Baldwin effects in early stone tools

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ISSUES

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Abstract
A sizeable dataset comprising millions of lithic artifacts sampling over two million years of early paleolithic tool technology from Africa and Eurasia is now available. The widespread presupposition of an exclusively cultural, that is, socially learned, nature of early stone tools from at least Acheulean times onwards has been challenged by researchers who hypothesize that these tools, a crucial element of early hominin survival strategies, may partly have been under genetic control, next to the effects of various other determinants. The discussion this hypothesis has sparked off in the present journal is here explored somewhat further, focusing on the Baldwin effect.

KEYWORDS
Acheulean, animal construction, Baldwin effect, genetic transmission, Oldowan, social learning

1 | INTRODUCTION

Partitioning the temporal, regional, inter-site and intra-site variability in pre-Acheulean (Lomekwian, Oldowan) and Acheulean stone technology to its drivers has proven to be notoriously difficult. A number of determinants on various scales of space and time are generally acknowledged, but weighed differently by various authors. These determinants include ecological circumstances, the fracture mechanics and shapes of raw materials, functional and ergonomic constraints, reduction and resharpening processes, various forms of learning, aesthetic preferences, and drift effects.

In 2017 Corbey et al., focusing on Acheulean cutting tools in particular and in line with earlier suggestions, pleaded for more attention to a hitherto neglected additional driver of variability. Using bird nest building, song and tool use, among other animal behaviors, as heuristic models they argue that next to the abovementioned determinants a role for genetic transmission should be considered more seriously.

John McNabb, elaborating on an earlier publication with Robert Hosfield and James Cole, has expressed skepticism on the genetic transmission hypothesis, as have others. In the following I address the main doubts of this seasoned Acheulean specialist, with special attention to the so-called Baldwin Effect as a possible additional determinant of early stone tool variability.

2 | FACTORING THE BALDWIN EFFECT IN

McNabb argues that any genetic component is unnecessary: cultural transmission can explain it all. "At no point can a hominin's own understanding of a hand axe be parsed from its social context," he writes, "... [this] is not the fine social tuning overlying a genetic basis, this is the basic social substrate of how and where hand axes were made." McNabb rejects dual inheritance (gene-culture co-evolution) arguments explicitly.

However, if phenotypically plastic individuals grow up time and again, over hundreds if not thousands of generations, in a technological niche while manipulating stone, and provided that the cost/benefit ratio is right: would not selection in the long run favor features of the organism befitting their technological capacities, so crucial for survival? This is a Baldwin Effect, a progressive encoding in the genome of...
initially non-genetic, plastic responses, acquired by learning, to changing environmental conditions. In the long run, phenotypic plasticity for a particular trait is reduced in favor of stereotyped, experience-independent, innate routines which mimic the initial plastic response.8–10

McNabb renders Corbey et al. as arguing that "the foundations upon which the social explanation of the Acheulean is built can in fact be more simply explained by genetics."4:11 This is not a correct reading, for they explore "the possibility that the production of Acheulean hand axes was under at least partial genetic control.1:8 They write: "The combination of genetic transmission and social learning is predicted to produce uniformity of overall design (due to the fixed component) and slight local variance (due to the process of socialization), which is the pattern observed with Acheulean hand axes" (my italics; cf. Figure 1). Corbey et al. also point to the role of "niches containing stimuli related to hand axe production ... [which] would have provided cues for individual learning." This shows that their position is, in fact, closer to McNabb’s than he credits. There is a fair amount of common ground with his position.

3 | PHENOTYPIC PLASTICITY

McNabb admits that certain features of early Acheulean tools "indicate a cognitive evolution in Homo ergaster, which distinguishes them from earlier hominins and their material culture." This might imply a Baldwinian change as just described, specifically regarding tool manufacture, but in view of his stress on social learning McNabb attributes such cognitive evolution to a general phenotypic plasticity, as do most workers on early Homo.

Here the Baldwinian argument runs into a possible objection. Phenotypic plasticity10,20 permits flexible reactions which facilitate survival under conditions of considerable ecological and climatic variation, such as in Africa c.2.5–1.5 myr ago, along the routes when Erectines spread into Eurasia, or when, much later, hand axe wielding Heidelbergs lived in Pleistocene Europe.21 The objection is that under such circumstances efficient plasticity would have prevented the appearance of automatized, Baldwinian solutions which, inflexible as they are, at first sight seem at odds with the malleability and learning capacities required for coping with environmental novelty and constantly moving targets.

