

The Nature of Culture: an eight-grade model for the evolution and expansion of cultural capacities in hominins and other animals

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Summary - *Tracing the evolution of human culture through time is arguably one of the most controversial and complex scholarly endeavors, and a broad evolutionary analysis of how symbolic, linguistic, and cultural capacities emerged and developed in our species is lacking. Here we present a model that, in broad terms, aims to explain the evolution and portray the expansion of human cultural capacities (the EECC model), that can be used as a point of departure for further multidisciplinary discussion and more detailed investigation. The EECC model is designed to be flexible, and can be refined to accommodate future archaeological,*

paleoanthropological, genetic or evolutionary psychology/behavioral analyses and discoveries. Our proposed concept of cultural behavior differentiates between empirically traceable behavioral performances and behavioral capacities that are theoretical constructs. Based largely on archaeological data (the 'black box' that most directly opens up hominin cultural evolution), and on the extension of observable problem-solution distances, we identify eight grades of cultural capacity. Each of these grades is considered within evolutionary-biological and historical-social trajectories. Importantly, the model does not imply an inevitable progression, but focuses on expansion of cultural capacities based on the integration of earlier achievements. We conclude that there is not a single cultural capacity or a single set of abilities that enabled human culture; rather, several grades of cultural capacity in animals and hominins expanded during our evolution to shape who we are today.

Keywords - *Cultural capacity, Cultural performance, Cultural evolution, Animal culture, Human culture.*

Introduction

"Culture ..., taken in its wide ethnographic sense, is that complex whole which includes knowledge, belief, art, morals, custom, and any other capabilities and habits acquired by man as a member of society. The condition of culture among the various societies of mankind, in so far as it is capable of being investigated on general principles, is a subject apt for the study of laws of thought and action. On the one hand, the uniformity which so largely pervades civilization may be ascribed, in great measure, to the uniform action of uniform causes; while on the other hand its various grades may be regarded as stages of development or evolution, each the outcome of previous history, and about to do its proper part in shaping the history of the future" (Tylor, 1871, p. 1)

In his 1871 volume on "Primitive culture: researches into the development of mythology, philosophy, religion, art, and custom" the English anthropologist Edward Burnett Tylor laid the groundwork of cultural evolutionism. On one level, his classic definition of culture is straightforward, but on another level, 'major issues' are already implicit in the passage cited above. At the time of his writing, not much was known about the course of human evolution. "Man as a member of society" referred to modern humans (*Homo sapiens*); earlier hominin species and their cultural expressions were not part of the frame of reference. "Stages of development or evolution" were not seen in an extended, chronological

perspective across different genera; it simply referred to the categorization of different 'modern' cultural performances and possible connections between these groupings. Since then, our understanding of humankind, our place in nature and the processes of change and continuity has changed fundamentally. The concept of evolution, based on Darwin's ideas, has been refined by genetic research, the concept of an organism as a biological system, epigenetic studies, and it is applied to fields beyond biology, including culture and cognitive evolution. Knowledge of hominin species richness has increased considerably, as has knowledge of the artifacts used by the fossil hominins. We now have evidence for around 20 fossil hominin species between 7 Ma and 18 Ka (MacLachy *et al.*, 2010), while the origins of technology – a widely accepted indicator of culture – have been traced back to at least 2.6 Ma (McPherron *et al.*, 2010; Semaw *et al.*, 2003). The concept of 'culture' has become a frequently used, but controversial notion to describe special behavioral phenomena. Still regarded by some as a uniquely human attribute, the term 'culture' has been increasingly applied to a special subset of behavioral patterns associated with some animal groups such as New Caledonian crows (Bluff *et al.*, 2010), whales and dolphins (Allen *et al.*, 2013; Rendell & Whitehead, 2001; Whitehead & Rendell, 2015), and great apes including chimpanzees (Lycett *et al.*, 2007, 2011; Whiten *et al.*, 1999), orangutans (van Schaik *et al.*, 2003), and bonobos (Hohmann & Fruth, 2003) (for critical discussion see Laland & Janik, 2006).

