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Original Article

The impact of imitative versus emulative learning mechanisms on artifactual variation: implications for the evolution of material culture☆

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ABSTRACT

Cultural evolutionary approaches highlight that different social learning processes may be involved in the maintenance of cultural traditions. Inevitably, for traditions to be maintained, they must be transmitted with reasonably fidelity. It has been proposed that 'imitation' (i.e., the direct copying of actions of others displayed in tasks such as toolmaking) generates relatively low rates of copying error. As such, imitation has often been ascribed an important role in the maintenance of traditions and in the 'ratcheting' of technological complexity over time. Conversely, 'emulation' (i.e., the copying of a result but not the behaviors that have led to that result) is allegedly associated with the production of relatively higher rates of copying error. However, to what extent these different social learning mechanisms generate distinct patterns of variation during the manufacture of material traditions remains largely unexplored empirically. Here, a controlled experiment was implemented using 60 participants who copied the shape of a 3D 'target handaxe form' from a standardized foam block. In an 'imitation condition', 30 participants were shown manufacturing techniques employed in the production of the target form *and* the target form itself. Conversely, in an 'emulation condition', 30 participants were shown only the (target) form. Copying error rates were statistically different, being significantly lower in the 'imitation' condition compared to the 'emulation' condition. Moreover, participants in the imitation condition matched the demonstrated behaviors with significantly higher copying fidelity than the alternative condition. These results illustrate that imitation may be imperative for the long-term perpetuation of visibly distinct archaeological traditions, especially in the case of lithic (reductive) traditions, where copying error rates can be expected to be relatively high. These findings, therefore, provide evidence that imitation may be required to explain the prolonged continuity of broad shape fidelity such as that seen in traditions of 'handaxe' manufacture during the Pleistocene.

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1. Introduction

Models of cultural evolution highlight the importance of understanding the social mechanisms that underlie historic trends in human technological continuity and change (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Jordan, 2015; Lycett, 2015; Mesoudi, 2011; O'Brien & Shennan, 2010). One challenge, however, is to understand precisely how social learning can explain lasting, stable trends in the artifactual record, which draws the focus onto how different social learning mechanisms act as vehicles of 'cultural inheritance'.

In the context of cultural evolutionary models, social learning is defined as the non-genetic transmission of behavioral patterns by observation of another individual and/or their behavioral outcomes and products (Heyes, 1994). In contrast, individual learning is a non-social process whereby an individual learns to achieve a goal by 'trial-and-error'. The study of the specific social learning mechanisms that can explain the perpetuation of distinct cultural variants has been undertaken predominantly within the field of comparative psychology (Dean, Kendal, Shapiro, Thierry, & Laland, 2012; Galef, 2012; Heyes, 2012; Whiten & Mesoudi, 2008). Indeed, convincing evidence for social learning capabilities in animals closely related to humans has been derived from controlled experimental studies on tool-use in chimpanzees (*Pan troglodytes*). For example, separate captive groups of chimpanzees have been shown to pass on distinct multi-action tool-use techniques along multiple-participant 'generations' (Horner, Whiten, Flynn, & de Waal, 2006). Such studies lend support to the notion that social learning processes lead to the perpetuation of separate stable behavioral 'traditions' over the course of long-term cultural transmission in wild populations (Whiten, Horner, & de Waal, 2005; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). Such comparative research, of course, allows us to draw a common base with our ancestors, in the sense that commonly shared (i.e., phylogenetically homologous) cultural capacities may have shaped the earliest examples of prehistoric artifactual traditions seen in the archaeological record (Lycett, Collard, & McGrew, 2009; McGrew, 1992; Whiten, Schick, & Toth, 2009).

Few ethnographic and experimental approaches to date, however, have actively researched the impact of different social learning

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mechanisms on patterns of variation in the archaeological record. In a rare example, Bettinger and Eerkens (1999) suggested that copying successful or prestigious individuals leads to greater homogeneity in artifact form (projectile points) than guided variation (i.e., social learning followed by individual trial-and-error). In a related study, Mesoudi and O'Brien (2008) tested the effects of social versus individual learning experimentally in a virtual hunting game context where participants 'constructed' their own digital arrowhead. In the virtual game environment, hunting success depended on the compositional nature of the arrowheads. The study provided support for the hypothesis of Bettinger and Eerkens (1999), showing that experimentally-induced indirect bias (the copying of successful group members' virtual arrowheads) generated greater artifactual homogeneity than experimentally-induced guided variation. Such studies help to highlight the important contribution that can be made to understanding material cultural evolution, specifically by examining how different social transmission mechanisms potentially generate detectable macroevolutionary changes in artifactual culture.

Definitions of different social learning mechanisms relevant to such issues, have been formulated on the basis of extensive studies across the animal kingdom (Fisher & Hinde, 1949; Galef, 1992, 2012; Heyes, 1994; McQuoid & Galef, 1993; Visalberghi & Fragaszy, 2002; Whiten, McGuigan, et al., 2009; Zentall, 2003). Distinctions between different forms or 'mechanisms' of social learning are ultimately based on distinctions between the precise means by which one individual 'copies' aspects of another individual's behavior (Whiten, McGuigan, et al., 2009). One distinct form of social learning is 'imitation' (Thorndike, 1898), which is differentiated from other forms of social learning mechanisms because the social learner copies the precise details and sequences of behavioral actions employed by a 'model' (Byrne, 2003; Heyes, 1993; Tomasello, Kruger, & Ratner, 1993). Hence, a straightforward operational definition of imitation (see e.g., Whiten, McGuigan, et al., 2009) states simply that it is the copying of demonstrated behavior(s) exhibited by a model (e.g., the actions involved in the production of an artifact). Conversely, 'emulation' refers to observational learning whereby only the outcome of an individual's behavior on an object or objects is copied by another, but not necessarily the exact actions used by the demonstrator (Nagell, Olguin, & Tomasello, 1993; Tomasello, Davis-Dasilva, Camak, & Bard, 1987; Whiten, McGuigan, et al., 2009). This is sometimes referred to as 'end-state copying' in a sense that emulation "is classed within copying, but it is only the end-state(s) of what the model has done that is copied" (Whiten, McGuigan, et al., 2009, p. 2419). The crucial distinction with 'imitation', therefore, is that emulation is purely a 'result-oriented' form of learning, and the behavioral actions or 'techniques' employed by the model are not copied directly.

