
Learning in the Acheulean: Experimental Insights Using Handaxe Form as a ‘Model Organism’

11

Stephen J. Lycett, Kerstin Schillinger, Marius Kempe, and Alex Mesoudi

Abstract

‘Learning’ is a process by which an individual gains new information. In the case of ‘social learning’, this process occurs because at least one individual has undertaken an activity that results in another individual learning something new. For an individual, therefore, ‘learning’ is an active process that takes place *in vivo*. For those faced with the challenge of studying learning in the Palaeolithic, however, all we are left with are inert objects (e.g., stone artefacts). Yet, understanding social learning during the Palaeolithic is a fundamental step toward understanding matters of our cultural evolution. Evolutionary biology, faced with similar problems, has made substantial progress in understanding matters of transmission, the effects of transmission on phenotypic variation, rates of mutation, etc. via the use of laboratory experiments, especially through the use of so-called ‘model organisms’. Here, we describe two experiments that use handaxe form in the manner of a ‘model organism’ in order to understand the effects of copying error. We go on to discuss why understanding these micro-evolutionary effects can ultimately lead to a greater understanding of learning dynamics in handaxe-making hominin populations. These experiments illustrate that the characteristic size and shape parameters of handaxe traditions will have been inherently unstable. In the case of shape, in particular, this suggests that a learning mechanism other than pure observation of others’ artefacts was used. Individual (trial-and-error) learning could conceivably constrain variation somewhat, but costs associated with knapping would encourage the adoption of social learning mechanisms that would countermand the inevitable effects of copying error with reduced risk to tool manufacturers.

Keywords

Acheulean handaxes • Copying error • Cultural evolution • Cultural mutation • Social learning

S.J. Lycett (✉)
Department of Anthropology, University at Buffalo SUNY, 380
MFAC-Ellicott Complex, Buffalo, NY 14261, USA
e-mail: sjlycett@buffalo.edu

K. Schillinger
Department of Anthropology, University of Kent,
Canterbury CT2 7NR, UK

M. Kempe • A. Mesoudi
Department of Anthropology and Centre for the Coevolution
of Biology and Culture, Durham University, Durham DH1 3LE, UK

11.1 Introduction

One of the enduring challenges facing Palaeolithic archaeology is to understand its basic database—i.e., knapped artefacts—in terms of behavioural, social, and cognitive implications, especially as these relate to wider questions of human evolution over the longer term (e.g., Isaac 1972; Gowlett 2010). It is, therefore, the hope of everyone working with the Palaeolithic record that key insights into these factors can be provided by examining, at various scales

of analysis, patterns observable in knapped stone artefacts, especially as recorded in terms of their variable attributes, form, and/or character (Clarke 1968; O'Brien and Lyman 2000; Lycett and Chauhan 2010). Major changes or trends in the Palaeolithic record inevitably draw particular attention, perhaps none more so than the appearance and temporal durability of so-called "handaxes" (Gowlett 2011).

The appearance of bifacial handaxes is often taken as evidence of a major behavioural shift in the production of stone tools by hominins, particularly in comparison with the preceding Oldowan (e.g., Roche 2005; Gowlett 2006; Lepre et al. 2011; Beyene et al. 2013). This is fuelled by the fact that their manufacture, either through the production and shaping of large flake blanks or via the reduction of stone nodules, involved not merely the production of discrete flake tools as was the case with the Oldowan, but serial knapping events strung together to produce the resultant form (Edwards 2001; Roche 2005). Formally, 'handaxes' are defined by the imposition of a long axis by means of invasive bifacial knapping to produce a relatively large (generally >10 cm in length) elongated, bilaterally-organized form, with a sharp edge that extends around a major portion of their extremities (Roe 1976; Isaac 1977; Schick and Toth 1993; Gowlett 2006). Evidence from experiments, residue analysis, usewear, design theory, cut-marks, and archaeological context has led many to contend that the form of such artefacts was driven, at least in part, by functional requirements relating to demands imposed by their use as cutting and/or chopping tools (e.g., Jones 1980; Keeley 1980; Roberts and Parfitt 1999; Domínguez-Rodrigo et al. 2001; Simão 2002; Gowlett 2006; Bello et al. 2009; Yravedra et al. 2010). Such artefacts first appear in the archaeological record of Africa ~1.75–1.5 MYA (Lepre et al. 2011; Beyene et al. 2013), but they subsequently appear in Western Europe and large parts of Asia, and remain a persistent feature of the archaeological record for over one million years (Clark 1994; Lycett and Gowlett 2008; Gowlett 2011). In specific terms, production of these artefacts represents a shift from the manufacture of relatively simple cutting tools (flakes) produced by bouts of knapping not necessarily directed toward the production of deliberate core forms (Toth 1985), to a situation where knapping events were strategically oriented toward *shaping* the residual block of stone (Roche 2005; Gowlett 2006).

Models of cultural evolution highlight the importance of understanding the mechanisms that underlie particular historical trends seen in the archaeological record (e.g., Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; O'Brien and Lyman 2000; Henrich and McElreath 2003; Mesoudi and O'Brien 2008; Mesoudi 2011; Shennan 2011; Lycett and von Cramon-Taubadel 2015). Following Darwin (1859), these models emphasize the co-existence of three essential factors in bringing about historical change via a process of 'descent with modification': (1) a mechanism

of inheritance, or 'learning' (2) the existence of variation in inherited properties, and (3) the differential representation of inherited variants through time (Mesoudi et al. 2004). What do we know about learning in prehistoric hominins from the production of artefacts such as handaxes? 'Social learning', in any form, is effectively a means by which certain information about a particular behavioural 'pattern' (however defined) is transmitted from one individual to another such that the behavioural pattern is, in turn, repeated (Heyes 1994; Byrne and Russon 1998; Whiten et al. 2004). It is sometimes (e.g., Mithen 1999) assumed that the repeated production of handaxe artefacts over time and space alone implies not only social learning, but specific forms of social learning such as imitation (i.e. copying of behavioural factors involved in their production, in addition to information gleaned from seeing the artefact alone). Such assumptions are certainly consistent with the macro-scale phenomenon of the 'Acheulean' technocomplex, whereby handaxes were repeatedly produced over large swathes of time and space (see above). Inevitably, however, any statement about learning from temporal and spatial patterns alone is limited in potency and would benefit from strengthening by other lines of enquiry. It may be worth considering in greater detail *why* the repeated production of broadly similar artefacts might be telling us something about social learning, especially in terms of the specific parameters that characterize the artefacts referred to as 'handaxes', using an evolutionary framework that moves from the micro to macro perspective.

Binford (e.g., 1983) noted some time ago that archaeology faces a fundamental dilemma in terms of trying to understand dynamic processes (human activities) from 'static' data (i.e. artefacts). Anthropologists, of course, can say things about people by studying *people*; archaeologists on the other hand, are forced to say things about people by studying *objects* people in the past left behind. This is the both the wonder and the curse of archaeology (Clarke 1968). In terms of understanding cultural evolutionary factors in the Palaeolithic, the basic problem is that we want to know something about learning and transmission from artefacts such as handaxes. In terms of their dislocation from the population dynamics and social processes that produced them, however, handaxes dug out of the ground are as dead as the fossils that palaeontologists use to reconstruct dynamic biological processes of transmission, the generation of variation, and the processes responsible for the sorting of that variation over time (i.e. evolution).