That, in fact, is a sensible protest. But however drastic the ecological variation, the challenges posed by manufacturing tools from various types of stone are the same in all settings: the fine tuning of the force and direction of blows, the weight balance between hammer stone and core, short term planning, handling spatial proportions, and so on. While generally speaking environmental variability on an ecological timescale maintains plasticity and prevents genetic adaptation, as far as this stable, predictable and reliable setting is concerned not flexible but rigid solutions pay off.10,22

Possible benefits include less time and energy spent in learning to knap quickly and effectively; less susceptibility to loss of traditional skills through demographic bottle necks; less cognitive load; and less

FIGURE 1 Acheulean hand axes from various regions (to scale; biface 7 is 22.5 cm tall). Sites: (1) Boxgrove, England; (2) North of Bridge Acheulean, near Gesher Benot Ya’aqov, Israel; (3) Erg Tihodaïne, Algeria; (4) Sterkfontein, South Africa; (5) Olduvai Gorge, Tanzania; (6) Bose, China; (7) Isampur, India.12–18 The picture conveys the puzzling combination, over huge spans of space and time, of uniform basic shapes with spatiotemporal variation. Acheulean cutting tools of the cleaver type are not included, but offer an analogous mixture of similarity and difference. Figure by Shumon Hussain, from Corbey et al.1
susceptibility to injury or failure to learn. It gives pause that it takes both chimpanzees in the Tai Forest in Côte d’Ivoire and Mbendjele-Yaka foragers in the Republic of Congo many years to learn how to crack nuts with stone hammers, despite support by teachers in both cases.11

Phenotypic plasticity allows organisms to search the space of adaptive possibility until they hit upon viable solutions. “In constant environments,” Avital & Jablonka summarize their detailed discussion of the trade-off between learning and instinct, “genetic assimilation of learned behavior may lead to behaviors becoming increasingly less dependent on experience, and finally culminate in the evolution of innate ‘instinctive’ behaviors. In frequently changing environments, where genetic changes are not fast enough to track recurring change, individual and social learning are more beneficial.”22:346 In the latter case the Baldwin effect enhances the learning capacity itself rather than “starting the individual off in a state closer in learning space to the mature practice, so there’s simply less to learn.”22:344

Sterelny3:297–8 suggests that Avital & Jablonka’s assimilate-and-stretch scenario22:330–1 may be of interest in connection with the evolution of technological capacity. If certain parts of a sequence of behaviors become genetically assimilated it will take less time for fledgling nest builders or flint knappers to acquire the sequence. This creates room for the individual to play and try out, adding any beneficial actions it discovers. If this happens time and again the behavioral sequence is elaborated, stretched, by making parts of it automatic, while it remains a mix of learned elements and automatized basic skills. The learned elements may be imitated by others and become a local tradition.

4 | WHAT FEATURES MAY HAVE BECOME AUTOMATIZED?

As minimal features of early stone tool technology that may have been targeted by Baldwin effects Corbey et al. proposed “probably … not just a simple target form, but rather a predisposition toward the basic behavioral routines involved, such as invasive bifacial reduction while realizing cutting edges in the secant plane, working from the tip down, and keeping symmetry. These routines would have operated in combination with causal understanding, manipulative skill, and intuitive (‘folk’) physics.”11:4

Thomas Wynn and John Gowlett provide a cogent complementary suggestion, without realizing how well it combines with Baldwinian selection: a constellation of six ergonomic constraints on all handheld stone cutting tools. These constraints comprise: a center of gravity of the hand ax which is positioned toward a base (but) by which the tool fits readily in the hand; forward extension, which gives leverage and a longer cutting edge; some lateral extension in order to provide stability; support for the cutting edge; thickness adjustment; and a slightly skewed shape according to handedness. Together these basic characteristics constitute “one solution to the need for a sturdy, hand-held cutting tool whenever and wherever the basic technology is that of knapped stone tools, hafting is unknown, and the available raw material comes in large enough clasts.”22:7

This is a plausible characteristic of attractors in design space23— or fitness peaks in a metaphorical adaptive landscape10—toward which various shapes must have gravitated. The bone of contention here is not the role of various restrictions providing direction during that process, such as ecological circumstances, the affordances of the technological niche, accumulated cultural experience, raw material structure, resharpening processes, and drift effects. Nor is it the possible contributions of various forms of learning, although these factors are weighed differently by various authors.