The definition of the term ‘culture’ is, however, diverse and debated in its various fields of application. Philosophy, social and cultural sciences use multiple definitions (Kroeber & Kluckhohn, 1952; Hammel, 2007), but generally consider it to be a trait exclusive to *Homo sapiens* (Ramsey, 2013). Culture has been defined as: “behavior, peculiar to the human species, acquired by learning, and transmitted from one individual, group, or generation to another by mechanisms of social inheritance” (White, 1959, p. 228), or as “an abstraction from behavior” (ibid. p. 227), instead of behavior itself. The term may be used in a restrictive way as “things and acts dependent on symboling” (ibid. p. 230), or as symbolic things and acts “considered and interpreted in an extrasomatic context, i.e., in terms of their relationships to one another rather than to human organisms” (ibid. p. 231). The focus, for example, has been on cultural patterning (ibid. pp. 232-233), or on culture as a set of ideas (ibid. pp. 236-237), including or excluding material culture (ibid. pp. 238-239). Other definitions are used to trace animal culture and emphasize the social transmission of information in the process of development of population-level characteristics, in contrast to genetic inheritance (Whiten *et al.*, 1999, p. 682). As Richerson & Boyd (2005, p. 6) state: “Culture is information stored in individuals’ brains that is capable of affecting behavior and that got there through social learning.”

The two approaches are reflected in the culturalistic versus naturalistic views on culture in philosophical anthropology (Bloch, 1991; Hallpike, 2008; Pihlström, 2003). Culturalism emphasizes humans (generally *Homo sapiens*) as intentionally and purposefully acting cultural beings, and cultural achievements as meaningful and self-determined. Humans are seen to live, not only in a physical world, but also in a symbolical world formed by language and other symbolic expressions. Culture, which shapes human life, is “continuously reconstitut[ed] through our social action and linguistic encounter with our symbolic world” (Pihlström, 2003, p. 263). In contrast, naturalism explains cultural achievements, like other natural phenomena, by

natural forces and laws. Thus, animals can also be thought of as bearers of culture, with the development of culture being driven by evolution (Laland & Galef, 2009; Whiten *et al.*, 2011). Both of these positions have problems. The culturalistic approach lacks a broad evolutionary perspective of how symbolic, linguistic, and cultural capacities emerge, while the naturalistic one falls short when it comes to dealing with certain specificities of cultural expressions, transformations, and processes, especially in explaining the active component of human culture (Perry, 2009; Hill, 2009). Both the culturalist and naturalist approaches refer to living organisms and their directly observable behavior. Paleolithic archaeology and paleoanthropology, however, are not only interested in a given state of expression of cultural behavior at any specific time. Rather, these fields also examine the long-term development of culture within evolutionary and processual contexts. Research on these aspects of culture is complicated by the fragmentary record of past behaviors resulting from partial materialization, incomplete embedding and preservation over thousands of years, fractional discovery, poor dating resolution and hence limited possibilities of analysis and interpretation.

Several attempts have been made in the last decade to approach the concept of culture from a more integrative point of view. These attempts aim to understand “culture across species” (Byrne *et al.*, 2004) and “the evolution of cultural evolution” (Henrich & McElreath, 2003), to explore “the evolution of animal culture” (Whiten & van Schaik, 2007) and the association of cognitive and cultural evolution (Haidle, 2008), to look for “a unified science of cultural evolution” (Mesoudi *et al.*, 2006), and to gain insight into how “culture evolves” (Whiten *et al.*, 2012). These authors discuss evolutionary aspects of culture defined in varying ways, providing insight into mechanisms of cultural development and their evolution (see also Andersson *et al.*, 2014; El Mouden *et al.*, 2014), supported by a growing corpus of empirical studies. However, they also reveal that two major elements required for synthesis are lacking:

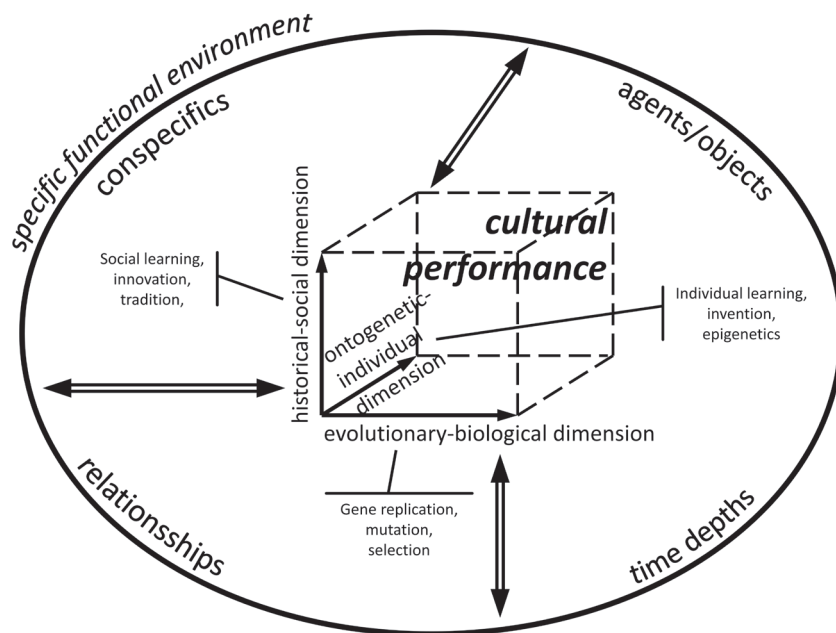


Fig. 1 - Cultural performance with three dimensions of development (evolutionary-biological, historical-social, and ontogenetic-individual) and their main mechanisms of development. The cultural performance of a group is interdependent with the group-specific environment. This includes conspecifics, agents and objects as affecting or affected elements with specific relationships to the group and in a certain time depth of perception, conception and action.

- 1) A concept of culture and of cultural evolution that covers not one single idea of culture, but discriminates different specificities of culture among, as well as within species. Such a concept should include several types of mechanisms that determine cultural peculiarities.
- 2) A model of cultural evolution that incorporates grades of pre-cultural, proto-cultural and cultural behavior identified in animals and the major cultural changes known in human evolution.

In the present paper, we—a multidisciplinary group of archaeologists, biological anthropologists, sociocultural anthropologists, primatologists, and psychologists—attempt to fill these gaps by developing a new conceptual model for the analysis of culture and cultural evolution. The

core components of the model were developed at a symposium that was organized by “The Role of Culture in Early Expansions of Humans” research center of the Heidelberg Academy of Sciences and Humanities in 2011 (Haidle & Conard, 2011).

An integrative concept of cultural behavior and evolution

The proposed integrative concept of cultural behavior and evolution differentiates between empirically traceable behavioral *performances* and behavioral *capacities*, as theoretical constructs.

Cultural Performances

Cultural performances are a subset of the behavioral performances of an individual, group, or population. Cultural performances can be observed in a variety of behavioral fields, such as

nutrition and food acquisition, communication, social organization, settlement patterns, and they can manifest in material products. Cultural performances possess three dimensions of development, i.e.: evolutionary-biological, historical-social, and ontogenetic-individual (Fig. 1). Cultural performances, per definition, require a historical-social dimension of development, while other non-cultural behavioral performances do not. Cultural performances represent the actual set of attributes with historical-social and developmental aspects, including activities and manners and their material or notional manifestations. Cultural performances (transmitted by social learning) can be observed in living organisms as well as partly (due to preservation and interpretation constraints) through archaeological assemblages.

The *evolutionary-biological dimension* affects the biological potential and constraints for a cultural performance set in genes and gene expressions, and expressed in anatomical blueprints and physiological standards of a group of organisms. Developments in this dimension enable or hamper a performance, either by directly affecting its emergence (as the activation of a specific gene or set of genes influences the expression of a certain trait), or by indirectly constraining developmental possibilities – for example, via the range of possibilities for a behavior given by the structure of the nervous system and the brain, sensory perception, principle motor and articulation skills, the memory system, the form of sociality, and the abilities to communicate, plan, and reason. The evolutionary-biological dimension affects the basic course of life history, the physiological-cognitive potential to perceive, create, learn and remember cultural traits, and the ways in which they can be expressed. For example, with flippers and flukes (instead of hands and feet), with a sound production system within the blow hole, with a different brain structure (despite external similarities such as a remarkable size and extensive folding of the neocortex; see Marino *et al.*, 2007), and with different social structures and life histories, a dolphin (Norris, 1966) possesses markedly different biological equipment for cultural behavior compared to that of a chimpanzee or a human. The

species-specific characteristic of the evolutionary-biological dimension of behavioral performances enables the finding of species-specific solutions to species-specific problems. Continuity or change in this dimension underlies evolutionary mechanisms such as gene replication, mutation and variation in selection. However, although material engagement with the environment and, as part of it, material culture cannot change the deep properties of a neural network, it can change the process of functional specialization, which is related to a historical/social and ontogenetic dimension (Coward & Grove, 2012; Fisher & Ridley, 2013; Jäncke, 2009; Malafouris, 2010, 2013; Woollett & Maguire, 2011).

