Skill Learning and Human Brain Evolution: An Experimental Approach

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Increasing reliance on skill-intensive subsistence strategies appears to be a hallmark of human evolution, with wide-ranging implications for sociality, brain size, life-history and cognitive adaptations. These parameters describe a human technological niche reliant on efficient intergenerational reproduction of increasingly complex foraging techniques, including especially the production and effective use of tools. The archaeological record provides a valuable source of evidence for tracing the emergence of this modern human condition, but interpretation of this evidence remains challenging and controversial. Application of methods from psychology and neuroscience to Palaeolithic tool-making experiments offers new avenues for establishing empirical links between technological behaviours, neurocognitive substrates and archaeologically observable material residues. Here we review recent progress and highlight key challenges for the future.

Introduction: the human technological niche

Humans are a highly successful species. Even without agriculture, it has been estimated that *Homo sapiens* would have attained a global population of more than 70 million and a total biomass greater than any other large vertebrate (Hill *et al.* 2009). Such demographic potential seems paradoxical in a large-brained primate known for its slow and costly development. A growing consensus finds the solution to this paradox in a human strategy of alloparenting (Hrdy 2009; Kramer 2010,) or 'biocultural reproduction' (Bogin *et al.* 2014), in which individuals other than the parents donate resources to help support offspring. This allows human mothers to produce large-brained children (Isler & van Schaik 2012) with the shortest interbirth interval of any ape and a total fertility rate three times that of chimpanzees (Kramer 2010), all funded by the surplus production of helpers. How is it that Pleistocene human foragers, in contrast to other apes, were able to reliably produce the surpluses that fuelled their demographic success?

Embodied capital theory (Kaplan *et al.* 2000; 2010) proposes that humans have evolved a tightly integrated strategy in which a focus on high-value, difficult-to-acquire food resources provides the surpluses needed to fund growth, survival and reproduction and is in turn enabled by the increased longevity and brain size that allow learning of the requisite foraging skills. Cognitive and affective adaptations for prosociality (Hill *et al.* 2009), necessary for biocultural reproduction, also provide a venue for social learning and teaching, ultimately leading to what Boyd *et al.* (2011) describe as a human 'cultural niche' of 'well-adapted tools, beliefs and practices that are too complex for any one individual to invent during their lifetime'. Integrating these various theoretical strands leads to a picture of a uniquely human way of life reliant on cognitive, affective, and life-history adaptations supporting the intergenerational reproduction and accumulation of foraging skills (Shennan & Steele 1999), including the production and use of tools. We refer to this particular aspect of the human cultural niche as the human 'technological niche' to reflect a specific focus on production.

How can we learn about the origins and evolution of this modern human technological niche? It is increasingly apparent that all elements of this bio-behavioural package did not arrive at the same time (Antón *et al.* 2014), and various authors have

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proposed co-evolutionary scenarios and timelines (Hill *et al.* 2009; Isler & van Schaik 2012; Sterelny 2011). These scenarios are framed by comparative evidence of 'human uniqueness' along inter-related social, biological and cognitive dimensions, but arguments about relative timing and causation will necessarily rely on direct evidence from the fossil, archaeological and palaeoenvironmental records (Antón *et al.* 2014). Critical to this endeavour is evidence of increasingly skill-intensive human technological activity (Nowell & White 2010), including extractive foraging, hunting and butchery, tool-making in stone, wood, bone, and antler, and signalling technologies such as pigments and personal adornment. Here we focus on knapped stone tools, which offer some of most prolific and detailed evidence of pre-modern hominin behaviour. Before this evidence can be used to develop or test evolutionary scenarios, however, it must be interpreted. This will require a solid base of middle-level theory allowing for secure inferences about the skills, cognition, and social context implied by particular ancient technologies.