The analogy between 'dead' fossils and 'dead' artefacts in terms of understanding dynamic evolutionary processes is potentially an interesting one in terms of looking for prospective solutions. Over several decades, evolutionary biology has made substantial progress in understanding matters of transmission, the effects of transmission on phenotypic variation, rates of mutation, etc. via the use of laboratory

experiments (Bataillon et al. 2013). What is needed are experiments that attempt to understand how the dynamics of micro-evolutionary processes affect artefactual variation, in order to better understand what the macro patterns seen in the archaeological record imply on a more secure basis. Experiments have a long history in the study of archaeological artefacts, including stone tools (Johnson 1978). Surprisingly, however, there are only a small number of experimental studies that have expressly studied microevolutionary effects in artefacts in order to derive their macroevolutionary implications for the study of culture as seen in the archaeological record (Eerkens 2000; Mesoudi and O'Brien 2008; Kempe et al. 2012; Schillinger et al. 2014).

Interestingly, biologists frequently use so-called 'model organisms' in experimental studies of evolutionary processes. 'Model' organisms are used because they enable a more secure understanding of phenomena of wide interest, from seemingly discrete, even trivial, laboratory experiments. Commonly used model organisms, such as fruit flies (*Drosophila spp.*), tend to have a variety of characteristics that make them particularly suitable for such experiments, including economy, speed of replication, and controllability (e.g., Ashburner and Novitski 1976; Greenspan 2004; Ashburner et al. 2005). The most suitable model organisms thus display some of the complexities of the phenomenon of interest, yet are generally not so complex that they are unwieldy in experimental settings. Elsewhere (Schillinger et al. 2014), we have argued that in regard to the study of cultural evolutionary phenomena, simple experiments that replicate certain aspects of handaxe form (e.g., their size and/or shape) make a particularly useful subject of study.

Here, we describe two experiments that we have undertaken using handaxe form in the manner of a 'model organism' in order to understand the effects of copying errors, or 'mutation' in cultural evolutionary models. We go on to discuss these experiments in terms of why understanding micro-evolutionary effects, such as copy error, can ultimately lead to a greater understanding regarding issues of 'learning' in handaxe-making hominin populations of the Palaeolithic.

11.2 Experiment 1: Considering the Effects of Size Mutation in the Acheulean

In the context of artefactual variation, the study of variation generation at a microevolutionary level is the equivalent of studying genetic mutation in biology (Cavalli-Sforza and Feldman 1981; Eerkens and Lipo 2005). In principle, a number of potential mechanisms (e.g., deliberate embellishment) might lead to the generation of new cultural variants, and it is important to note that the deliberate, intentional introduction of variation does not invalidate an evolutionary

theory of cultural change (Mesoudi 2008). However, it is also recognized that unintentional copying errors (i.e. imperfect replication) during the manufacture of artefacts can lead to the introduction of novel variation in material traditions (Clarke 1968: 161; Eerkens and Lipo 2005; Hamilton and Buchanan 2009).

In our first experiment (Kempe et al. 2012) we were interested in testing the 'accumulated copying error' (or 'ACE') model proposed by Eerkens and Lipo (2005), in which random error in a quantitative artefact dimension (e.g., handaxe 'length') is generated by the physiological limitations of the hominin perceptual system. Eerkens and Lipo drew on experimental findings suggesting that the accuracy of human perception has physiological limits, which influences our ability to perceive differences between objects (e.g., Coren et al. 1994). If the difference in size between two objects is below some threshold, then this size difference will tend to be imperceptible. Such error thresholds are always relative to the size of the object, rather than absolute. The perceptual threshold below which humans fail to discriminate variation in the size of different objects is termed the 'Weber fraction' and is now established at a level of $\sim 3\%$ difference for a dimensional variable such as 'length' (Eerkens 2000; Kempe et al. 2012). In other words, if a person is presented with two objects and the difference in their length is less than 3%, they will generally fail to perceive this difference. Such insights provide a basis for comparing patterns of size variation in artefactual assemblages (Eerkens 2000; Eerkens and Bettinger 2001; Kempe et al. 2012).

Eerkens and Lipo (2005) applied this basic principle to the repeated cultural transmission of artefacts. They assumed that when attempting to copy the morphology of an artefact as faithfully as possible, and in the absence of formal measurement aids (e.g., scaled rules), the manufacturer will inevitably make copying errors that are imperceptible due to the aforementioned perception thresholds. If that person's copied artefact is in turn copied by another person, and so on along a transmission chain, then copying errors will compound over time, possibly creating significant morphological change compared to the original artefact. Moreover, if multiple such transmission chains evolve independently, then the variation between these diverging chains is likely to become substantial and to increase over time. Note that this process will take place regardless of whether any other cultural evolutionary forces are at work. Eerkens and Lipo presented a simple simulation model of this process in which a continuous trait value is transmitted over successive generations of individuals with a 3% random normal error rate, and with 10 independently evolving chains. Their simulation showed that, as expected, the independent chains diverged over time as some became larger and others became smaller. Due to the randomness of the error, the overall mean value

did not change over time, while the between-chain variation did increase over time.

The aim of our experiment was to provide an explicit empirical test of Eerkens and Lipo's (2005) ACE model of artefact transmission. Although their assumption that 3 % is the perceptual threshold below which humans fail to discriminate variation in the size of different objects is based on previous experimental findings from psychophysics, it is unclear (1) whether this 3 % error threshold is uniform across a large population of individuals, given that psychophysicists typically obtain their estimates from just one or a handful of experimental participants; (2) whether this 3 % threshold, originally obtained for simple lines or abstract geometric shapes, also applies to more realistic artefact shapes, such as handaxes; and (3), whether it is valid to simply extrapolate a single individual's perceptual error along successive transmission episodes or whether there are, for example, unexpected dynamics introduced by the compounding of individual errors.

In order to address these three points, we (Kempe et al. 2012) first derived the ACE model within an explicit mathematical framework and simulated its effects. The model operated on the basis that an individual copies a continuously-valued artefactual trait (e.g., handaxe 'length') with a set amount of copying error, drawn randomly from a normal distribution. Given that copy-error is scaled proportionally to that of the attribute being copied, the resultant value is obtained by multiplying the original (starting) value by the randomly sampled copying error. Full details are provided in Kempe et al. (2012). Simulating this model in 10 independently evolving chains over 400 generations of copying demonstrated that mean artefact size (across all 10 chains) will remain stable (Fig. 11.1). This is because, although most chains become smaller across time, the few transmission chains that get larger become increasingly large because error is scaled relatively to the attribute being copied. Equally, chains that tend toward the production of smaller artefacts deviate less overall from the original value in absolute terms. Hence, perhaps counter intuitively, the average artefact value across independently evolving chains will remain relatively stable across time, even though *variance* across the different transmission chains increases. These results were, therefore, broadly in agreement with Eerkens and Lipo's (2005) original formulation of the effects of the ACE model.