Fidelity inevitably plays a role in the 'cultural inheritance' or long-term maintenance of detectable patterns of cultural variation, such as those seen in the archaeological record. Hence, in discussions concerning which social processes might potentially explain the emergence of stable artifactual traditions, debate has often centered on the social learning mechanisms required for the high-fidelity transmission of cultural information (Galef, 1992; Heyes, 1993; Lewis & Laland, 2012; Shea, 2009). There seems to be wide agreement that imitation has the capacities for faithful propagation (i.e., 'high fidelity' copying) because of the more 'complete' and 'accurate' acquisition of both manufacturing actions and the end-state product of an artifact (e.g., Byrne & Russon, 1998; Hill, Barton, & Hurtado, 2009; Whiten et al., 2004). Thus, imitation – in theory – has important implications for the emergence and long-term propagation of distinct artifactual traditions (Mithen, 1999). Such a link between imitation and high-copying fidelity has been expressed by Tomasello (1999), Heyes (2009), Whiten, McGuigan, et al., (2009), and more recently, Lewis and Laland (2012). Importantly, imitation is also argued to sufficiently reduce cultural mutation rates necessary to sustain the long-term propagation of modifications in the course of cultural transmission (Shea, 2009). It is for these reasons that many scientists argue that imitation may also mediate the gradual and incremental nature of human cumulative cultural evolution, a process also referred to as 'ratcheting' (Boyd & Richerson, 1985; Dean et al., 2012; Kempe, Lycett, & Mesoudi, 2014; Shea, 2009; Tomasello, 1999; Tomasello et al., 1993). In other words, imitation has the capacity for change via descent ('descent with modification') because high copying fidelity allows for the long-term perpetuation of cultural traditions (descent) where novel modifications can be additionally incorporated. Therefore, a capacity for descent via high copying fidelity is a fundamental component of ratcheting.

Emulation is often contrasted with imitation in terms of copying fidelity, in the sense that emulation may not have the same capacity to sufficiently sustain cultural variants in the long-term (Galef, 1992; Tomasello, 1999; Tomasello et al., 1993). Since emulation involves only the 'end-state' copying of an object or behavior, but not the precise action sequences or 'behavioral means' to achieve the goal, emulation is, therefore, argued not to contain the sufficient capacity to maintain cultural traditions to the same extent as imitation (Tomasello, 1999). Therefore, emulation could (theoretically) be seen as a 'low-fidelity copying mechanism', at least on a relative basis with imitation.

Despite a general consensus that imitation provides a means for high fidelity transmission (e.g., Shea, 2009; Tomasello, 1999), cultural transmission parameters have not yet been well studied from an experimental viewpoint in specific regard to material culture, especially contrasting the outcomes of one learning mechanism against another (Mesoudi & O'Brien, 2009). Indeed, while material artifacts have been utilized within experimental models of cultural evolution, they have been primarily employed as tools for investigation of the social and psychological mechanisms involved in learning and transmission of cultural variants, rather than as a means of studying the impact of social learning mechanisms on artifactual variation for their own sake (e.g., Caldwell & Millen, 2009; Caldwell, Schillinger, Evans, & Hopper, 2012; Wasielewski, 2014). However, such studies are essential if we are to connect cultural evolutionary models to long-term empirical datasets such as the archaeological record. Indeed, there has been some doubt regarding the differential impact of contrasting social learning mechanisms on the long-term transmission of morphological artifactual modifications. For instance, in Caldwell and Millen's (2009) cultural transmission experiment, human participants were asked to each manufacture a paper airplane with the aim to make them fly the greatest possible distance. The findings of this study suggested that participants were equally good at incrementally improving the flight distance of the previous generation's paper airplanes, irrespective of whether they were placed in a teaching, imitation or emulation context. A recent experiment by Wasielewski (2014) expanded on Caldwell and Millen's (2009) findings by demonstrating that for less 'transparent' (i.e., 'opaque') tasks, such as those tasks where information from the end-state product are not enough to reconstruct the product at high fidelity, imitation may indeed be essential for the sustainability of cultural traditions. Thus, further experimental endeavor would certainly illuminate the cultural transmission mechanisms necessary for the long-term perpetuation of the earliest of stable artifact lineages known from the archaeological record (e.g., Mithen, 1999).

One of the main problems for the stable continuity (i.e., fidelity) of artifactual traditions is the introduction of 'copying errors', which are inevitably produced during repeated bouts of artifact replication due to perception limitations or other error-inducing factors (Eerkens, 2000; Eerkens & Lipo, 2005; Hamilton & Buchanan, 2009; Kempe, Lycett, & Mesoudi, 2012; Schillinger, Mesoudi, & Lycett, 2014a, 2014b). Indeed, Eerkens and Lipo (2005) showed via a computer simulation that copy errors may accumulate in a stochastic fashion over the repeated course of cultural transmission events. This model, which was later termed the "accumulated copying error model" or "ACE" model by Hamilton and Buchanan (2009), highlighted that compounded copying error has the potential to ultimately generate macro-scale level trends and cultural change. Schillinger et al. (2014a) meanwhile, recently investigated experimentally whether rates of shape copying error were affected

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differentially in reversible, or 'additive–reductive' manufacturing traditions such as basketry and pottery (i.e., where material can be both added and removed), as opposed to irreversible or 'reductive-only' traditions, such as stone-tool knapping (i.e., where material can only be removed during the manufacturing process). The results of these experiments demonstrated that cultural mutation rates are indeed process dependent, with reductive manufacturing traditions, such as stone knapping, carrying an inherently larger 'mutation load' compared to other forms of manufacturing processes. While such high mutation rates have implications for the 'evolvability' of cultural products (Schillinger et al., 2014a), there is also an increased potential that cultural traditions associated with high mutation loads face erosion in the long-term (Lycett, Schillinger, Kempe, & Mesoudi, 2015; Schillinger et al., 2014b). Hence, wherever specific shape properties are an important component of an artifactual tradition, these may require the implementation of 'fidelity mechanisms', specifically to counteract such high mutation rates. Such issues again stress the importance of better understanding the impact of specific social learning mechanisms on artifactual variation.