The experimental method

Experimental archaeology aims to identify principles of transformation linking material evidence to human behaviours, and has been a critical component of archaeological enquiry for many decades. Experimental studies of skill and cognition are a straightforward extension of this endeavour using new methods to collect previously unavailable behavioural data regarding, for example, bodily movements (Nonaka *et al.* 2010) and neurophysiological responses (Stout *et al.* 2015). As with any actualistic research, this involves analogical arguments that must be justified (Wylie 1985). No experiment will ever be a perfect 'replication' of the past, and so the aim is to identify and manipulate particular variables relevant to the question at hand. For example, several experiments (Morgan *et al.* 2015; Nonaka *et al.* 2010; Stout *et al.* 2011) have used flint to model 'Oldowan' tool-making for reasons of practicality and/or experimental control. Though obviously inaccurate, this choice reflects a theoretical emphasis on studying the 'least effort' or 'mindless' (Moore, 2011) flaking thought to characterize the Oldowan (and other 'Mode 1' or 'Mode C' technologies: Shea 2013) generally rather than on exploring raw-material specific effects. In support of this abstraction, two studies (Stout & Chaminade 2007; Stout *et al.* 2008) that used cobbles (limestone, quartzite and greenstone) to model Oldowan tool-making obtained very similar neuroimaging results to a study with flint (Stout *et al.* 2011). Nevertheless, future work might aim to test specific hypotheses about the implications of different raw materials for knapping skill acquisition and performance (cf. Eren *et al.* 2011b).

A related concern is the match between experimental and archaeological tool-making techniques, a preoccupation of experimental knapping from the outset (Crabtree 1966). Again there is a question of specificity *versus* abstraction. Palaeolithic tool making occurred over a vast time period and many millions of square miles—to study patterning, some generalization is needed. For example, Stout (2011) attempted a theory-driven analysis of Lower Palaeolithic technology to identify cognitively relevant features present across diverse archaeological instantiations. One result was to identify platform preparation as a key technique contributing to the greater procedural complexity of Late *versus* Early Acheulean knapping. Subsequent research (Stout *et al.* 2014) identified direct evidence of preparation on *débitage* from the Late Acheulean site of Boxgrove, and showed that the technique was employed in a similar manner, to achieve similar effects (relatively thin flakes with small platforms) as in a sample of experienced experimental knappers. At the same time, systematic misapplication of platform preparation by a sample of less experienced experimental knappers illustrated the learning difficulties associated with this technique. This use of theory and experiment to generate behavioural hypotheses with testable archaeological predictions is a textbook (Kelly & Thomas 2013) example of middle-level theory building to strengthen analogies. The prevalence of platform preparation across Late Acheulean sites other than Boxgrove is not yet known, but where it occurs it has behavioural and cognitive implications and may be linked to brain-imaging studies (Stout *et al.* 2008; 2011; 2015) of experimental knappers using this technique.

Experimental archaeology of the Lower Palaeolithic faces the added challenge of modelling the behaviour of extinct hominin species with modern human (and other primate: Toth & Schick 2009) subjects. Limited reflection might make this appear as a fatal difficulty for experimental 'neuroarchaeology', especially if unfamiliarity with brains and cognition lends an air of mystery to the topic. However, brains are organs and cognition a form of behaviour: their proper study is simply another example of the need to develop appropriate middle-level theory. Consider, for comparison, experimental studies of tool making and hand morphology (Marzke 2013). Modern human experiments are used to identify morphological features supporting modern human tool making. These are compared with extant primates to identify derived elements of the human pattern, the emergence of which can then be traced in the fossil record and interpreted in terms of functional capacities for tool making. A similar logic applies to experimental neuroarchaeology. For example, an early brain-imaging study by Stout and Chaminade (2007) found Oldowan tool making to be especially reliant on an evolutionarily ancient frontoparietal system that also supports tool use in monkeys. It may be concluded that this system was shared with Pleistocene hominins and was a likely target of selection acting on tool making ability. Indeed there is now comparative evidence of derived human modifications to this system that are directly relevant to distinctive human tool-use abilities (Orban & Caruana 2014), and are differentially recruited by Oldowan *versus* Acheulean knapping (Stout *et al.* 2011). Neuroarchaeological experiments, like any experimental archaeology, should not be thought of as straightforward 'replications' of the past, but rather as contributing to an inferential framework of middle-level theory linking variation in brain systems, cognitive processes and archaeologically observable behaviours (Stout *et al.* 2015).