The experimental portion of the study aimed to determine more accurately the variance of the distribution seen in such copying errors and also to test whether mean and sample variance values obtained from experimental data matched their model-predicted values. The experiment consisted of individual volunteers, randomly allocated to independent transmission chains, resizing an image of a handaxe using an iPad (Fig. 11.2). Each participant was shown the handaxe of the previous person in their chain and then asked to resize

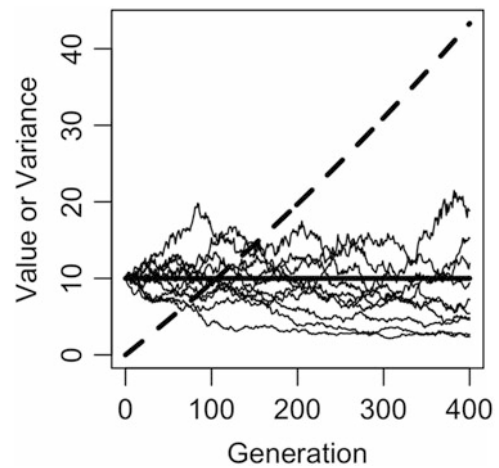


Fig. 11.1 Results of simulation based on copy error model. Output shows 10 chains evolving over 400 generations (*black lines*) and theoretically predicted mean (*thick black line*) and variance (*thick dashed line*)

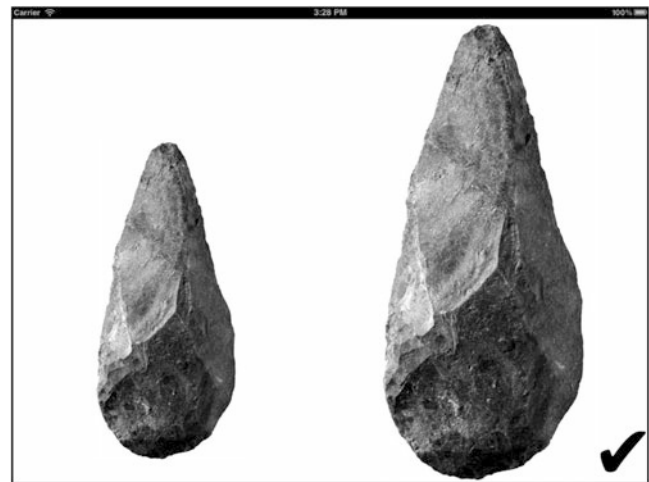


Fig. 11.2 Example of the resizing experiment using electronic touchscreen. Each participant was asked to resize the handaxe image on the *right* so as to match the size of the previous participant's as closely as possible, which is shown on the *left*. Participants pressed the tick mark to complete the copying task

a second handaxe to match the size of the previous person's handaxe as closely as possible. This experimental set-up, as with the use of 'model organisms' referred to earlier, has the advantage of procedural simplicity, in that it required only application of a pinching gesture on the electronic screen and no time limit was imposed. Hence, perceptual error was emphasized over manufacturing error, as is necessary given the aims of our study. A video demonstration of the experiment is provided in the online supplementary information (open access) of Kempe et al. (2012).

A total of 200 participants were asked to faithfully copy the size of the previous participant's handaxe image using this experimental set up, divided into 20 independent

transmission chains of 10 participants each. Two alternative conditions were implemented. In the first condition, the size of the image to be rescaled began at the maximum possible, which in this instance was 14.4 cm, given the height of the electronic screen. The second condition involved the starting size of the image to be rescaled being set at 1/3 of maximum (i.e. 4.8 cm). The transmission chains divided equally between these 'start-larger' and 'start-smaller' conditions. Copying errors were found to be normally distributed and on the order of 2.69 % for the larger condition and 3.99 % for the smaller condition, with an overall mean of 3.43 %, which corresponds well to the 3 % value reported in the psychophysiological literature. The experimental findings also supported the model's prediction that between-chain variance should increase over time and did so in a manner quantitatively in line with the model. However, when the initial size of the image that the participants resized was larger than the size of the image they were copying, subjects tended to increase the size of the image, resulting in the mean size increasing rather than staying constant, as the raw model would predict. This latter observation represents a novel and unanticipated empirical finding that, to our knowledge, has no precedent in psychology, illustrating the value of experimental simulations of cultural transmission over multiple generations rather than inferring long-term dynamics from the characteristics of single individuals.

The final part of the study involved comparing our results to a dataset of genuine Acheulean handaxes. This dataset provided quantitative data for 2061 complete handaxes from 21 different sites located in a total of five countries (Israel, Morocco, South Africa, Tanzania, United Kingdom) covering an age range of some 1.2 million years (Marshall et al. 2003). The coefficient of variation (CV) for length in this sample was 0.30 and for breadth was 0.23. We then simulated the output of the ACE model, setting copy-error rates to the 3.43 % determined by our experiments. These simulations determined that CV values of greater than 0.30 will be produced by copying error in less than 200 copying generations. Conservatively setting each generation at 20 years would imply that in $\leq 4,000$ years of copying, variation would exceed that seen in the genuine Acheulean sample. Indeed, copying error would need to be only on the order of 0.17 % (i.e. 20 times smaller than the 3.43 % seen in our experiments) in order to produce the level of total variation seen in the 1.2 million years covered by the handaxes concerned. Clearly, what these results imply is that certain factors must be countermanding the inevitable effects of size copying error and lineage mutation implied by the model.

Further experiments and models might examine such factors, as well as test the effect of relaxing our simplifying assumptions. For example, we assume in the model and experiment that transmission is one-to-one, with individuals

acquiring the trait from a single individual. Ethnographic evidence (e.g. Stout 2005) suggests that the transmission of artefacts may often be many-to-one, with individuals acquiring the trait from multiple cultural parents, which our design could easily be modified to explore (see Kempe and Mesoudi 2014 for an experimental methodology that incorporates multiple cultural parents).

11.3 Experiment 2: Considering the Effects of Shape Mutation in the Acheulean

It bears emphasizing that our first experiment, as described above, considers only mutation in the *size* (i.e. scale) of handaxe attributes, and the patterns of variation that will be produced through inevitable copying errors induced by physiological limits to perceive such differences. Although the analyses we describe suggest that Acheulean handaxes exhibited a definite range of size variability (see also Crompton and Gowlett 1993; Gowlett 2009), a fundamental distinguishing feature of handaxes are their characteristic *shape* properties (Roe 1976; Wynn 1995; Roche 2005). Shape properties of artefacts, independently of their size, may have specific functional or aesthetic significance (Lycett 2008; Winter-Livneh et al. 2013). Indeed, although size and shape are often conflated ('form' = size + shape), both conceptually and empirically, size and shape are fundamentally distinct (Bookstein 1989; Jungers et al. 1995). While the size of an object is a univariate property and can therefore be described quantitatively by a single measure of scale such as volume, shape is inherently a multivariate property. A quantitative concept of shape, therefore, relies not on the appreciation of a single variable such as 'length', but on the relative relationships between multiple aspects of morphometric variation in a given object. As Gowlett (2006) has noted, the deliberate manufacture of handaxe shape requires—minimally—the interrelated manipulation of the *relative* length variable (s), width (s) and aspects of thickness variability on the part of their manufacturer, and control of those interrelated properties during the knapping process.