The *ontogenetic-individual dimension* refers to individual agency and pertains to the potential and constraints of an individual organism, set by an individual's talents or poor aptitudes, social setting and life histories of physical, mental, and emotional experiences. The ontogenetic-individual dimension is reflected in individuals' range of preferences, aversions, skills and abilities. Already in the womb, monozygotic twins, with the same genetic complement, have different experiences with different epigenetic effects (Petanjek & Kostović, 2012). Siblings can be raised in the same family, within the same historical-social setting, but experience different influences by parents, relatives, friends, teachers, etc., by support or deprivation, by diseases, fortuitous timing or traumatic accidents. All these factors affect the mechanisms of change that operate on this dimension: individual learning, personal inventions, and epigenetics, "factors that influence gene expression without modifying the DNA sequence" (Ledón-Rettig *et al.*, 2013, p. 311).

Behavioral performances may express solely a biological program like reflexes (although these may also be influenced by individual factors such as disorders of the nervous system). They may also combine genetically inherited factors with individual aspects, such as nest building behavior of birds, squirrels and beavers. In these cases, the behavioral program may be largely instinctively initiated, but the execution is improved and adjusted to the specific situation by individual learning.

Cultural performances, in contrast, involve *historical-social dimension* that represents historical and social cues opening potential scenarios or raising constraints. The set of historically acquired knowledge and skills, customs, views and opinions represents a basis of behavior derived from experiences made by group members. For example, the organism can use the performance of expert group members as a scaffold for learning behavioral tasks. In this way, he can reduce costs of acquisition and risks of failure. The social access to the cultural set affects the possibilities of an individual to benefit from the experiences made by other members of a group. The forms and extent of storage, transmission, permutation, and transformation of the historical-social set support or hamper the unfolding of cultural performances. Cultural behavior is grounded on factors developed by evolutionary-biological processes and it is learned and executed in individual ways. A learning path is, however, also provided by the behavior of the social group to which an individual belongs. This social learning path is created and functions within a historical time frame (cf. Sterelny, 2012).

The historical-social dimension, in general, affects the ways in which the evolutionary-biological basics are used for cultural behavior, but it can also affect the plasticity of some biological bases developed in phylogeny (Coward & Grove, 2012; Fisher & Ridley, 2013; Jäncke, 2009; Kim & Sasaki, 2014; Malafouris, 2010, 2013; Woollett & Maguire, 2011). This dimension unfolds via social transmission, from stimulus enhancement to the capacity of teaching, via group-wide adoption of innovations and via transgenerational traditions. The characteristics of the historical-social dimension are influenced by factors that themselves are under the impact of historical-social variables like population density, communication systems, child-raising habits, teaching systems, and systems of religious and political participation. This means that the historical-social dimension is self-enhancing; cultural behavior influences factors that foster cultural transmission and creativity (Enquist *et al.*, 2008). An example that illustrates the importance

of the historical-social dimension is provided by the culturally different forms of color perception in humans. This is biologically generally limited by trichromatic vision. The ways in which colors are seen and categorized, however, are culturally influenced by historical-social factors and can range from bipartite concepts that differentiate only between black and white, to concepts with eight and more categories for different shades of colors (Hill & Hill, 1979; Kay *et al.*, 1991). How an individual perceives the color of an object depends on the phylogenetic prerequisites, the historical-social system of color categorization in which he/she was raised, and the individual affection to and training of applying it.

Musical performances provide another example. Musicality, the capability for musical perception and expression, is a biological potential developed in phylogeny (Peretz, 2006). Historical-social aspects influence the different ways music is perceived and expressed in different social groups of humans (Cross, 2001). While general musicality is allowed by biological factors, the preference for classical music with baroque instrumentation, for rock music with electric bass, or for Indian sitar music is biased by historical-social aspects. The individual performance in playing one of these instruments depends on individual training and verve. Wolfgang Amadeus Mozart was an individual genius who received special support from his musician father. He possessed human capacities of musicality, not those of a blackbird. And he lived in the historical-social context of Austria in the 18th century with large orchestras and a broad, fascinated audience, which was favorable for his special efforts, and not in a small mobile foraging group in the mammoth steppe of the last ice age.