Given the foregoing, this study aimed to elucidate whether emulation and imitation exhibit significantly different levels of copying fidelity when material artifacts are produced manually. This experiment particularly emphasized the effects of social processes on shape variation, which is inevitably a component of many artifactual traditions. 'Shape' is inherently a *multivariate* property of artifacts in that it describes the association between multiple morphological features of 3D cultural artifacts, as opposed to 'size' which can be described adequately in univariate terms (e.g., via a single measure such as volume). Shape has long been utilized in the biological sciences to understand variation, evolutionary change, and the adaptations of biological organisms (Rohlf & Marcus, 1993; Slice, 2007) as well as by archaeologists to study temporal patterns of human behavioral change (see e.g., O'Brien and Lyman (2000) for review). Shape in the archaeological record may have specific functional and/or aesthetic relevance, which is one potential reason explaining its long-term preservation in lineages of artifactual products, and also makes it an appropriate target of study in cultural evolutionary analyses of artifactual variation (e.g., Chitwood, 2014; Lycett & von Cramon-Taubadel, 2015; O'Brien, Lyman, Mesoudi, & Van Pool, 2010; Okumura & Araujo, 2014). In that respect, shape may have come under the direct influence of evolutionary transmission biases promoting the preservation of shape components in the artifactual record (e.g., Buchanan & Collard, 2010), yet may also be affected by drift processes (Eren, Buchanan, & O'Brien, 2015; Lycett, 2008). Some of the first prehistoric cultural artifacts known to exhibit shape preservation across spatial and temporal spans are Acheulean handaxes, which were manufactured by extinct hominins from around 1.7 million years ago and continued to be made for over one million years thereafter (Gowlett, 2011; Roche, 2005). The reproduction of shape properties seen in the reductive stone tool technology of the Acheulean is particularly interesting given the experimental findings that 'reductive' manufacturing processes produce higher cultural mutation rates (i.e., copying errors) compared to 'additive' manufacturing traditions; thus, making stone tool traditions particularly prone to shape degradation in cultural systems (Schillinger et al., 2014a). In this respect, the study of the effects of different social learning mechanisms on shape preservation may offer answers as to how a decrease in cultural shape mutation rates might have been achieved under such conditions. Hence, findings from this study could further provide crucial implications regarding the specific mechanisms required for the emergence and spread of lasting artifactual shape traditions.

The purpose of this study was thus to understand whether contrasting social learning mechanisms generate diverging patterns of shape copying error within an experimental context where rates of variation can be compared in a controlled laboratory environment. Two contrasting experimental conditions were employed, utilizing a simple copying task. Participants were asked to faithfully copy a foam handaxe 'target' form using a standardized block of foam and a plastic table knife. The experimental conditions differed in respect to the learning conditions provided. In an 'imitation condition', participants were shown both the end product (i.e., target handaxe form) as well as a video that allowed them to directly observe a variety of techniques that were employed in the manufacture of the original target form. In the 'emulation condition', participants observed only the target form. Morphometric properties (size-adjusted shape data) of the 'handaxes' produced in each condition were then subjected to statistical analysis. It was predicted that if indeed imitation is a 'high fidelity' copying mechanism, then, this should result in significantly lower rates of copying error compared to the emulation condition. Additionally, we analyzed video data to test specifically whether differences in the rates of shape copying errors can confidently be attributed to the differences in the experimental learning contexts of each group. This second set of analyses involved statistical analysis of the videos, which recorded the participants manufacturing their handaxes in each condition. It was predicted that if participants in the 'imitation' condition were indeed imitating, then accordingly, they should match their behaviors to the video to a significantly greater extent compared with participants in the 'emulation' condition.

2. Methods and materials

2.1. Participants

A total of 60 participants took part in this experiment. The majority of these participants were undergraduates from the University of Kent who were recruited via advertisement. Of these, 30 were female (mean age = 23, SD = 5.2, age range = 18–44 years) and 30 were male (mean age = 24, SD = 4.8, age range = 18–34 years), thus facilitating even distribution of male and female participants between experimental conditions (see below). All participants were reimbursed with £4 for their participation. Ethical approval for this study was provided by the University of Kent Research Ethics Committee. All participants read a summary that briefed them about the nature of the experimental task and signed a consent form prior to the task.

2.2. Materials

The 'target model form' copied by participants in this experiment was made from foam blocks (described in Schillinger et al., 2014b and below) and modeled after the shape of an 'Acheulean handaxe' (Fig. 1). Handaxes of the 'Acheulean techno-complex' first appear in the archaeological (Palaeolithic) record around 1.75–1.5 million years ago in Africa (Beyene et al., 2013; Lepre et al., 2011). They later appeared in large parts of Asia and western Europe (Beyene et al., 2013; Lepre et al., 2011) and subsequently remained a persistent feature of the archaeological record for over one million years (Clark, 1994; Lycett & Gowlett, 2008). Handaxe artifacts are widely agreed to constitute a shift from the manufacture of relatively simple cutting tools (i.e., flakes), via knapping procedures not necessarily directed towards producing deliberate forms in the residual block of stone (Toth, 1985a), to the strategic shaping of the eventual artifact (Gowlett, 2006; Roche, 2005; Schick & Toth, 1993).

There were specific reasons why we elected to conduct a copying task that involved the production of handaxe replicas from foam blocks. For safety and feasibility reasons actual stone knapping exercises were not employed, especially given that large numbers of participants were required to make statistical analysis viable. The manufacture of stone handaxes requires extensive practice and relevant skills which are learned over months or even years (Edwards, 2001) and may result in serious injury (e.g., Whittaker, 1994). By contrast, foam handaxe manufacture was sufficiently easy such that it facilitated the recruitment of suitable numbers of participants who do not have specialized manual manufacturing skills. The production of foam 'handaxes' is a relatively simple artifact manufacturing task, but one that requires