The potential importance of shape copying errors in the case of handaxe production is particularly emphasized given that it has been proposed that the production of artefacts via knapping may be a particularly 'error prone' process. For instance, some time ago, Deetz (1967) noted that in the case of a 'reductive' process of manufacture, such as the knapping of stone artefacts, errors are not easily reversed. As Baumler (1995: 11) put it more recently, in the case of stone tool manufacture "each [flake] removal is irrevocable and its consequences are permanent". Conversely, Deetz (1967) contended that in the case of more readily reversible (or 'additive') processes of manufacture, such as basketry or pottery, errors are readily corrected due to the ease by

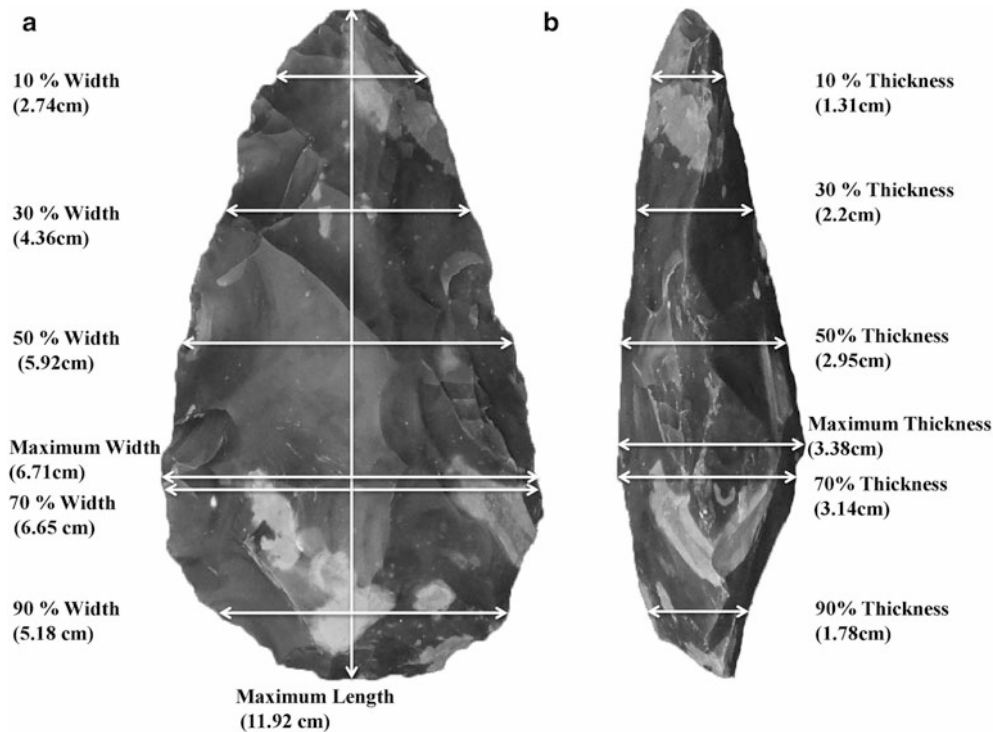


Fig. 11.3 Flint replica handaxe provided to participants as the ‘target’ model during the copying task. Participants in each condition were asked to copy the shape of this handaxe from standardized plasticine blocks using a steel table knife (Replica knapped by SJL.)

which material can be either added or removed. According to Deetz, differences between such alternative manufacturing processes would lead inevitably to greater levels of variation in non-reversible manufacturing traditions, such as those used in handaxe production.

Testing predictions of this form through studies of the archaeological record would be fraught with difficulty given the differing situational conditions under which alternative sets of artefacts (e.g., pots versus baskets) might be made, even within the same community. Moreover, comparing variation in artefacts across differing raw materials may be problematic given that the medium of manufacture itself (e.g., stone versus clay) might influence variation patterns in particular ways. A further specific problem in the case of artefacts such as handaxes is that their production requires skilled behaviour built over months, if not years, of practice (Edwards 2001) and is an activity that can even prove dangerous (Whittaker 1994). Such issues provide serious challenges to the implementation of an experimental approach that requires ready-recruitment of participants in numbers amenable to the implementation of statistical analysis. What is needed is a ‘model organism’ approach that enables implementation of fundamental controls such that the key contrasts between the two alternative manufacturing conditions are emphasized, while replicating the essential (i.e. ‘additive’ and ‘reductive’) features of the processes of interest under safe conditions.

Given these considerations, we (Schillinger et al. 2014) implemented an experimental procedure that consisted of a simple copying task. Participants were asked to copy the shape of a replica Acheulean handaxe (Fig. 11.3) as accurately as possible using a standardized block of plasticine and a stainless steel table knife. Following Deetz (1967), the central prediction that we tested is that the implementation of reductive manufacturing processes, where material can be removed but not added, automatically leads to an overall higher rate in copying error for shape than under reversible manufacturing conditions. In the context of this hypothesis, we specifically targeted the statistical effects of copying error on shape attributes, using a dataset of size-adjusted morphometric variables. It should be noted, therefore, that in contrast to the type of experiment described earlier, this experiment is not so much aimed at the issue of perceptual bias (in terms of establishing a baseline error rate), as procedural bias (i.e. additive versus reductive manufacturing processes) and establishing whether one procedure has intrinsically greater error rates than the other.

A total of 60 participants were recruited to take part in this experiment. Of these, 30 were female (mean age = 26, s.d. = 5.4, age range = 18–44 years) and 30 were male (mean age = 28, s.d. = 9.8, age range = 18–64 years). Equal numbers of males and females were employed deliberately in order to control for any potential confound in terms of sex differences in visuo-spatial abilities (see e.g., Wynn et al.

1996). The participants were divided equally between two experimental conditions: an ‘additive-reductive’ condition, whereupon participants were instructed that they were free to both remove and add plasticine during the manufacture of their replica, and a ‘reductive-only’ condition in which participants were strictly required only to remove material in producing their copy. In order to control for memory effects (see e.g., Eerkens 2000), participants were permitted to examine the target handaxe for 1 min prior to beginning the copying task, and were free to compare their model to the target at any point during the 30 min allotted for completion of the task. All participants were able to complete the task within this timeframe.

Upon completion of the task, each participant’s model was photographed in plan- and profile-views according to a standardized orientation protocol (see Schillinger et al. 2014 for full details). Thereafter, measurements were obtained digitally for 42 standardized variables (28 plan-view and 14 profile-view) from each plasticine handaxe using the freely available morphometrics software tpsDig v2.16 (Rohlf 2010). Given that our analysis specifically focused on monitoring shape-related changes, the data were size-adjusted via use of the geometric mean method (Jungers et al. 1995; Lycett et al. 2006). This method of size-adjustment effectively removes size (scaling) variation between specimens by equalizing their volumes, yet retains their relevant shape data (Jungers et al. 1995). The geometric mean of a series of n variables ($a_1, a_2, a_3 \dots a_n$) is equivalent to $\sqrt[n]{a_1 \times a_2 \times a_3 \times \dots \times a_n}$. Simply, the geometric mean is the n th root of the product of all n variables (Sokal and Rohlf 1995: 43). 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 handaxe replica was calculated separately and thereafter each of the 42 morphometric variables for each specimen were divided by the geometric mean for that particular specimen. The size-adjusted values of the 42 morphometric variables for each of the 60 replicas were subtracted from the equivalent 42 variables of the target flint replica. Thereafter, mean shape error was computed for each of the 42 morphometric variables across the 30 replicas obtained in each experimental condition.

In terms of results, the additive-reductive condition had an overall mean copying error rate of 0.115 (s.d. = 0.040) across all variables. The reductive-only condition had a mean of 0.134 (s.d. = 0.053) across all variables. The results of a conservative Mann-Whitney U test demonstrated that copying error rates for the 42 variables in the reductive-only condition were statistically greater than in the additive-reductive condition ($U = 621.5$; asymptotic $p = 0.0191$; Monte Carlo $p = 0.0199$). Figure 11.4 shows the overall distribution of the

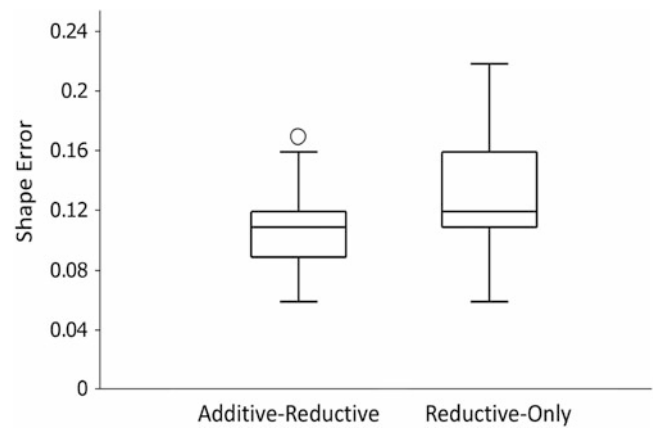


Fig. 11.4 Box plots showing shape error distribution in each of the two experimental conditions. *Horizontal lines* indicate the median error in each case, boxes depict the 25–75 percentile, while whiskers mark the largest datum point $\leq 1.5 \times$ box range

copy errors from the two conditions in the form of 25–75 percentile box plots.