All of these three major dimensions are multi-factorial. The axes in the diagram (Fig. 1) do not represent a quantitative measure, but qualitative factors opening potentials for behavior. Each of these factors has its individual developmental path, that is affected by factors of the same and the other developmental dimensions of the same and other performances of the organism, the group, or elements of the environment. The three dimensions and their factors are

conceptually distinguishable but not independent in their effects. To the contrary, they interact with one another directly or indirectly via reciprocal effects in the context of a specific functional environment (cf. Andersson *et al.*, 2014; Brooke & Larsen, 2014). The specific functional environment (or resource space, ecological niche) is the sum of the cultural and social aspects of the environment of an organism or a group, plus the section of the natural environment which affects, or is affected by, the organism or the group (Haidle, 2008a). The specific functional environment (resource space, ecological niche) is composed of other performances of the same organism as well as of performances of conspecifics (e.g. other Neandertals), of agents (e.g. cave bear, anatomically modern humans, a parasite) affecting, and of objects (e.g. tree, deer, water, chert, scraper) affected by the individual organism and its performances. These components are in specific functional relationships with the individual performance or the organism (as predator, competitor, shelter, food resource, raw-material for tools, tools etc.), which are effective within a certain time depth in perception, conception, and action (ranging between an instant and generations in both past and future directions, being singular or recurring). The functional relationships of a group of organisms with elements of the specific environment (resource space, ecological niche) vary according to the affordances the organisms perceive in the environment, given the state of their evolutionary-biological, historical-social and ontogenetic-individual dimensions. Although the natural landscape of a lion and *Homo ergaster* may have been the same, their specific environments differed markedly.

The specific functional environment (resource space, or ecological niche) is also not static, but a set of other developing entities with several developmental dimensions. It depends on variation in biogeographic distribution of the group or species in focus; on geological and climatic changes and consequences in vegetation, fauna, and landscape on different scales; on the evolution and changing performances of other organisms. The specific environment shapes an organism and its

behavior. Some aspects are pleasant, raise well-being and fitness, others are uncomfortable or even lethal. Thus, some environmental factors are sought after, whereas others should be avoided or altered. And an organism, respective of its behavior, can also shape the environment by changing the frequency of vegetation and fauna elements, eating other organisms, spreading seeds with excrement, suppressing competitors, opening landscapes, providing nutrition, etc., thus constructing its specific niche respectively (Kendal *et al.*, 2011; Laland & Sterelny, 2006; Odling-Smee *et al.*, 1996, 2013; Scott-Phillips *et al.*, 2014), by effects of factors of the historical-social dimension, the cultural niche (Laland & O'Brien 2011).

On the one hand, the specific functional environment (resource space, ecological niche) is the sphere where evolutionary-biological adaptations are brought forward. On the other, it is also effective as the learning environment of an organism, in the ontogenetic-individual as well as in the historical-social dimension. Via individual and social learning the behavior can be rapidly adjusted to a specific, heterogeneous and changing environment, and behavior is constantly forming the future adaptive and learning environment. In human evolution, not only do the three developmental dimensions of behavior expand, but consequently, the specific environments of hominins (that serve as basis) become increasingly altered and/or enriched. Figure 1 can provide only a broad outline of the different developmental lines of cultural performance – neither a mere biological product, nor solely a historical issue – and their embedding into the specific functional environment in which the lives of individuals play out.

Cultural capacities

While cultural performances represent the actual sets of cultural attributes expressed by an organism or a group (subunit), cultural capacities of a defined analytical unit (species, population, or group) are theoretical constructs and express the potential range of cultural performances in different subunits at a given time. The different performances are based on different factors of the three