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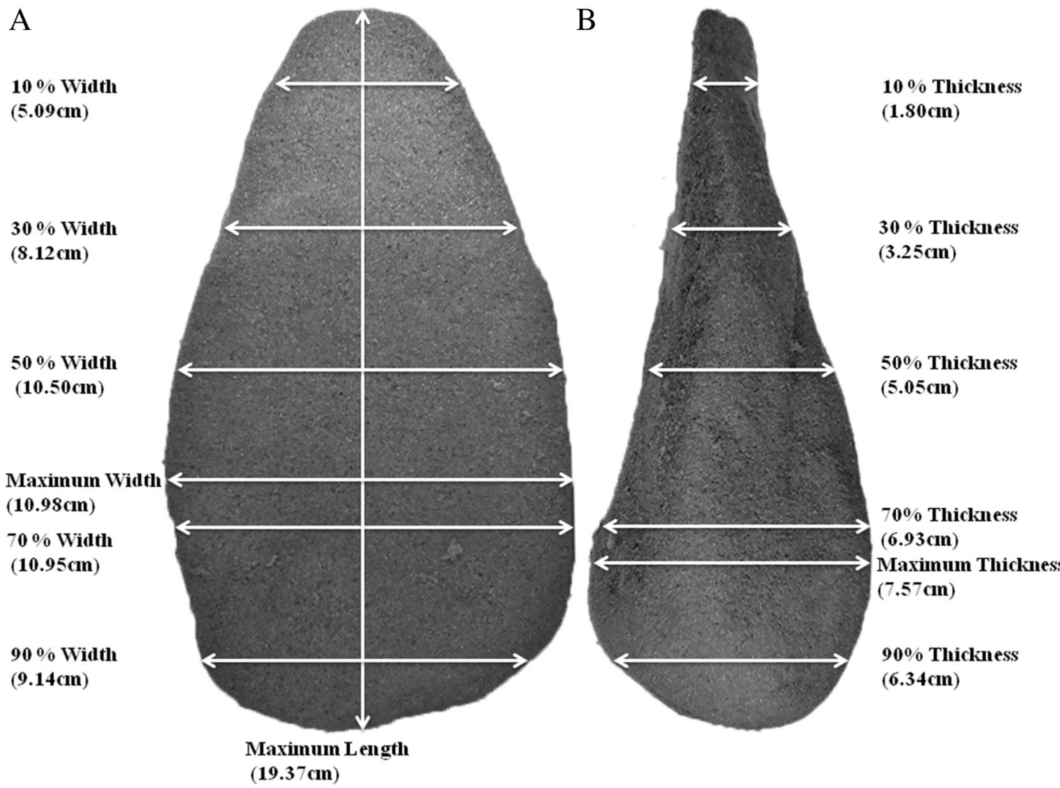

Fig. 1. Target foam model handaxe used during experiment.

participants to manipulate multivariate and interrelated three-dimensional shape properties such as relative lengths, widths and thicknesses in order to invoke the characteristic shape of these artifacts (Gowlett, 2006). Given this, we have argued that in regard to the study of *cultural* evolutionary phenomena, simple experiments that require participants to replicate certain aspects of handaxe form (i.e., their size and/or shape) make a particularly useful subject of study, for directly analogous reasons to those that lead biologists to use 'model organisms' in the context of evolutionary studies (Lycett et al., 2015; Schillinger et al., 2014a, 2014b).

Standardized blocks supplied by OASIS DRY SEC foam, a type of dense, porous and hard floral foam, were used to make the handaxe replicas. These blocks are machine-cut in a pre-determined, standardized format and, therefore, allowed for maximum replicability of starting conditions. The blocks measured 22.3 cm in length, 11 cm in width and 7.8 cm in thickness. The experimental 'handaxe replicas' were produced from this foam using a simple plastic table knife. The plastic knife was suitable for use in either the left or right hand. Dimensions and visual display of the standardized foam block and the plastic table knife can be found in the supplementary material (Figs. S1 and S2). Participants were also provided with the option to use mouth protection and eye protection glasses to protect against irritations resulting from small parts of dispersing foam dust. All participants also wore a lab coat to protect their clothing from the foam dust. Video recordings were undertaken using a DSLR Fujifilm Finepix HS 20 (focal range of 24–720 mm) and a tripod.

2.3. Experimental conditions

The experiment was divided into two alternative conditions.

2.3.1. Condition 1: the imitation condition

The first condition tested the effects of imitative learning on the production of shape copying error. Participants were shown the relevant manufacturing techniques involved in the production of the target form and were also shown the end product of a 'target handaxe form' (Fig. 1). These action sequences were displayed in the form of a video demonstration that was 4 min and 50 s in length. The video illustrated, in sequence, the main procedures and steps taken to produce the target model. It should be noted that the video demonstration was produced and edited in a fashion where the prolonged exposure to the final target form was avoided. Thus, participants in the imitation condition were not exposed to the final target form any longer than the participants in the alternate condition. The choice of a video demonstration was the preferred method over the alternative option of a human demonstrator because the video format allowed for the 'total repeatability' of the demonstrated behaviors across all participants.

2.3.2. Condition 2: the emulation condition

The second condition assessed the effects of end-state copying (emulative learning) on the production of shape-copying errors in the copying task. A video demonstration was not provided in this condition. Participants were only given the opportunity to view the end product of the target handaxe model prior to the copying task. This condition was referred to as the 'emulation' condition.

2.4. Experimental design and procedure

All 60 participants were divided into the two experimental conditions so that there was an equal number of participants ($n = 30$) in each condition. Within each condition, participants were equally divided into 15 females and 15 males to control for sex differences. In addition, both sample groups consisted each of 27 right-handed individuals (90% of the group) and three left-handed participants (10% of the group). This distribution of left-and right-handed individuals is representative to that of the natural population distribution of modern human populations (Corballis, 1989; Raymond, Pontier, Dufour, Pape, & Møller, 1996; Toth, 1985b). Inconsistencies in handedness were unlikely to be of relevance given the overall experimental design and also because numbers were balanced across conditions.

In the experimental task, all participants were assigned to an experimental condition alternatively and took part only once in one of the two conditions. In both conditions, participants were asked to copy the shape of the foam target handaxe form as accurately as possible. All participants were advised to pay attention to the overall form and shape features of the target form but to prioritize the copying of the handaxe *shape*. The instructions also clarified that video recording would take place during the copying task for further analysis. To encourage their motivation to perform well, all participants were informed that the person who produced the most accurate handaxe copy (the replica with the lowest shape copying error), would win a prize in the form of a £20 book voucher from a well-known internet book seller in addition to their £4 reimbursement.

All participants read the task instructions before beginning the experimental task. In the imitation condition, participants were then shown the video demonstration illustrating the action sequences employed in the production of the target form (participants in the emulation condition proceeded immediately with the next step in the experimental procedure). In both conditions, participants were provided with one minute to inspect and handle the target handaxe form from all sides and were verbally reminded of the instructions. When the minute was over, they were placed at a table and provided with one standardized foam block and a plastic knife for the manufacturing task. They were given a time frame of 20 min to complete the copying task. Previous analyses have shown that this is ample time for participants to conduct the required replication task effectively (Schillinger et al., 2014b). To control for memory effects, the target handaxe remained with the participants throughout the experiment. The participants were also advised that they may compare the target handaxe form with their own foam replica from any side or angle at any point desired during the experimental task. All participants were provided with a countdown clock which allowed them to track the remaining time of the experiment whenever desired. In addition, at five minute intervals the participants were reminded of the remaining time left until task completion. There was only one attempt at the experimental task but all participants managed to complete the task within the time limit given.