Overall, the results of these analyses were, therefore, entirely consistent with the proposition of Deetz (1967) that copying errors, at least in terms of shape, will be higher in artefacts produced via processes of irreversible reduction, than in artefacts produced via reversible processes of manufacture. In other words, ‘mutation’ rates in the shape attributes of artefacts produced under irreversible, or ‘reductive’, conditions—such as handaxes produced via stone knapping—are intrinsically greater than those produced via alternative means.

11.4 Discussion

Here, we have reviewed the results of two experiments designed to examine mutation rates produced by copying error in cultural evolutionary models. At this juncture, however, the reader may well be asking what any of this implies for questions concerning the learning of handaxe production in the hominin societies that made them.

The value of these experiments in approaching questions of this type, we would contend, lies in their microevolutionary perspective. Evolution is a process in which inherited variants are replicated differentially, and imperfectly, through time. Variants are replicated differentially because certain variants fail to be reproduced either due to ‘selective’ factors (i.e. differences between variants lead to a differential likelihood of successful replication in given circumstances) or due to some random (chance) factor, which results in ‘drift’ of characteristics within populations. The replication process in any genuine evolutionary system is, however, always imperfect (even if only in very subtle ways), thus ensuring that

new variants may appear across time. These new variants, of course, become the engine for yet further evolutionary change. In the case of artefacts, this was recognised some time ago by Harrison (1930: 111) who noted:

it is clear that the size and form of any one-piece artifact, or of any such component of a compound artifact, may be altered very considerably by the cumulative effect of a number of changes each small in itself . . . In some instances, variational modifications arise through the copying from other artifacts of features of form, with resultant changes in shape and proportions; . . . It also plays a part in mutational progress.

The results of the first experiment we describe (Kempe et al. 2012), considered the role of size mutation in these terms. We simulated the assumptions of the accumulated copying error model under realistic size copying-error rates established via empirical experiment. These analyses were able to show that drift alone would lead to size variation exceeding that seen in archaeological samples of handaxes in, conservatively, as little as 4,000 years. In other words, it seems that in the case of a learning model in which individuals simply copied the size of handaxes made by those nearby, mutation effects over time would inevitably lead relatively quickly to unrealistic levels of size variation.

Simple learning (size copying) plus a level of random variation does not, therefore, explain the relatively constrained levels of size variation seen across the samples of handaxes considered in our study (Kempe et al. 2012). What this plausibly suggests is that functionally-related cultural selection, such as the need to fit into the hand comfortably (Gowlett 2006), was constraining variation in ways that do not fit the simple drift-copying model. Such constraints may have been inducted by individual ('trial-and-error') learning, whereby an individual hominin 'scaled' their handaxes to what worked well in a functional capacity given their own physical size, strength, etc. Indeed, the importance of 'feedback' mechanisms between considerations of this nature and the attributes of artefacts such as handaxes was mentioned some time ago by Clarke (1968: 181–182, 649). However, within any socially-mediated context of observation of, and learning about, handaxe production and usage, some notion of suitable size parameters is also likely to have been inducted in novice handaxe producers through direct observation of others' tools (Fragaszy et al. 2013), essentially 'resetting' the drift clock with each generation, especially in terms of the population mean.

Our second experimental analysis (Schillinger et al. 2014), considered copying error in terms of *shape* mutation, independently of size factors. The participants engaged in one of two alternative conditions; one representing an irreversible ('reductive-only') manufacturing process, and the other representing a reversible ('additive-reductive') manufacturing process. Participants in each condition were asked to copy the shape of a target form (a flint replica

handaxe) as accurately as possible utilizing a standardized block of plasticine and a stainless steel table knife. Our analysis found that replicas produced in the reductive-only condition displayed statistically greater levels of shape-copying error than those produced in the additive-reductive condition. In other words, mutation rates in the shape properties of material traditions produced under reductive conditions (such as stone knapping) are intrinsically greater than those produced via alternative means. Hence, shape mutation rates are process dependent, and in the case of traditions produced through knapping will be inherently prone to copying error, especially via an imitative (i.e. goal copying) form of learning. This point is especially notable given that the characteristic shape of handaxes was imposed by hominins through the knapping sequence itself, and is not easily determined merely by selection of starting form as might more easily be the case with 'size' parameters. Indeed, handaxes were produced on tabular material, rounded nodules and cobbles, and flake blanks, the latter of which sometimes involved the instigation of regionally distinctive knapping routines that produced such flake 'blanks' (Sharon 2009). Hence, the characteristic form of handaxes seen in the archaeological record was imposed on materials comprised of a variety of differing 'start' points. Indeed, at least one study suggests that handaxes made of stone and bone at the same locality show no statistical differences in outline shape, despite the differing nature of these materials (Costa 2010).

Elsewhere, we have noted that the appearance rate of new cultural variants may conceptually be linked to potential for evolutionary change (Schillinger et al. 2014: 137) akin to the concept of 'evolvability' in biology (Ridley 2004: 587). It must be stressed, of course, that while 'evolvability' in these terms might be used to describe the potential for change brought about by selective factors (either natural or cultural), it can also be used to describe potential for the degradation of culturally transmitted traits, leading eventually to their extinction, or cultural 'collapse' of a particular tradition. Indeed, although variation is required for selection to operate, and is therefore a prerequisite of cumulative cultural evolution, equally it has been known for some time in biology that 'mutation load' is a factor that may ultimately prove fatal to population viability (Simpson 1953). Hence, in the case of items of material culture, such as handaxes produced via reductive processes, their potential for evolutionary 'corruption' in terms of shape would be higher than artefactual traditions produced via processes in which errors are more easily corrected. A visual demonstration of this effect is shown in Fig. 11.5, which illustrates merely 15 'generations' of different experimental participants copying the previous participant's copy in the form of a transmission chain, when the initial shape starts out in a form similar to that of a handaxe. In this (albeit anecdotal) example, it is readily visible that erosion due to effects of copying error can

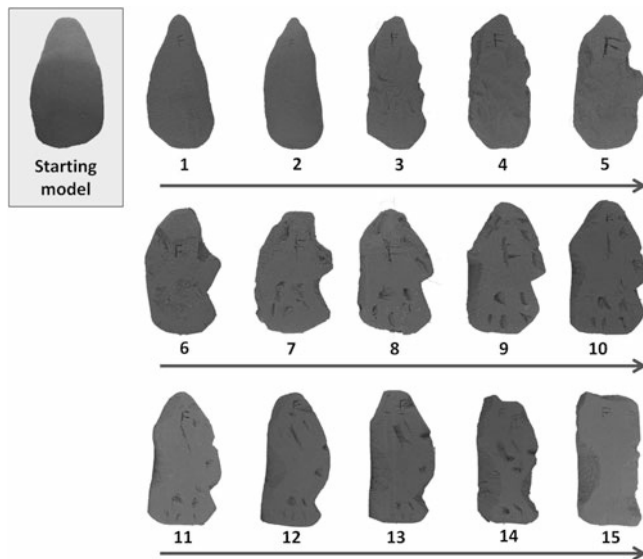


Fig. 11.5 Transmission chain produced by 15 participants copying the 3D shape of the 'artefact' of the previous participant (starting initial 'target' shown *top left*). Each of these 3D models was carved from standardized foam blocks ($22.3 \times 11 \times 7.8$ cm) using a plastic table knife. It should be noted, therefore, that the production of these shapes requires no specialized skills or knowledge, and they are produced on an easily malleable material

potentially have potent effects on the integrity of 'handaxe' shape within a limited number of generations.