Learning to knap stone

Obviously, one major reason to study stone artefacts is the simple fact that they are there—one of the most consistently preserved and prolific sources of evidence available to Paleolithic archaeologists. But there is more to it than that. Stone knapping is a prototypical human skill, requiring a combination of perceptual-motor coordination and conceptual understanding to which archaeologists have applied the terms *savoir-faire* and *connaissance* (Pelegrin 1990). The acquisition of even relatively simple, Lower Palaeolithic, knapping skills requires extended practice (Hecht *et al.* 2014; Khreisheh 2013; Nonaka *et al.* 2010) of a kind that, in modern humans, is supported by a scaffold of culturally structured knowledge, practices, environments, interpersonal relationships and values (Stout 2002) as well as explicit teaching and language (Morgan *et al.* 2015). This raises the question of why exactly knapping is so hard to learn.

Knapping is a percussive technology. It requires forceful and accurate striking motions that are executed too rapidly for correction via sensory feedback. Knapping is also a 'reductive' technology involving the progressive removal of material. Together, these two facts account for much of the difficulty in learning to knap, in that even small errors in percussive delivery can result in uncontrolled, failed or incipient fractures that are very difficult to correct and may compromise the entire reduction plan. To make matters worse for those learning how to knap, many of the relevant parameters (e.g. appropriate kinetic energy of the blow) are not easily perceived or copied by watching more experienced practitioners. This problem of understanding and copying observed actions (the 'correspondence problem') has been heavily debated in neuroscience (e.g. Brass & Heyes 2005), with many now concluding that it is accomplished by associating preexisting internal models of one's own body and actions with the observed behaviour of others through stimulus generalization (Laland & Bateson 2001). Critically, this mechanism requires the preexistence of appropriate skills/experience to be matched with observed behaviours. Although this would seem to be a fatal problem for any kind of imitation learning, it may often be possible to 'copy' complex behaviours by assembling them from familiar constituents (Buccino *et al.* 2004). In cases where variation in lower-level action details does not make a difference to intended outcomes, the purely observational learning of novel actions may be possible (Byrne 1999). Unfortunately for stone knappers, however, details of the percussive act do matter quite a bit. Thus, learners must begin by (incorrectly) imitating the observed gesture, checking the actual outcome against the predicted outcome and then embarking on a lengthy process of goal-oriented behavioural exploration (deliberate practice: Ericsson *et al.* 1993) in order to (re)discover the relevant task constraints and develop corresponding internal models. Because there are a huge number of variables to be explored, this skill acquisition process may be quite lengthy and its completion may require substantial motivation and self-control.

Experimental studies

Seminal field experiments by Bril and colleagues (Bril *et al.* 2000; Roux *et al.* 1995) working with modern stone-bead knappers in India have shown that the 'elementary' percussive gesture of stone knapping requires a highly coordinated and precise strike, control over which is a more reliable indicator of expertise than years of experience or amount of technical knowledge (Bril *et al.* 2005). This work has now been extended to deal with simple flake detachment under laboratory conditions (Nonaka *et al.* 2010), with the finding that only experienced (>20 years) knappers were able properly to adapt the kinetic energy of their strikes to variable conditions of the core and thus to reliably predict and control flake detachment. Establishing this control is a critical learning bottleneck for any kind of efficient knapping; leading the authors to suggest that even Oldowan technology implies some form of social and/or environmental (e.g. frequent exposure to tool-making materials and residues) support to provide recurring opportunities for observation and practice. Indeed, such 'scaffolding' is characteristic of tool learning in non-human primates (Fragaszy *et al.* 2013), and the question becomes when and how this primitive condition developed to the much more elaborate set of transmission mechanisms exemplified in modern human lithic technology (Stout 2002), including especially teaching (Morgan *et al.* 2015) and social motivation (Hiscock 2014).