Participants were also allowed to wear spectacles and contact lenses if so required for close-up tasks to avoid major inconsistency in visual perception. The use of additional external aids to improve perceptual accuracy (e.g., scaled rules) was not permitted.

2.5. Video analysis

An analysis of the video recordings of participants' behavior was conducted to test whether participants in the imitation condition matched the behaviors seen in the video demonstration to a higher degree compared to participants in the emulation context. Thus, the aim of the video analysis was to collect direct evidence for imitation.

Every video was systematically tested for the degree to which each participant's manufacturing behaviors matched the video demonstrations, therefore evaluating the level of copying fidelity. Copying fidelity was assessed by assigning one 'fidelity code' to every video in both the imitation and emulation condition. The fidelity code ranged from 0 to 7; the lowest degree of copying fidelity being scored as zero and the highest degree of copying fidelity being scored as seven.

Overall, the assignment of one fidelity code to every video could be understood as the *combined result* of three factors: 1) number of demonstrated behaviors that were copied from the video demonstration (also termed 'matched behaviors'), 2) sequence adherence, and 3) presence of 'aberrant behaviors' (i.e., behaviors not shown in the video demonstration). In the first instance, the fidelity code reflected the numbers of demonstrated behaviors that were copied. Thus, the higher the number of 'matched behaviors', the higher the fidelity code assigned. However, the assignment of the final fidelity code was also influenced by the sequence adherence and presence of 'aberrant behaviors'. The coding system systematically 'clustered' varying combinations of these three factors within one fidelity code. The fidelity coding system can be found in the digital supplementary material (Text S1). The three main constituents of the coding procedure are also described in the following sections.

2.5.1. Number of demonstrated behaviors

Scores of 'matched behaviors' were counted for each video. Matched behaviors were identified as the behaviors that were copied from the demonstration video (Fig. 2). Table 1 lists the six behavioral categories that would count as 'matched behaviors'. More detailed definitions of the six behavioral categories identified in the video demonstration can also be found in the supplementary material section (Text S2). The highest achievable copying score would be a score of six (i.e., one score for each of the six demonstrated behaviors). For two specific behavioral categories (i.e., categories [1] cutting corners and [2] cutting margins), the score was based on the number of their occurrence. Here, participants could score in one of two subcategories for each of those behaviors. One subcategory identified if the exact consecutive count was reached as displayed in the video (categories 1.1 and 2.1 in Table 1). The second subcategory identified whether at least 50% of the count was reached (categories 1.2 and 2.2 in Table 1). The purpose of the additional behavioral categories was to show that participants still copied the demonstrated behavior despite failing to match the exact count as displayed in the video. However, it may be noted that a score in the subcategory which identified a 50% count of corner and margin cutting could affect the final fidelity code awarded (i.e., result in a potentially lower-ranking code).

2.5.2. Sequence adherence

Each video was also assessed as to whether it followed the exact sequence of manufacturing behaviors as illustrated in the video demonstration (chronology as displayed in Fig. 2). If the sequence was also matching with that of the demonstration, the video would be given a 'complete sequence' status. If a video's sequence of manufacturing techniques was not matching with that of the video demonstration, it would be given a 'mixed sequence' status. In order to score a 'complete sequence' participants were expected to copy *all* demonstrated behaviors. Mixing up the sequence and/or otherwise missing one or more demonstrated behaviors was treated as a deviation from copying fidelity and resulted in a fidelity code below the 'complete sequence' category.

2.5.3. Presence of aberrant behaviors

'Aberrant' behaviors were also incorporated into the composite fidelity score. Aberrant behaviors were defined as any behaviors exhibited by a participant that were not displayed in the demonstration. If aberrant behaviors were also present, this additionally affected the final fidelity code awarded. Aberrant behaviors were assessed on an 'absence or presence' basis. The presence of aberrant behaviors was regarded as deviation from full copying fidelity and a sequence violation. In the presence of one or more aberrant behaviors, the final fidelity code awarded was one below the recorded number of matched behaviors in combination with the 'mixed sequence' status.

Generally speaking, the fidelity coding system followed a systematic procedure by which a higher level of matching to the demonstrated behavior resulted in the assignment of a 'higher' fidelity code. In other words, the more of the demonstrated behaviors were copied, the higher the number of the fidelity code. Yet, this coding system also took into consideration multiple factors of deviations from the video demonstration and incorporated these within one integrated multi-dimensional definition of 'copying fidelity'. To establish intra-rater reliability, we also double-coded a subset of the videos. Intra-class correlation demonstrated a strong agreement between the original set of scores and the retest analysis of 10 participant videos (i.e., 30% of the video data), thus confirming intra-rater reliability ($r(10) = 0.996$, $p = 0.0001$).

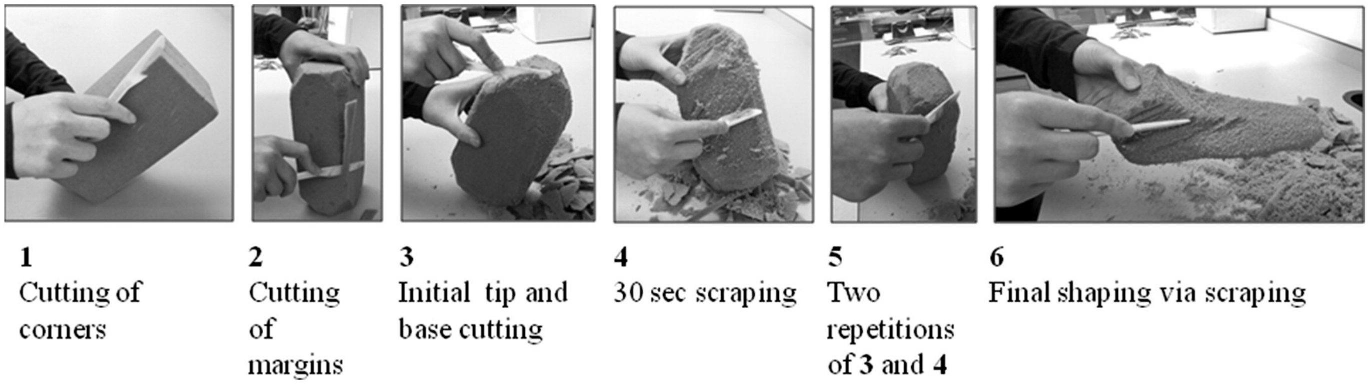

Fig. 2. The six manufacturing techniques displayed in the video demonstration.