Given these findings, what does this imply for the learning of 'shape' in handaxe-producing communities of the Palaeolithic? One possibility is that individual (trial-and-error) learning helped to mitigate the relatively strong effects of shape mutation in handaxe traditions, at least once the 'concept' of handaxe tools had been instigated via other means (e.g., stimulus enhancement learning and emulation). There are reasons, however, to be cautious that individual learning alone explains phenomena of the scale attested in the archaeological record. One pertinent factor to consider here is the inherently dangerous nature of flintknapping involving the percussive removal of razor sharp stone flakes, which inevitably also leads to small flakes and sharp chips of stone being thrown into the air. Ethnographically and historically recorded comments on such injury risks are attested in the literature (e.g., Pope 1918: 117; Kroeber 1961: 184; Hampton 1999: 267). Today, many flintknappers who produce stone artefacts for academic purposes or recreation deliberately wear protective gear in the form of safety glasses, gloves and thick padding. One contemporary academic flintknapper is known to have severed a tendon with a small flake ($\sim 5 \times 20$ mm) requiring corrective surgery and causing permanent debilitation of movement in his hand (Whittaker 1994: 3–4). Painful open wounds, blood loss, risk of infection to injuries, eye damage/loss are noted risks, in addition to damaged ligaments that might be

caused by incorrect form. These factors are important when we consider that there is widespread agreement that social learning strategies will be favourable to asocial learning strategies (i.e. trial-and-error learning) whenever the activity to be learned is costly or hazardous (Boyd and Richerson 1985; Feldman et al. 1996). This is strongly supported by empirical evidence from studies of learning in non-human animals, which indicate that social learning will be favoured wherever asocial learning is more costly (e.g., Mineka and Cook 1988; Chivers and Smith 1995; Kelley et al. 2003), as well as in contemporary humans using similar computer-based learning tasks as those described above (Mesoudi and O'Brien 2008).

One social learning mechanism potentially available to handaxe-producing hominins, beyond pure copying of artefact shape (i.e. emulation), is imitation. This would imply some copying of not only the form of the object (the goal, or 'end state') but also some fidelity in terms of copying the actual behaviours used by others in the manufacture of their handaxes. Subtle differences in the details of manufacture, or 'process controls' (sensu Patten 2005) that aim to increase the likelihood of intended outcomes during the knapping process would make obvious targets for such bouts of imitation. Such possibilities would also explain why metric studies of handaxe form have persistently indicated *statistical* differences between assemblages of handaxes from different regions or sites (e.g., Wynn and Tierson 1990; Lycett and Gowlett 2008; Lycett and von Cramon-Taubadel 2015), which remain difficult to explain solely on the basis of reduction and/or raw material factors (Sharon 2008; Eren et al. 2014; Lycett and von Cramon-Taubadel 2015). However, further support for the instigation of imitative learning must be further substantiated via independent means.

11.5 Conclusions

Assertions of social learning are often invoked for handaxe production, sometimes even invoking specific mechanisms of social learning such as imitation (e.g., Mithen 1999). These assertions are made largely on the strength that these mechanisms most plausibly explain the repeated pattern of handaxe production over considerable swathes of time and space. Given the scale of the phenomenon under consideration, these assertions are not necessarily unreasonable. This is especially the case given what we have learned in recent decades about the role of social learning in the acquisition of tool use behaviours of our closest living primate relatives (e.g., Lonsdorf et al. 2004; Whiten and Mesoudi 2008; Horner and de Waal 2009; Humle et al. 2009; Biro et al. 2010), and what we know from the ethnographic record in terms of the learning of stone artefacts that are similar to handaxes (e.g., Stout 2005). However, such assertions are

problematic in the case of prehistoric handaxes without considering the role, scale, incidence and potential magnitude of cumulative copying errors in precise terms. In essence, what our experiments show is that inevitable copying error in size and shape factors would relatively quickly lead to the disintegration of handaxe traditions attested empirically in the archaeological record. Handaxe traditions are not inherently stable; in fact, a combination of factors relating to copying error in both size and shape factors would make them inherently *unstable*. In the case of shape, in particular, this suggests that a learning mechanism other than *pure* observation of others' artefacts (i.e. goal emulation, or 'end-state' copying), was used in the learning of handaxe manufacture. Individual (trial-and-error) learning could conceivably constrain variation somewhat, but the costs associated with knapping would encourage the adoption of social learning mechanisms that would countermand the inevitable effects of copying error that we describe with reduced risk to tool manufacturers. Determining what such mechanisms are—in precise terms—will, however, require further work. Hence, do we still have a long way to go in order to fully understand the dynamics of learning in the Acheulean? Absolutely. What the preceding discussion should demonstrate, however, is the importance of an evolutionary perspective that can work from a micro- to macro-scale level, and importantly, is informed by data derived from experimental work of the type we describe.

11.6 Final Remarks in the Context of the RNMH Project Objectives

As Nishiaki (2013: 173) noted recently, a primary objective of the RNMH research project is to investigate potential factors in the replacement of hominin populations referred to as 'Neanderthals' by those commonly referred to as 'Modern Humans'. If the points we have made here regarding imitation capacities in handaxe producing hominin populations are correct (and we re-emphasize the need for further corroboration), then imitative capacities were a plesiomorphic feature, present in the last common ancestor of both groups of populations. Hence, if we are correct, differences in imitative capacities are unlikely to have played a major role in the replacement process. This, it should be noted, is despite the fact that imitation may be a key variable in the fidelity of social learning systems, which a priori, may make it a potential explanative candidate. If modal differences in the innate (i.e. genetically determined) social learning capacities of these two hominin populations played any role in the replacement of one by another, this leaves only two potential candidates: (1) that capacities for more sophisticated social learning mechanisms, such as teaching (Tehrani and Riede 2008), were different or (2) that one population possessed greater

capacity for innovation than the other, which in turn, provided an advantage in a competitive environment. Personally, we are doubtful that innate differences between these two groups of populations will provide a *fully* satisfactory answer to the question of population replacement, partly because of the demonstrable resilience of Neanderthal populations over millennia prior to their disappearance, and the proximity of their biological relationship to contemporary populations of *H. sapiens*. However, we acknowledge the considerable amount of work that needs to be done to fully support our position.

Acknowledgements The research discussed in this chapter was funded by a Leverhulme Trust Research Project Grant (F/07 476/AR) awarded to AM and SJL. For numerous invaluable conversations and comments while undertaking this work we are grateful to Noreen von Cramon-Taubadel. We are also grateful to Ken Aoki and Jamie Tehrani for helpful comments on a previous version of this paper.