These are difficult issues to address experimentally precisely because they concern prolonged learning. Most studies of knapping skill to date have used a cross-sectional design, comparing subject groups of differing skill and/or experience (Geribas *et al.* 2010; Nonaka *et al.* 2010; Roux *et al.* 1995; Shelley 1990; Stout 2002; Stout *et al.* 2008; 2011; Winton 2005). Such studies have great value, but are unable directly to observe or manipulate learning processes. Longitudinal studies have been less common and have been compromised by small numbers of individuals (e.g. one: Eren *et al.* 2011a,b), short training periods (Morgan *et al.* 2015; Ohnuma *et al.* 1997; Putt *et al.* 2014), or both (Stout & Chaminade 2007). For example, two recent studies addressed the role of verbal teaching in tool-making skill acquisition. Morgan *et al*. (2015) found a facilitatory effect of verbal teaching on simple flake production, whereas Putt *et al.* (2014) found no (or even a negative) impact on bifacial shaping. As pointed out by Morgan *et al.*, this discrepancy may be more apparent than real, reflecting the attempt of verbal-condition subjects in the Putt *et al.* study to execute correct, verbally transmitted strategies (i.e. *connaissance*) without sufficient motor skill (*savoir-faire*). Indeed, the training period consisted of only one hour a week for five weeks. Previous research has found some conceptual (e.g. appropriate edge angles) learning, but limited motor improvement over such time scales (4 hours Oldowan flaking: Stout & Chaminade 2007). Even 16 hours was insufficient for subjects to produce bifaces comparable to archaeological examples (Novice group: Stout *et al.* 2014). Conversely, it is also possible that the verbal teaching advantage observed by Morgan *et al.* might diminish or disappear over more realistic practice durations. This study involved an unprecedented 184 participants, but suffered from a correspondingly truncated learning period (5 minutes). These two studies make important contributions by manipulating learning conditions, but ambiguities linger due to short learning periods. What are ultimately needed are studies with sufficient sample sizes to manipulate learning conditions (e.g. instruction, motivation) and assess individual variation (e.g. performance, psychometrics, neuroanatomy) that *also* have realistic learning periods. This would be expensive in terms of time, effort and money but offer new traction on key issues in the evolution of the human technological niche.

Another recent project did achieve a more realistic training period, but without a sufficient sample size to manipulate learning conditions systematically. As detailed by Khreisheh (2013), subjects were trained for two years in three Palaeolithic knapped-stone technologies (Oldowan flaking, Acheulean handaxe manufacture and Levallois preferential core technology). A wide range of data were collected, from subject training time, content and outcomes to practice-related brain functional and structural changes. Knapping skill was assessed through structured observational assessments as well as artefact metrics. All subjects received introductory teaching and attended three flint-knapping field trips but (for practical reasons) the remainder of learning was through self-paced individual practice and discretionary participation in taught sessions. In the event, not all subjects practised consistently (see Hecht *et al.* 2014; Fig. 1). In particular, subjects reported frustration with Levallois flaking and largely avoided practising this technology, logging less than 30 hours Levallois practice on average. Perhaps as a result, there was little evidence of improvement and no significant association between Levallois practice time and skill scores. Sadly, these data do not provide much information on the course of Levallois skill acquisition, but do re-emphasize: 1) the critical importance of motivation and self-regulation (Stout 2010) in knapping skill learning, and 2) the need for more systematically controlled studies.