2.6. Morphometric procedure and computation of shape error data

For all 'handaxe replicas' including the 'target' model, a set of measurements was recorded comprising a total of 42 morphometric variables. 28 of these measurements were obtained from the plan-view and 14 from the profile-view. To capture the 42 bilateral and lateral measurements, a digital grid was placed on the photographic images of the plan-view and profile-view perspectives of each handaxe replica (Fig. S3). All measurements were recorded digitally by importing photographic images of each handaxe replica into a freely accessible morphometric software tpsDig (v2.16, Rohlf, 2010). Photographic images were obtained by placing each handaxe replica on a lightbox which facilitated the capturing of the shape outline in the photographs. A Fujifilm DSLR camera (30× zoom lens: 24–720 mm) was used to take the photographic images and was firmly attached to a copystand. To acquire homologous measurements, a standardized orientation protocol was applied. The orientation protocol utilized here was a slightly modified variant from that originally employed by Callow (1976) and also recently applied by Costa (2010). A detailed description of the orientation protocol can be found in the digital supplementary material (Text S3).

Since the main aim of the analyses was to investigate the effects of social learning mechanisms on shape attributes, the next step included the extrapolation of shape data from the raw measurement data. This was achieved by size-adjusting the raw data using the geometric mean method (Falsetti, Jungers, & Cole, 1993; Jungers, Falsetti, & Wall, 1995). Size-adjustment via the geometric mean method has been demonstrated to efficiently control for scaling variation between objects by creating a 'dimensionless scale-free variable' whereby the original shape data are preserved, and for these reasons is widely used in biological studies of shape variation (Falsetti et al., 1993; Jungers et al., 1995). In more specific mathematical terms, the geometric mean derived from a series of n variables ($a1$, $a2$, $a3$ … an) is correspondent to $\sqrt[n]{a_1 \times a_2 \times a_3 \times \ldots \times a_n}$. Hence, the geometric mean may be described simply as the nth root of the product of all n variables (Jungers et al., 1995). The method proceeds on a specimen-by-specimen basis, dividing each variable in turn by the geometric mean of the variables to be size-adjusted. Hence, to implement the method, the geometric mean of each foam replica was calculated separately and, thereafter, each of the 42 morphometric variables for each specimen was divided by that particular specimen's geometric mean.

Table 1
Behavioral categories for 'matched' behaviors.

Categories	Knife	Foam
1.1	Cutting	'Corner cutting': minimum six consecutive corners
1.2	Cutting	'Corner cutting': minimum of three non-consecutive corners
2.1	Cutting	'Margin cutting' minimum six consecutive margins
2.2	Cutting	'Margin cutting': minimum of three non-consecutive margins
3	Cutting	Initial tip and base cutting
4	Scraping	30 s scraping (dominant foam removal technique)
5	Both	Two repetitions of scraping and tip and base cutting
6	Scraping	Final shaping via scraping

For corner and margin cutting, participants could only score in one of each behavior's subcategory (e.g., 1.1 *or* 1.2).

To compute the shape error data used in the subsequent statistical analyses, the 42 size-adjusted variables for each handaxe replica were simply subtracted from the equivalent 42 variables of the target model. Lastly, mean shape errors were calculated for each of the 42 variables across the 30 handaxe copies produced in each of the two experimental conditions. It is these 42 mean error rates for each experimental condition that were used in the subsequent statistical analyses.

2.7. Statistical analysis

2.7.1. Analysis of shape copying error

In a first statistical analysis, the shape error data between the imitation and emulation conditions were compared using a non-parametric Mann–Whitney U test, where $\alpha = 0.05$. Both the Monte Carlo p-value (10,000 random assignments) and the asymptotic p-value were documented. The comparison of the rates of shape copying error was undertaken in PAST v2.17 (Hammer, Harpner, & Ryan, 2001).

2.7.2. Analysis of 'fidelity codes'

To test whether participants in the imitation condition displayed a significantly higher level of copying of the relevant manufacturing techniques compared to the emulation condition, the fidelity codes assigned to the videos were compared statistically between conditions. A Pearson's chi-square test was used to assess whether there was a significant difference in the frequencies of the categories of fidelity codes between conditions. The Pearson's chi-square test was undertaken in IBM SPSS Statistics v20.

The Pearson's chi-square test was further supported by an additional quantitative analysis of the participants' scores of *matched behaviors only* between the imitation and emulation condition. This analysis simply compared the central tendencies (median values) of the matched behaviors in each condition. The purpose of this analysis was to establish whether any effect for contrasting levels of behavioral matching would emerge when using only the 'matched behaviors' element of the coding system. Note that scores from the two behavioral subcategories for removing corners and margins were merged into one for each of the behavioral criteria to facilitate the data analysis. The merged behavioral categories incorporated the possibilities of cutting three to six corners or margins. Since the data failed normality tests, a non-parametric Mann–Whitney U test was used to compare the data statistically. This second set of statistical analyses was again undertaken in IBM SPSS Statistics v20.

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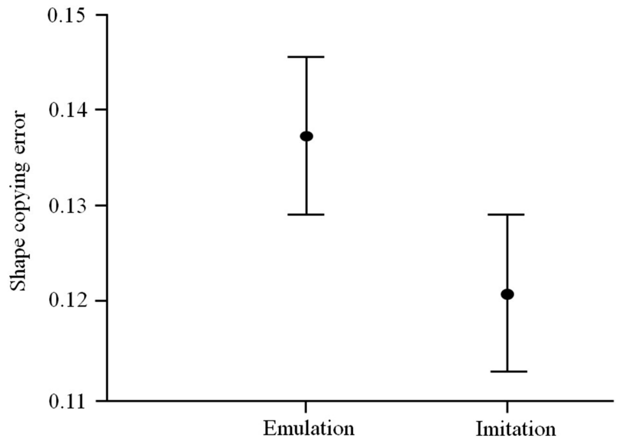

Fig. 3. Mean shape error in the emulation and imitation conditions. Whiskers mark +/− one standard error.