My disagreement concerns the assumption that, in McNabb’s words, “parsimony affirms a social basis for hand axes and does not require a genetic predisposition,”4 or, as Wynn & Gowlett state in a converging argument,7:21 that hand axes are “fully accountable in cultural terms without recourse to genetic causation.” The latter think it highly unlikely that hand ax making by foraging Erectines and Heidelbergers “required other neural resources in support of production routines than those mandated by the anthropoid object manipulation network.”7:25

Paradoxically, Wynn & Gowlett in passing allude to “cognitive developments, primarily the emergence of a true tool concept, and an ability to coordinate spatial and shape information.” This renders their culturalist arguments ambiguous, for it begs the question what may have driven these evolutionary developments, which in their scenario appear out of the blue? Baldwinized, stable solutions may provide an answer, creating derived divergence in the hominin lineage from that ancient, phylogenetically primitive, anthropoid object manipulation network.

It is time now to heed recent research on the evolution of hominid neural resources more seriously. Baldwin effects have in fact been suggested regarding, among other features, neural tracts involved in visuo-spatial and visuo-motor skills24 as well as self-action control in stone knapping and copying others.19:25–27

However, these contributions stress skills for acquiring motor repertoires, not the repertoires themselves, content wise, as possible Baldwin effects. Under discussion here is that latter, more radical suggestion. In a number of bird species cited by Corbey et al. like Galápagos woodpecker finches (Camarhynchus pallidus), specific tool use appears spontaneously in naïve, untutored individuals, which suggests genetic assimilation into the genome of content, not (just) of learning capacities. The same goes for at least the basics of nest building in many bird species (see below).

The limited physical cognition of other primates in particular suggests dramatic derived developments in the hominin lineage, from reasoning in the earliest hominins based on what is observable, tangible, spatiotemporally associated on to a proper understanding of causal relationships in present-day humans.28 At the same time gradual changes befitting stone knapping occurred in the functional morphology of the hand and wrist while manual dexterity evolved in response to tool use. Key & Lycett think that the evolutionary advantages provided by efficient stone tool use may have selected for anatomical changes observed in the hand.29
McNabb remarks that Corbey et al. give too much focus on bifacial hand axes, neglecting other Acheulean products such as flake cleavers and picks, as well as the related problem how diversity in core techniques squares with basically uniform products.

The Baldwinian scenario suggests multiple attractors in design space: pebble tool, flake cleaver, trihedral pick, bifacial hand ax. It also implies that such solutions, once emerged under various constraints, possibly more often, would be long-lasting when adaptively optimal. The latter effect has often been described—or should we say: misunderstood—as “stasis,” for example, “Acheulean stasis.”

McNabb, cf. and Hosfield et al. are right to criticize Corbey et al. when, as an argument for partial genetic control, the latter assume that under a cultural transmission model copying errors should have eroded Acheulean shapes at a rate that is not reflected in the archeological record. Any such effect would indeed be masked by constraints which force the products toward optimal shapes, apart from the fact that the effect would be hard to ascertain archeologically because of weak vertical resolution.

At least seven different techniques have been used to produce more or less ready-made flake cleavers from large prepared cores (eg, Figure 2). Such cores permitted the production of many large flake blanks with a minimal investment of time and labor. The various core types are astonishingly similar between sites spread over large parts of Africa and Eurasia, as are the resulting cleaver types. Gonen Sharon postulates “one lithic tradition” to account for what is, in his view, a cultural phenomenon, comprising a “unique and highly sophisticated technology designed to achieve maximum control of the resulting large flake.”

But here too multiple, similar Baldwin effects on stone knapping, under various similar constraints, in particular limited technical possibilities (affordances), offer an alternative explanation which deserves further exploration. The result may have been convergence between distant sites toward a limited number of possible core types as attractors in design space.

**5 | CORES AND CLEAVERS**

Although hierarchically more complex than the preceding Oldowan, the appearance of Acheulean cleavers made of flake blanks struck...
from large cores was not as “fundamentally different, innovative, and sophisticated” as Sharon claims on the basis of his culturalist assumptions, like many others.

Both the core and to a lesser extent the flake blank, struck from that core to serve as a cleaver, undergo an essentially similar stepwise reduction. Whenever a flake is struck from a core there are always two obvious options for further reduction: of the core, or of the flake. Using either a reduced core or, alternatively, a more or less reduced flake as a tool are always obvious possibilities, and switching from the first to the latter action basically is not a large step, nor is the reverse. Once the reducing of the—say, late Oldowan—core in order to serve as a (pebble) tool had shifted to the reducing of flakes into tools, both the cores which were subsequently discarded and the flake tools would likely have become larger.