Oldowan and Acheulean results were more informative. Following the theoretical distinction discussed above, skill assessments independently evaluated knapping execution (*savoir-faire*) *versus* planning (*connaissance*) on a 5-point scale (methods in Khreisheh 2013). Figure 1 depicts the first eight months (when the bulk of practice and improvement took place: see Hecht *et al.* 2014), showing that Oldowan skill on both dimensions was highly variable to start, but rapidly converged on higher values with practice. This is consistent with an artefact-based measure of performance (total flake area generated) that also indicates relatively rapid Oldowan skill acquisition (Stout *et al.* 2015). In the case of handaxe making, *savoir-faire* scores remained lower and showed no significant increase over practice. On the other hand, Acheulean *connaissance* scores show a similar rate of increase to the Oldowan but shifted to the right (i.e. requiring ~75 hours more to reach similar levels). These results are consistent with artefact data showing no group level improvement in handaxe 'refinement'

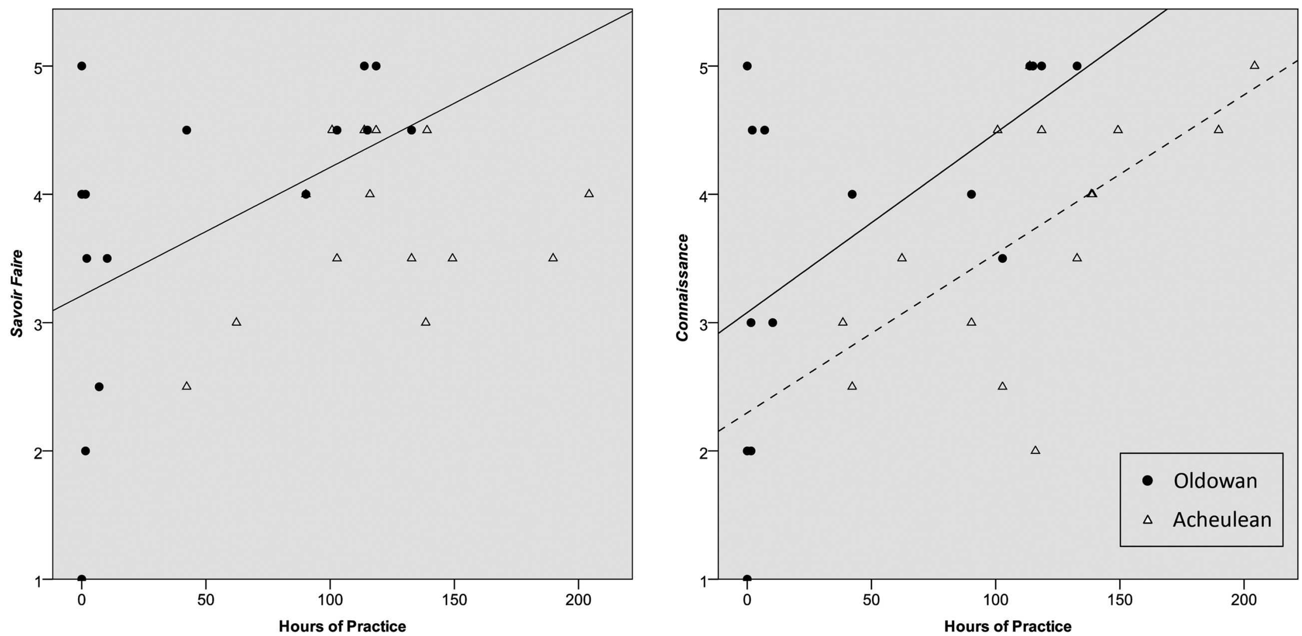

Figure 1. *The relationship between total practice hours and skill assessment scores for* savoir faire *(left) and* connaissance *(right). Significant (p<0.05) regression lines are plotted for Oldowan (solid) and Acheulean (dashed) evaluations.*

(Br/T) and with fMRI task performance showing improvement in strategic judgement but not fracture prediction (Stout *et al.* 2015). They also reinforce interpretations of the Putt *et al.* (2014) study presented above. Taken as a whole, these findings support and begin to quantify archaeological intuitions regarding the relative difficulty of Oldowan and Acheulean technologies, as well as the more specific hypothesis (Bril *et al.* 2000; 2005; Roux *et al.* 1995) that practical motor-skill acquisition is a greater constraint on complex skill development than is conceptual learning. Interestingly, hours of teaching had no apparent effect on skill assessment scores for either technology, suggesting that explicit instruction may be less helpful than individual practice. However, there was also relatively little variability in the amount of teaching (mean = 30 hours, s.d. = 15.6) as compared to practice (mean = 82.5 hours, s.d. = 60.7), so potential teaching effects may not have been adequately tested.