3. Results

3.1. Shape copying error

In the imitation condition, shape error displayed a mean of 0.121 (SD = 0.05) and in the emulation condition the mean shape error was 0.137 (SD = 0.047) (see Fig. 3). The mean shape copying error rates for every morphometric variable for the imitation and emulation conditions can be viewed in the supplementary material (Figs. S4 and S5). The Mann–Whitney *U* test demonstrated a significant difference in overall copying error rates for shape in the imitation condition compared to the emulation condition ($U = 652$, asymptotic $p = 0.0393$, Monte Carlo $p = 0.0383$). The test illustrated that participants created significantly less shape copying errors when they viewed the video in the imitation-learning context compared to participants in the emulation context.

3.2. Video analysis

The majority of participants in both conditions scored between 0 and 5 fidelity coding categories. Since none of the participants in either condition scored in the two highest ranking fidelity codes 6 and 7, this led to those two code categories to be removed from the chi-square analysis (Table 2). In addition, due to the low numbers of participants in code 5, the participant who scored in this category was merged with the lower-ranking fidelity code 4, resulting in the code category 5 to be collapsed with category 4. Therefore, the contingency table for the chi-square analysis contained five fidelity copying categories (fidelity codes 0–4) versus the two learning contexts (imitation/emulation) (i.e., a 2 × 5 contingency table). In the statistical test assessing the main video analyses, a Pearson's chi-square test established a significant difference in the frequencies of the categories of fidelity codes between the two experimental conditions ($\chi^2 = 26.065$, DF = 4, n = 60, asymptotic $p = 0.00003$, Monte Carlo $p = 0.0001$). Hence, the test provided evidence that participants in the two experimental conditions possessed contrasting fidelity scores.

When considering the frequency distribution across the fidelity codes that represented higher levels of copying fidelity (Table 2), more than 50% of the participants in the imitation condition reached fidelity codes three to five. By reaching codes three to five, this meant that the majority of participants in this condition copied between three to six demonstrated behaviors. Conversely, only seven percent of participants in the emulation condition reached fidelity code three which means that a minority matched, maximally, three to four of the demonstrated behaviors. In this case, these seven percent of participants in the emulation context innovated behaviors such as those demonstrated in the video demonstration through individual learning. By contrast to participants in the imitation condition, the majority of participants in the emulation condition (76%) were placed in lower-ranking fidelity codes, such as zero and one. Only around 27% of participants in the imitation condition are found in these lower-ranking fidelity codes.

In the final step of the behavioral analysis, the differences in the scores of only the 'matched behaviors' between the experimental conditions were assessed. Fig. 4 shows that higher percentages of participants in the imitation condition copied the six demonstrated behaviors, compared to participants in the emulation condition. When averaging the scores for all participants in each condition across the six demonstrated behaviors, participants in the imitation condition scored an average of 3.533 matched behaviors (SD = 1.408). Participants in the emulation condition had a mean score of 1.233 matched behaviors (SD = 1.331). When comparing the different individual scores for all six behaviors between the two experimental groups, a Mann–Whitney *U* test established that participants in the imitation condition copied significantly more of the demonstrated manufacturing techniques compared to participants in the emulation condition (Mann–Whitney *U* test: $U = 115$; $n_1 = 30$; $n_2 = 30$; asymptotic $p = 0.0001$; Monte Carlo $p = 0.0001$). Therefore, the results of the Pearson's chi-square and Mann–Whitney *U* test reveal a clear pattern that participants in the imitation condition matched the behaviors displayed in the video to a considerably higher degree compared to participants in the emulation condition.

Altogether, the results of this experiment demonstrated that participants in the imitation condition generated significantly lower levels of shape error, compared to the emulation condition. It could also be demonstrated that the low rate of shape error in the imitation condition was associated with participants copying demonstrated manufacturing techniques significantly more so than participants in the emulation condition. Thus, differences in the shape error rates between the two conditions could be confidently traced to the differences in the learning context.

4. Discussion

Recent experimental and ethnographic studies suggest that distinct individual-level social transmission processes generate different patterns of variation in material culture, which affect the evolution of detectable morphological attributes on the population-level (Bettinger & Eerkens, 1999; Kempe et al., 2012; Mesoudi & O'Brien, 2008). In the last two decades, research from the comparative psychology literature has emphasized the study of distinct social learning processes in the quest for the specific conditions required for the 'heritable continuity' underlying the emergence and long-term preservation of cultural traditions (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Galef, 2012; Tomasello et al., 1993; Whiten, McGuigan, et al., 2009). It is due to the 'complete' transmission of manufacturing techniques *and* end-state product that imitation is argued to contain the capacity to considerably reduce variation-generating rates of cultural mutation which threaten to erode emerging patterns of artifactual traditions (Shea, 2009). Conversely, emulation is often assumed not to be capable of transmitting cultural modifications at the level of copying fidelity required to maintain 'artifactual traditions' over the long-term, because only the end-state is copied rather than the exact behavioral patterns involved (Tomasello, 1999; Whiten, McGuigan, et al., 2009). For this reason, emulation has been hypothesized potentially incapable of sufficiently impeding rates of 'cultural mutations' to explain the long-term preservation of lasting artifactual 'traditions' in the archaeological record (Shea, 2009).

Consistent with the theoretical predictions, this study provides evidence for the hypothesis that imitative learning (i.e., the goal-directed copying of a model's manufacturing techniques) can significantly reduce shape copying error compared to a contrasting social learning mechanism where the manufacturing techniques are not directly

Table 2
Percentages of participants that fit the respective fidelity codes of the main coding system in the imitation and emulation conditions.

Fidelity Code	Copying behaviors	Emulation (in %)	Imitation (in %)
0	0 to 1 matched (plus aberrant behavior)	66.67	10.00
1	1 to 2 matched (plus aberrant behavior)	10.00	16.67
2	2 to 3 matched (plus aberrant behavior)	16.67	16.67
3	3 to 4 matched (plus aberrant behavior)	6.67	20.00
4	4 to 5 matched (plus aberrant behavior)	0	33.33
5	5 to 6 matched (plus aberrant behavior)	0	3.33
6	6 matched (mixed sequence)	0	0
7	6 matched (perfect sequence)	0	0

copied (i.e., emulation). These findings suggest that imitation has the capacity for high-fidelity copying and so would better ensure the preservation of detailed morphological manifestations (i.e., 'heritable continuity'), underlying cultural lineages of 'shaped' artifactual traditions. The results further suggest that in the absence of high-fidelity copying of *manufacturing techniques*, the cultural mutation rate in the shape morphology of cultural artifacts is considerably higher, which potentially renders 'emulated' cultural traditions relatively unstable over the course of cultural transmission.