References

- Ashburner M, Novitski E (1976) The genetics and biology of *drosophila* 1A. Academic, London
- Ashburner M, Golic K, Hawley RS (2005) *Drosophila: a laboratory handbook*, 2nd edn. Cold Spring Harbor Laboratory Press, New York
- Bataillon T, Joyce P, Sniegowski P (2013) As it happens: current directions in experimental evolution. *Biol Lett* 9:20120945
- Baumler MF (1995) Principles and properties of lithic core reduction: implications for levallois technology. In: Dibble HL, Bar-Yosef O (eds) The definition and interpretation of levallois technology. Prehistory Press, Madison, pp 11–23
- Bello SM, Parfitt SA, Stringer C (2009) Quantitative micromorphological analyses of cut marks produced by ancient and modern handaxes. *J Archaeol Sci* 36:1869–1880
- Beyene Y, Katoh S, WoldeGabriel G, Hart WK, Uto K, Sudo M et al (2013) The characteristics and chronology of the earliest Acheulean at konso, Ethiopia. *Proc Natl Acad Sci U S A* 110:1584–1591
- Binford LR (1983) In pursuit of the past. Thames & Hudson, London
- Biro B, Carvalho S, Matsuzawa T (2010) Tools, traditions, and technologies: interdisciplinary approaches to chimpanzee nutcracking. In: Lonsdorf EV, Ross SR, Matsuzawa T (eds) The mind of the chimpanzee: ecological and experimental perspectives. Chicago University Press, Chicago, pp 141–155
- Bookstein FL (1989) 'Size and shape': a comment on semantics. *Syst Zool* 38:173–180
- Boyd R, Richerson P (1985) Culture and the evolutionary process. University of Chicago Press, Chicago
- Byrne RW, Russon AE (1998) Learning by imitation: a hierarchical approach. *Behav Brain Sci* 21:667–721
- Cavalli-Sforza LL, Feldman MW (1981) Cultural transmission and evolution: a quantitative approach. Princeton University Press, Princeton
- Chivers DP, Smith RJF (1995) Chemical recognition of risky habitats is culturally transmitted among fathead minnows, *Pimephales promelas* (osteichthyes, cyprinidae). *Ethol* 99:286–296
- Clark JD (1994) The Acheulian industrial complex in Africa and elsewhere. In: Corruccini RS, Ciochon RL (eds) Integrative paths to the past. Prentice Hall, Englewood Cliffs, pp 451–469
- Clarke DL (1968) Analytical archaeology. Methuen, London
- Coren S, Ward LM, Enns JT (1994) Sensation and perception. Harcourt Brace, San Diego

- Costa AG (2010) A geometric morphometric assessment of plan shape in bone and stone Acheulean bifaces from the middle Pleistocene site of Castel di Guido, Latium, Italy. In: Lycett SJ, Chauhan PR (eds) *New perspectives on old stones: analytical approaches to paleolithic technologies*. Springer, New York, pp 23–41
- Crompton RH, Gowlett JAJ (1993) Allometry and multidimensional form in Acheulean bifaces from Kilombe, Kenya. *J Hum Evol* 25:175–199
- Darwin C (1859) *On the origin of species*. John Murray, London
- Deetz J (1967) *Invitation to archaeology*. The Natural History Press, Garden City
- Domínguez-Rodrigo M, Serrallonga J, Juan-Tresserras J, Alcalá L, Luque L (2001) Woodworking activities by early humans: a plant residue analysis on Acheulean stone tools from Peninj (Tanzania). *J Hum Evol* 40:289–299
- Edwards SW (2001) A modern knapper's assessment of the technical skills of the late Acheulean biface workers at Kalambo falls. In: Clark JD (ed) *Kalambo falls prehistoric site: volume III*. Cambridge University Press, Cambridge, pp 605–611
- Eerkens JW (2000) Practice makes within 5 % of perfect: visual perception, motor skills, and memory in artifact variation. *Curr Anthropol* 41:663–668
- Eerkens JW, Bettinger RL (2001) Techniques for assessing standardization in artifact assemblages: can we scale variability? *Am Antiq* 66:493–504
- Eerkens JW, Lipo CP (2005) Cultural transmission, copying errors, and the generation of variation in material culture and the archaeological record. *J Anthropol Archaeol* 24:316–334
- Eren MI, Roos CI, Story B, von Cramon-Taubadel N, Lycett SJ (2014) The role of raw material differences in stone tool shape variation: an experimental assessment. *J Archaeol Sci* 49:472–487
- Feldman MW, Aoki K, Kumm J (1996) Individual versus social learning: evolutionary analysis in a fluctuating environment. *Anthropol Sci* 104:209–232
- Fragaszy DM, Biro D, Eshchar Y, Humle T, Izar P, Resende B, Visalberghi E (2013) The fourth dimension of tool use: temporally enduring artefacts aid primates learning to use tools. *Philos Trans R Soc B* 368:20120410
- Gowlett JAJ (2006) The elements of design form in Acheulean bifaces: modes, modalities, rules and language. In: Goren-Inbar N, Sharon G (eds) *Axe age: Acheulean tool-making from quarry to discard*. Equinox, London, pp 203–221
- Gowlett JAJ (2009) Artefacts of apes, humans, and others: towards comparative assessment and analysis. *J Hum Evol* 57:401–410
- Gowlett JAJ (2010) The future of lithic analysis in palaeolithic archaeology: a view from the Old World. In: Lycett SJ, Chauhan PR (eds) *New perspectives on old stones: analytical approaches to paleolithic technologies*. Springer, New York, pp 295–309
- Gowlett JAJ (2011) The empire of the Acheulean strikes back. In: Sept J, Pilbeam D (eds) *Casting the net wide: papers in honor of Glynn Isaac and his approach to human origins research*. American School of Prehistoric Research, Cambridge, MA, pp 93–114
- Greenspan RJ (2004) *Fly pushing: the theory and practice of drosophila genetics*, 2nd edn. Cold Spring Harbor Laboratory Press, New York
- Hamilton MJ, Buchanan B (2009) The accumulation of stochastic copying errors causes drift in culturally transmitted technologies: quantifying Clovis evolutionary dynamics. *J Anthropol Archaeol* 2:55–69
- Hampton OW (1999) *Culture of stone: sacred and profane uses of stone among the Dani*. Texas A&M, College Station
- Harrison HS (1930) Opportunism and the factors of invention. *Am Anthropol* 32:106–125
- Henrich J, McElreath R (2003) The evolution of cultural evolution. *Evol Anthropol* 12:123–135
- Heyes CM (1994) Social learning in animals: categories and mechanisms. *Biol Rev* 69:207–231
- Horner V, de Waal FBM (2009) Controlled studies of chimpanzee cultural transmission. *Prog Brain Res* 178:3–15
- Humle T, Snowdon CT, Matsuzawa T (2009) Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Anim Cogn* 12(S1):37–48
- Isaac GL (1972) Early phases of human behaviour: models in lower palaeolithic archaeology. In: Clarke DL (ed) *Models in archaeology*. Methuen, London, pp 167–199
- Isaac GL (1977) *Ologesailie: archaeological studies of a middle Pleistocene lake basin in Kenya*. University of Chicago Press, Chicago
- Johnson LL (1978) A history of flint-knapping experimentation, 1838–1976. *Curr Anthropol* 19:337–372
- Jones PR (1980) Experimental butchery with modern stone tools and its relevance for palaeolithic archaeology. *World Archaeol* 12:153–165
- Jungers WL, Falsetti AB, Wall CE (1995) Shape, relative size, and size adjustments in morphometrics. *Yearb Phys Anthropol* 38:137–161
- Keeley LH (1980) *Experimental determination of stone tool uses: a microwear analysis*. University of Chicago Press, Chicago
- Kelley JL, Evans JP, Ramnarine IW, Magurran AE (2003) Back to school: can antipredator behaviour in guppies be enhanced through social learning? *Anim Behav* 65:655–662
- Kempe M, Mesoudi A (2014) An experimental demonstration of the effect of group size on cultural accumulation. *Evol Hum Behav* 35:285–290
- Kempe M, Lycett SJ, Mesoudi A (2012) An experimental test of the accumulated copying error model of cultural mutation for Acheulean handaxe size. *PLoS One* 7(11):e48333
- Kroeber T (1961) *Ishi in two worlds*. University of California Press, Berkeley
- Lepre CJ, Roche H, Kent DV, Harmand S, Quinn RL, Brugal J-P et al (2011) An earlier origin for the Acheulean. *Nature* 477:82–85
- Lonsdorf EV, Eberly LE, Pusey AE (2004) Sex differences in learning in chimpanzees. *Nature* 428:715–716
- Lycett SJ (2008) Acheulean variation and selection: does handaxe symmetry fit neutral expectations? *J Archaeol Sci* 35:2640–2648
- Lycett SJ, Chauhan PR (2010) Analytical approaches to palaeolithic technologies: an introduction. In: Lycett SJ, Chauhan PR (eds) *New perspectives on old stones: analytical approaches to palaeolithic technologies*. Springer, New York, pp 1–22
- Lycett SJ, Gowlett JAJ (2008) On questions surrounding the Acheulean 'tradition'. *World Archaeol* 40:295–315
- Lycett SJ, von Cramon-Taubadel N (2015) Toward a "quantitative genetic" approach to lithic variation. *J Archaeol Method Theory*. doi: 10.1007/s10816-013-9200-9
- Lycett SJ, von Cramon-Taubadel N, Foley RA (2006) A crossbeam co-ordinate caliper for the morphometric analysis of lithic nuclei: a description, test and empirical examples of application. *J Archaeol Sci* 33:847–861
- Marshall G, Gamble C, Roe D (2003) The Acheulean biface project: a digital archive for teaching and research. *Antiquity* 77 (online)
- Mesoudi A (2008) Foresight in cultural evolution. *Biol Philos* 23:243–255
- Mesoudi A (2011) *Cultural evolution: how Darwinian theory can explain culture and synthesize the social sciences*. Chicago University Press, Chicago
- Mesoudi A, O'Brien MJ (2008) The cultural transmission of great basin projectile point technology I: an experimental simulation. *Am Antiq* 73:3–28
- Mesoudi A, Whiten A, Laland KN (2004) Is human cultural evolution Darwinian? evidence reviewed from the perspective of *The origin of species*. *Evolution* 58:1–11
- Mineka S, Cook M (1988) Social learning and the acquisition of snake fear in monkeys. In: Galef BG, Zentall TR (eds) *Social learning: psychological and biological perspectives*. Erlbaum, Hillsdale, pp 51–73