For the same subjects, Hecht *et al.* (2014) analysed structural MRI data from the beginning, middle and end of training and found practice-related changes in both grey and white matter. Interestingly, these changes did not simply accumulate across the learning period, but rather appeared and faded according to the actual amount of practice individuals engaged in immediately prior to the scan. This 'use it or lose it' effect illustrates the acute demands of tool-making activity on brain systems involved in complex action execution. In particular, effects were found in white matter connecting ventral frontoparietal regions of the brain previously linked to stone-tool making by functional studies (Fig. 2A), notably including prefrontal cortex of the right inferior frontal gyrus (rIFG). Prefrontal cortex generally is associated with the higher order cognitive or 'executive' control of action, with the right inferior frontal gyrus specifically supporting response inhibition and task switching (Levy & Wagner 2011). Indeed, a recent study found white matter changes associated with learning a classic 'Go/NoGo' inhibitory control task in almost exactly the same rIFG location as Hecht *et al.*'s tool-making effect. Right IFG inhibition is important for generating complex action sequences (Dippel & Beste 2015), which generally require different responses depending on changing contexts. This may underpin rIFG involvement in superficially diverse activities ranging from manual sequence learning (Seitz & Roland 1992) to language processing (Vigneau *et al.* 2011).

Following the 'neuroarchaeological' logic outlined above, evidence of tool-making effects in regions of overlap between praxis and communication (left ventral premotor and parietal, rIFG) led Hecht *et al.* (2014) to propose that human frontoparietal circuits were a likely target of selection for tool-making skill and that resulting adaptations may have been 'behaviourally co-opted ['exapted': Gould & Vrba 1982] to support proto-linguistic communication and