The same goes for the appearance of Levallois technology much later, c.300 kyr ago, which—as has been hypothesized before—may well have originated in the bifacial reduction of hand axes. Using not the hand ax but a large flake obtained during the hand ax’s production as a tool was, at any point, a clear alternative. Once this started to be done more often, the shape and size of the core probably quickly changed from being suitable for use as a handheld tool to being suitable to produce one or more large flakes, and then discarded. This, likely, happened multiple times, in various places.

In view of this possibility I am skeptical of the usual laudatory accolades conferred on core preparation because of presumably intelligent anticipation in terms of mental templates. I prefer a step-by-step Baldwinian scenario in terms of gradual developments in flaking and shaping which by their very nature—coincidence combined with constraints and path dependency—may have permitted punctuated shifts, such as the appearance of cleavers in the Acheulean, the Victoria West core method (Figure 2), or the appearance of very regular, well finished hand axes at about 700 kyr.

7 | ANIMAL STRUCTURE BUILDING

Tool making is seen as a case of animal construction by specialists in that field. This provides a heuristic for the study of early stone technology. The admittedly still rather sparse available research on nest building by birds, burrowing by rodents and dam building by beavers shows that these behaviors are under substantial genetic control—but also betray significant behavioral flexibility. They depend considerably on individual learning as well as, often, some weak social learning, within various constraints—ecological, functional, regarding raw material, and so forth.

The genetic underpinnings of such behaviors in the wild have hardly been studied directly, but a series of experiments with burrowing Oldfield mice (Peromyscus polionotus) sheds some light in this regard. This species, native to the south eastern United States, builds burrows with an entrance tunnel, a lounge and an escape tunnel in the opposite direction ending just below the surface. Cross-breeding with a closely related species with different burrows has permitted the identification of various surprisingly small regions of the genome, each controlling specific invariable parts and aspects of the burrow.

Animal niche construction in general shows how sophisticated emergent products usually result from a limited behavioral repertoire consisting of simple, repetitive, standardized routines in response to local stimuli. North American beavers (Castor canadensis, Figure 3), for example, build dams from logs cut down off-site, branches and mud—with a central living space, safe underwater entries, and refined air and water engineering. They pick suitable trees, fell them by gnawing a groove, transport them to the dam, and insert them into the dam structure. This chaîne opératoire and the resulting complex architecture are under genetic control while at the same time indicating much learning, insight and decision making. A young rescue beaver in Louisville Kentucky called JB (Justin Beaver) obsessively kept building dams from all sorts of household items in his caretaker’s house.

In the course of many generations of selection on characteristics befitting the construction behaviors of, for example, weaverbirds (Ploceidae) or long-tailed tits (Aegithalos caudatus), the smoothness, symmetry and regularity of their nests has increased continuously toward higher functionality. Research on nest-building behaviors and completed nest structures in several of over a hundred species of weaverbirds shows experience-dependence, variability and confluence on the individual, population and species levels. The same goes for bower architecture within 20 species of bower birds (Ptilonorhynchidae), which in particular show significant individual variation.

An analogous scenario can be considered, hypothetically, for the intriguing mix of similarity and difference in Acheulean stone tool manufacture. This research on bird nest building suggests how difficult it may be to disentangle the mix of learned elements, innate elements, and the effects of ecological, functional and other constraints—a mix which includes aesthetic preferences as well as...
social-sexual signaling and sexual selection. Claiming an exclusively cultural, learned character for early stone tool technology may well be premature.

Across different bird species cerebellar foliation increases as the complexity of the nest, manipulative skill and the amount of tool use increase. An increase in foliation may also explain the positive correlation between cerebellum volume, extractive foraging and tool use in primates. Various researchers have criticized the stress on central executive control as a distinct faculty, associated with the forebrain—dramatically expanded in the course of human evolution, and traditionally seen as separate from sensory input and motoric output. The as dramatically expanded cerebellum—arguably under Baldwinian selection—suggests the integrated character of distributed sensory-motor brain mechanisms, enabling embodied, adaptive "control, organization and comprehension of complex sequences involved in both technical and social intelligence."

According to this line of argument there exists no "Cartesian," disembodied reasoning device handling mental templates in the sense of McNabb’s “capacity to hold ideas in the mind and act on them,” or Wynn & Goullet’s cognitivist “true tool concept” which in Acheulean times "filled the supposed gap between sensory reception and motor output."