- Mithen S (1999) Imitation and cultural change: a view from the stone age, with specific reference to the manufacture of handaxes. In: Box HO, Gibson KR (eds) *Mammalian social learning: comparative and ecological perspectives*. Cambridge University Press, Cambridge, pp 389–399
- Nishiaki Y (2013) ‘Gifting’ as a means of cultural transmission. In: Akazawa T, Nishiaki Y, Aoki K (eds) *Dynamics of learning in Neanderthals and Modern Humans*, vol 1. Springer, Tokyo, pp 173–185
- O’Brien MJ, Lyman RL (2000) *Applying evolutionary archaeology: a systematic approach*. Kluwer Academic/Plenum, New York
- Patten B (2005) *Peoples of the flute: a study in anthropolithic forensics*. Stone Dagger Publications, Denver
- Pope ST (1918) *Yahi archery*. University of California Press, Berkeley
- Ridley M (2004) *Evolution*, 3rd edn. Blackwell, Oxford
- Roberts MB, Parfitt S (eds) (1999) *Boxgrove: a middle Pleistocene hominid site at eartham quarry, boxgrove, West Sussex*. English Heritage, London
- Roche H (2005) From simple flaking to shaping: stone-knapping evolution among early hominins. In: Roux V, Bril B (eds) *Stone knapping: the necessary conditions for a uniquely hominin behaviour*. McDonald Institute, Cambridge, pp 35–48
- Roe D (1976) Typology and the trouble with handaxes. In: Sieveking G de G, Longworth IH, Wilson KE (eds) *Problems in economic and social archaeology*. Duckworth, London, pp 61–70
- Rohlf FR (2010) *TpsDig2 v2.16*. Department of Ecology and Evolution, State University of New York, Stony Brook. <http://life.bio.sunysb.edu/morph/>
- Schick KD, Toth N (1993) *Making silent stones speak: human evolution and the dawn of human technology*. Weidenfeld and Nicolson, London
- Schillinger K, Mesoudi A, Lycett SJ (2014) Copying error and the cultural evolution of “additive” versus “reductive” material traditions: an experimental assessment. *Am Antiq* 79:128–143
- Sharon G (2008) The impact of raw material on Acheulian large flake production. *J Archaeol Sci* 35:1329–1344
- Sharon G (2009) Acheulian giant-core technology. *Curr Anthropol* 50:335–367
- Shennan S (2011) Descent with modification and the archaeological record. *Philos Trans R Soc B* 366:1070–1079
- Simão J (2002) Tools evolve: the artificial selection and evolution of paleolithic stone tools. *Behav Brain Sci* 25:419
- Simpson GG (1953) *The major features of evolution*. Columbia University Press, New York
- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. W.H. Freeman, New York
- Stout D (2005) The social and cultural context of stone knapping skill acquisition. In: Roux V, Bril B (eds) *Stone knapping: the necessary conditions for a uniquely hominin behaviour*. McDonald Institute, Cambridge, pp 331–340
- Tehrani JJ, Riede F (2008) Towards an archaeology of pedagogy: learning, teaching and the generation of material culture traditions. *World Archaeol* 40(3):316–331
- Toth N (1985) The Oldowan reassessed: a close look at early stone artefacts. *J Archaeol Sci* 12:101–120
- Whiten A, Mesoudi A (2008) Establishing an experimental science of culture: animal social diffusion experiments. *Philos Trans R Soc B* 363:3477–3488
- Whiten A, Horner V, Litchfield CA, Marshall-Pescini S (2004) How do apes ape? *Learn Behav* 32:36–52
- Whittaker JC (1994) *Flintknapping: making and understanding stone tools*. University of Texas Press, Austin
- Winter-Livneh R, Svoray T, Gilead I (2013) Shape reproducibility and architectural symmetry during the chalcolithic period in the southern Levant. *J Archaeol Sci* 40:1340–1353
- Wynn T (1995) Handaxe enigmas. *World Archaeol* 27:10–24
- Wynn T, Tierson F (1990) Regional comparison of the shapes of later Acheulean handaxes. *Am Anthropol* 92:73–84
- Wynn TG, Tierson FD, Palmer CT (1996) Evolution of sex differences in spatial cognition. *Yearb Phys Anthropol* 39:11–42
- Yravedra J, Domínguez-Rodrigo M, Santonja M, Pérez-González A, Panera J, Rubio-Jara S et al (2010) Cut marks on the middle pleistocene elephant carcass of Áridos 2 (Madrid, Spain). *J Archaeol Sci* 37:2469–2476