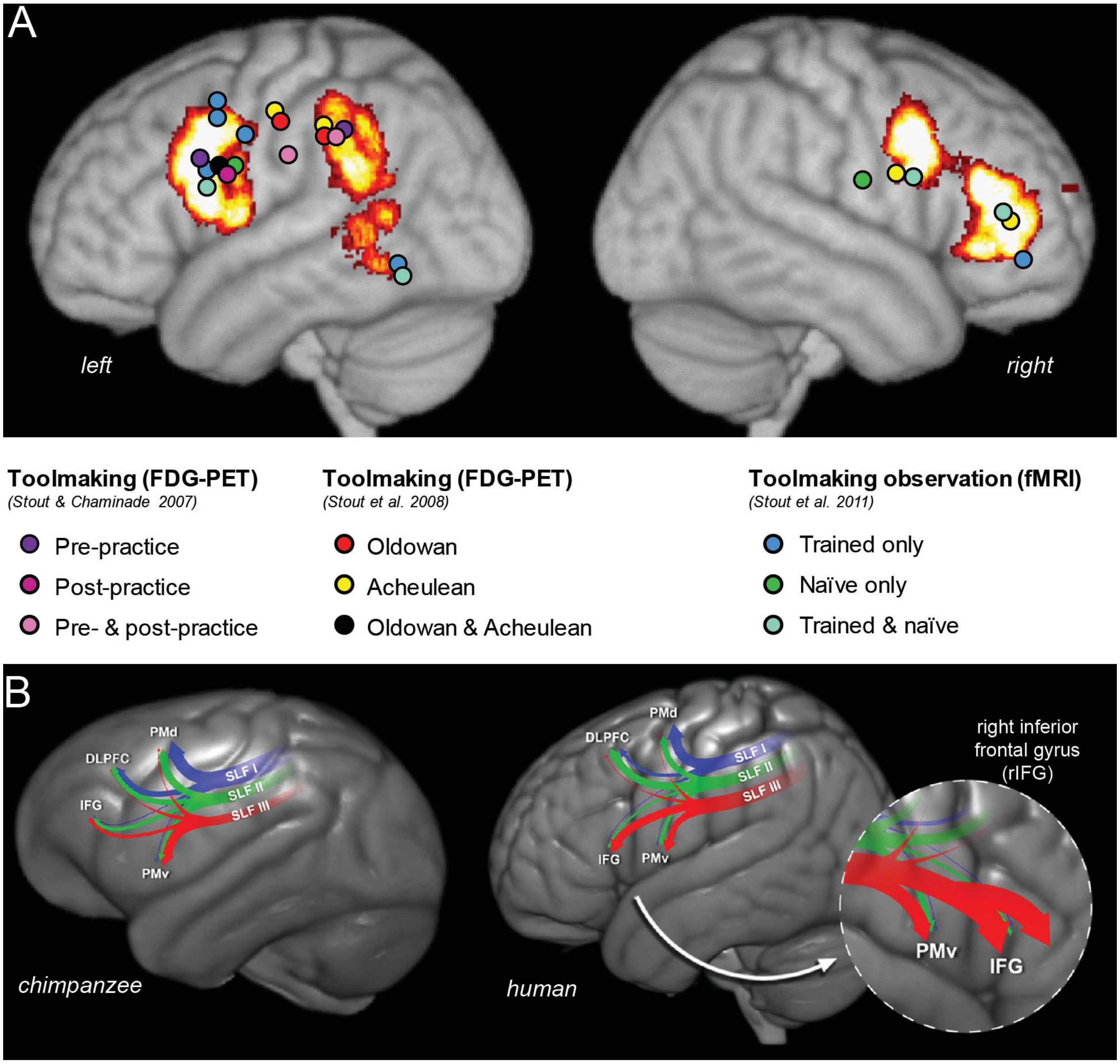

Figure 2. *A) Location of stone-tool making functional activations (coloured circles) adjacent to the cortical projections of white-matter tracts (coloured regions) that underwent structural changes in response to tool-making training. (Adapted from Hecht* et al. 2014.*) B) Frontal connectivity of the superior longitudinal fasciculus in chimpanzees and humans. Arrow size is proportional to the volume of grey-matter connectivity. Note greater human SLF III connectivity with IFG and (in circle) rightward asymmetric extension into more anterior IFG. (Adapted from Hecht* et al. 2015.*)*

then subsequently altered by secondary adaptations specific to language'. This proposal makes the prediction, testable by comparative data, that these circuits should in fact show adaptations in humans that parallel observed experimental effects (i.e. increased frontoparietal gray matter volume and connectivity). This does generally appear to be the case (Rilling & Stout 2014), and a targeted follow-on study (Hecht *et al.* 2015) comparing the relevant white-matter tract (superior longitudinal fasciculus III) found that it is indeed larger, more anteriorly projecting and right lateralized in humans (Fig. 2B).

Conclusion

Stone tools have the potential to provide valuable evidence regarding the evolution of the modern human technological niche, but much work remains to be done to establish the necessary middle-level theory leading from lithic data to behaviour, cognition and evolution. Recent experimental results confirm sensorimotor-skill acquisition as a key bottleneck in learning to knap. Abstract cognitive control and information manipulation may be needed to deploy effective knapping strategies (Stout *et al.* 2015), but, at least for modern humans, a greater investment of time and effort is required to develop the underlying ability to predict and control flake detachment. This suggests two major avenues of research. The first centres on the social, psychological and environmental conditions enabling prolonged skill learning and the potential co-evolutionary interactions of technology with social cognition (Stout & Chaminade 2012; Stout *et al.* 2011), communication (Morgan *et al.* 2015; Putt *et al.* 2014) and self-control (Stout 2010), all of which are also directly relevant to supporting biocultural reproduction. The second focuses more directly on identifying neural adaptations for skilled praxis, as indicated by human physiological (e.g. Stout *et al.* 2008) and structural responses (Hecht *et al.* 2014) and by comparative data (Hecht *et al.* 2015). Progress has been made on both fronts, but it remains for future work to achieve the simultaneously large, well-controlled and lengthy studies that will ultimately be needed.

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