8 | SIMPLE BEGINNINGS

The Baldwinian scenario as developed here implies simple beginnings. In an early phase of extractive foraging and occasional tool use a lucky blow on a stone block may reward a phenotypically plastic individual with a sharp edge, next there may be other rewards for accidental blows under the right angle, etc. In the long run flaking develops into shaping: patterned and hierarchical flaking occurs and directional changes toward optimal points in design space set in. The entire process is susceptible to Baldwin effects given the stable, predictable character of stone.

Moore & Preston show what this earliest phase of stone manipulation may have looked like while throwing doubt upon extrapolations from experiments with modern stoneworkers to early hominin design goals. In an ingenious series of experiments they disrupted the modern stone workers’ inclination to use higher-order reasoning to guide the stone reduction, thus randomizing flake removal. When multiple flakes were removed randomly from a stone core the geometrical constraints of fracture mechanics alone, without any mental templates, turned out to "give rise to what appear to be highly-designed stone working products and techniques," including hand ax-like "protobifaces" and cores with apparently "predetermined" flake removals.

In a converging line of reasoning Tennie et al. criticized alleged over-interpretations of both Oldowan and extant ape tool making in terms of high fidelity ("strong") social learning and cultural traditions. They see the (pre-Acheulean) Oldowan as resulting from individual learning steered by raw material affordances—through trial and error, play, least effort strategies and the like—combined with some low-fidelity ("weak") social learning such as stimulus enhancement.

However, why not consider a plausible next step in this line of argument, I would like to ask Tennie et al. as well as Moore & Preston, to wit selection in favor of initially plastic features contributing to the effectiveness of stone technology? Tennie et al. claim that their parsimonious approach works better than strong social learning models in view of frequent local extinction and repopulations, but the same goes for genetic transmission.

The same question can be posed to Stout et al., who, contrary to Tennie et al., see evidence of strong social learning skills in differences between three 2.6 myr old Oldowan sites in Ethiopia, possibly resulting, they add, from Baldwinian selection. They dismiss the possibility that "various different knapping possibilities already existed as evolved tendencies in the motor repertoire," content wise, rather than being acquired by copying. They dismiss this because "it is difficult to see how multiple, highly specific yet functionally neutral, alternative behavioral programs could have been constructed by natural selection in the earliest known Oldowan knappers." But it is not that difficult, as I have argued. Stout et al. specifically dismiss some form of Baldwinian genetic assimilation of content because "this would itself presuppose an earlier stage in which behaviors were learned rather than innate." Yes, it would—as argued.

9 | CONCLUSION

Recent work on animal construction rectifies a widespread assumption that "nest building requires little or no cognitive ability." It suggest a considerable role for cognition (learning, insight, decision making, planning) in behaviors which are under some degree of genetic control. It is not a matter of either instinct or cognition—as McNabb’s stress on the imposition of conceptual preconceived forms would seem to suggest. The good news is that the stress on learning and other cognitive aspects in the still pervasively culturalist mainstream research on early stone tool technology combines well with possible Baldwin effects as explored here, as does its stress on ecological and functional constraints on toolmaking.

Baldwinian selection as a biocultural co-evolutionary process is an understudied, hypothetical (sic) driver of early lithic variability, next to various forms of learning which themselves were susceptible to such selection. Any emergent Baldwinian selection on basic aspects of stone tool making by definition was not species-wide, but may have happened in various places and times, whenever inflexible solutions paid off, regarding various types of tools and cores. This suggests a new take on complex archeological macro-patterns, including dispersals, grade shifts and convergences, and the degree to which these patterns vary with taxonomic status.

There is a huge amount of quantitative data regarding pre-Acheulean and Acheulean tool technology out there waiting to be revisited from this particular perspective, combined with niche construction theory and inspired by the Extended Evolutionary Synthesis. This paradigm gives more weight to "non-programmed
components of environment, development and inheritance than the classic, mid-20th-century Evolutionary Synthesis which still forms the mostly implicit background of much lithic analysis.

One of various problems to be addressed not mentioned in the present, revisionist and out-of-the-box note is that of Acheulean endings. Acheulean hand axes vanished when Middle Paleolithic and Middle Stone Age industries appeared with arguably different kinds of bifaces and much more spatiotemporal variability, at smaller scales. This may point to a reverse Baldwin Effect under relaxed selection pressures because learned behaviors had higher payoffs.

A promising angle on genes and early stone tools, finally, is the parallel with the evolution of language. Here too Baldwin Effects have been invoked by which certain previously learned linguistic features may in the long run have become innate through selection on linguistic behavior. Manipulation and speech are both multilevel, hierarchically nested, goal-oriented motor sequences, implemented by neuronal circuities which partially overlap and are under strong genetic control.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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