of uniparental cultural transmission (Enquist et al., 2010). Enquist et al.’s model showed that having a single cultural “parent” cannot maintain cultural patterns of form transmission over time. Transmission would break down eventually and could not recover. One could say that “it takes a village to keep culture afloat”. And so, even the claim that apes copy actions only from their mothers does not stand – neither empirically, nor theoretically.

Another potential objection relates to the notion of a potential ‘sensitive learning period’ in ape action copying (3-5 years old in chimpanzees; Biro et al., 2003). The chimpanzees in our sample were aged 14-52 years old, thus, placing them outside most claimed sensitive learning periods (e.g., Biro et al., 2003). However, some chimpanzees in other ‘pure’ action studies were inside the claimed sensitive range, and still they did not copy actions (Tennie et al., 2012: minimum age = 5yo; Tomasello et al., 1997: minimum age = 2yo). In addition, in the previous bonobo study of ‘pure’ action copying (Clay & Tennie, 2017) bonobos across the age range (i.e., including juveniles; 3-29 years old) also failed to copy novel actions. Note that it has also been suggested that, at least in some ape species, a particularly young sample (within the sensitive learning period) might not be optimal for detecting action copying, as copying tendency may instead increase as a function of age (Custance et al., 2001). Thus, our overall older sample should not be a significantly limiting factor in our subjects’ clear lack of action copying even following majority demonstrations.

Given that the apes we tested were mostly born and raised in captivity, it may be claimed that our subjects are somewhat, or at least relatively more, human-enculturated than wild populations, perhaps also given the relatively high frequency of cognitive testing at the

813 WKPRC (e.g., Allritz et al., 2013; Buttelmann et al., 2013; van Leeuwen & Call, 2017;
 814 Wobber et al., 2014). However, this is not a problem for our conclusion, as any increase in
 815 human enculturation – including merely a relative increase over wild conspecifics – should
 816 be expected to *increase* the likelihood of action copying (Tomasello et al., 1993). This effect
 817 is not even limited to primates (Gajdon et al., 2004; Penndorf & Aplin, 2020). We therefore
 818 see our selection of sample population as unproblematic to critically examine the predictions
 819 of the ape action copying hypothesis – as, if our data were biased, it would have been instead
 820 biased in support of the action copying hypothesis. Instead, our conditions and sample
 821 represent a ‘best case’, conservative, approach as it was arguably designed to be the most
 822 likely to result in ape novel action copying occurring, compared to other samples, test
 823 situations, and arguably even when compared to wild populations. Therefore, the fact that
 824 even this “best case” scenario failed to copy novel actions – even when these were
 825 demonstrated by a majority – suggests evidence incompatible with the ape action copying
 826 hypothesis.

827 This lack of - or greatly reduced likelihood of - novel action copying in apes, or
 828 know-how copying (Bandini et al., 2020) might be a definitive feature that distinguishes
 829 human culture from the remainder of the great ape clade (Tomasello, 1999). The human
 830 tendency to copy novel – even causally opaque actions – might be the factor that has allowed
 831 our species to transcend ape-type cultures to produce and maintain our own, cumulative
 832 culture of know-how (Boyd & Richerson, 1996; Galef, 1992; Gergely & Csibra, 2005; Tennie
 833 et al., 2009; Tomasello, 1999). This highlights the importance of understanding the role (if
 834 any) that know-how copying plays in the cultures of our closest living relatives (and in early
 835 hominins; Tennie et al., 2017). In spite of this, studies of ‘pure’ action copying in apes have
 836 only started to be performed rather recently. Wherever these studies have been attempted (this
 837 being one), the marked absence of action copying, combined with data gleaned from other

experimental (e.g., Bandini & Tennie, 2017) and modelling studies (Enquist et al., 2010), speaks against the possibility that ape culture is often – or perhaps ever – underlain by action copying. In clarifying any potential differences between our own species and our closest extant relatives it becomes possible to help approximate the point in our evolutionary past when our remarkable capacity for culture evolved. Our results suggest that in contrast to previous assertions, novel action copying may have evolved within our own hominin lineage, i.e., after the split from other great ape lineages (Tennie et al., 2017). If true, this would mean that the ape action copying hypothesis is false.

In sum, ape behaviours can and do re-occur in the absence of action copying (Bandini & Tennie, 2019; Motes-Rodrigo et al., 2019) and apes reliably fail to copy novel actions under controlled conditions (Clay & Tennie, 2017; Tennie et al., 2012; Tomasello et al., 1997)– even when majority demonstrations are used (this study). The most parsimonious explanation for these and other patterns is that action copying plays a minimal or no role in wild ape cultures.

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