The video analysis that we conducted provided further evidence that the copy-error differences between the two conditions were indeed due to differences between the two social learning contexts. However, it should be noted that despite the significant differences in copying fidelity between the distinct learning contexts, the video analysis also demonstrated that even in the imitation condition, participants failed to copy the *entire* set of behavioral demonstrations. In addition, most participants who were exposed to the video demonstration also engaged in aberrant behaviors, such as innovative uses of the plastic knife or behavioral modifications of the techniques demonstrated. A few explanations and implications regarding these observations may be suggested. First of all, in the light of the experimental set-up, it can be noted that participants were given only one opportunity to view the video demonstration. This may have impacted memory recall to some extent and may explain why participants in the imitation condition did not copy all behaviors perfectly. In addition, there is also the possibility that participants deliberately engaged in novel behaviors in the attempt to complete the task to the best of their abilities (i.e., they may have attempted to 'improve' upon the demonstrated set of behaviors). Importantly, however, the analysis illustrates that while participants in the video condition did not perfectly copy all the behaviors demonstrated, they clearly engaged in imitative learning *sufficiently* more so compared to participants who have not viewed the demonstrations, to significantly reduce copy-error rates. In other words, the results from

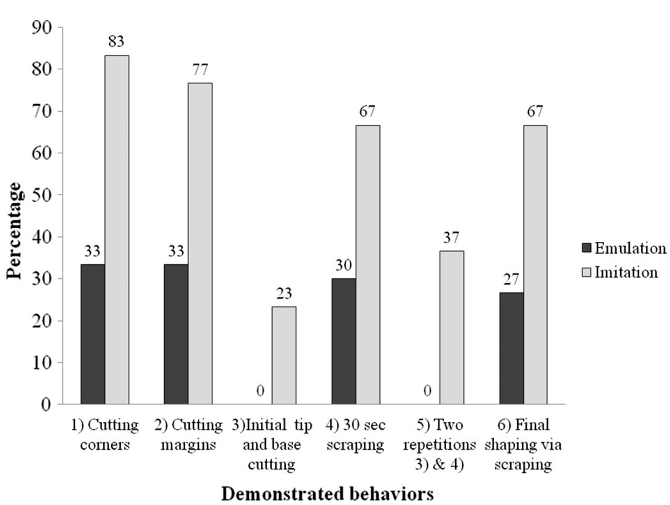

Fig. 4. Distribution of participants in the imitation and emulation conditions engaging in the six categories of matched behaviors.

the video analysis demonstrated that the *tendency* toward higher copying fidelity induced by imitative learning was sufficient to generate statistically significant effects, *even despite* the fact that participants in the imitation condition did not copy the demonstrated behaviors 'perfectly' and had only one demonstration and one attempt.

The findings of this research also have direct implications with regard to the social mechanisms required for the emergence and perpetuation of some the earliest of prehistoric artifactual traditions, such as is seen in the Acheulean. The Acheulean is famous for its imposition of high congruence in shape over time and space (Gowlett, 1984; Petraglia, Shipton, & Paddayya, 2005; Wynn, 2002). It is sometimes argued that social learning with high copying-fidelity was required for such high levels of homogeneity in shape to persist (Mithen, 1999; Nielsen, 2012; Wynn, 1993). Indeed, it has been argued that imitation may have been required in the Acheulean not only to countermand the effects of copying errors, but also to reduce specific costs (i.e., injury risks) involved in the manufacture of artifacts such as handaxes (Lycett et al., 2015). The results of this study support the idea that imitation could have been a means by which stability in shape traditions was maintained, especially in the face of relatively high copying errors (i.e., 'mutation loads') that are likely to accompany such 'reductive' processes of manufacture (Schillinger et al., 2014a). Hence, these findings suggest that hominin stone-tool manufacturers were employing imitation in order to obtain the manufacturing skills necessary for the cultural continuity of the Acheulean across time and space. Our results thus support Morgan et al.'s (2015) recent experimental work suggesting that relatively complex social learning mechanisms (beyond stimulus enhancement and emulation) would have been required to initiate, but more importantly sustain, Acheulean traditions. In particular, our results highlight the importance of imitation in the maintenance of a tradition involving shaping.

These findings, therefore, specifically inform about the role of social learning in the archaeological record and could be viewed as directly addressing what Mithen (1999, p.389) describes as "limited reference … to the nature of social learning of pre-modern humans, as reconstructed from the fossil and archaeological records". This also supports research literature stating that "the reliance on social learning suggests that complex technologies, which are costly to invent, learn, and maintain, should be more dependent on social learning than simpler technologies" (Mesoudi & O'Brien, 2008, p. 23). Imitation is often suggested to represent a prerequisite for cumulative cultural evolution (Boyd & Richerson, 1985; Dean et al., 2012; Lewis & Laland, 2012; Tomasello, 1999; Tomasello et al., 1993). However, the necessity for high fidelity transmission mechanisms, like imitation, to be present for the successful transmission of effective cultural variants in the face of cumulative copying error highlights a novel facet of cultural evolution that is perhaps underestimated in the current research literature. That is, that the longevity of cultural traditions depends largely on the active *containment* of variation (i.e., mutation) via high fidelity transmission mechanisms. The findings of this study support the hypothesis (see e.g., Shea, 2009) that imitation specifically allows for a significant reduction of continuously produced rates of mutation during intergenerational transmission, so facilitating the long-term continuity of selected cultural traits. Thus, by illustrating the capacity for imitative learning to reduce mutation loads that threaten to erode shape traditions during cultural transmission (Eerkens & Lipo, 2005; Hamilton & Buchanan, 2009; Kempe et al., 2012; Schillinger et al., 2014a, 2014b), it has been demonstrated *how* imitation assures the long-term survival of cultural traditions, despite the persistence of newly generated variation. It is not simply the case that imitation allows manufacturing techniques to be transmitted with greater ease culturally; but rather, that imitation, when incorporated into the cultural learning process, acts directly as a mutation-reducing 'repair' mechanism, actively countermanding the effect of copying errors that are also – inevitably – part of cultural processes over the longer term.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2015.04.003.

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