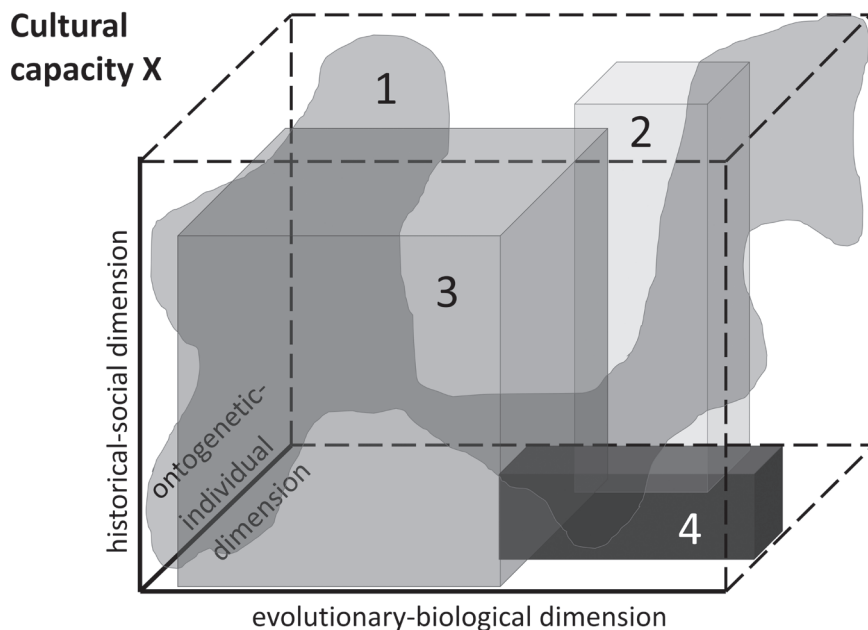


Fig. 2 - Contemporaneous cultural performances of different subunits (1, 2, 3, and 4) of an analytical unit (e.g. species X) with different expression within the three dimensions. The maximal outline of all the observed performances forms the cultural capacity of the analytical unit X. The axes in the diagram do not represent a specific quantitative measure, but qualitative potentials for behavior developed in evolutionary-biological, historical-social and ontogenetic-individual dimensions.

developmental dimensions and different segments of the specific functional environment; the sum of the performances expresses the sum of factors of the three developmental dimensions, documented in an analytical unit, and of the overall specific functional environment. The cultural capacity of, say, *Homo heidelbergensis* cannot be directly observed. It must be deduced from the sum of quasi-contemporaneous performances observed through the record of material culture preserved at different archaeological sites associated with *Homo heidelbergensis* (Fig. 2). The same principle applies to the assessment of cultural capacities of a specifically defined group: the cultural capacity of social groups (e.g., along linguistic lines) is derived from the sum of the possibly different sets of performances of the subgroups at different sites, within variable biogeographic areas with diverse ecological factors operating. ‘Capacity’ in the sense of this paper refers to the maximum range of

the evolutionary-biological, historical-social, and ontogenetic-individual dimensions, and the specific functional environment as expressed in the varying performances of the subgroups of the unit under examination. ‘Capacity’ is thus dependent on the layout of the unit to be analyzed. The cultural capacity of an analytical unit (group, population, or species) is never completely exhausted by each of the particular subunits (individuals, groups, or populations); rather, different aspects of the capacity are used and expressed. The cultural capacity of an analytical unit represents the potential of behavior given by the sum of factors developed in the phylogenetic, historical-social, and ontogenetic-individual dimensions, in interaction with a specific functional environment (resource space, ecological niche).

The range of cultural performances of different groups – and thus the corresponding cultural capacities – has expanded over the

course of human evolution. Nonetheless, a single cultural performance in an advanced grade of cultural capacity may be simpler in its developmental dimensions and interaction with the specific environment than another performance in an earlier grade, since different aspects of the full cultural potential can be applied selectively (Lombard & Parsons, 2011). The mechanisms of cultural development can be compared with the act of mountaineering (Lombard, 2012); it is always possible to proceed from any point reached so far, increasing behavioral or cultural complexity and flexibility, but it is also possible for individuals or groups to re-exploit seemingly simpler options, depending on the ruggedness of the specific fitness landscape (socio-ecological niche). Using the mountaineering metaphor, cumulative cultural capacity does not only include those cultural efforts that are built upon the highest level achieved, but also recursions following on seemingly more advanced solutions. Advanced cultural capacities are not necessarily accompanied by a progressive line of ever-more sophisticated and complex performances built on earlier ones, but allow increasing technological, cognitive, and behavioral flexibility from very simple to highly complex solutions depending on changing environmental constraints and cultural decisions (Lombard & Parsons, 2011; Lombard, 2012 in press). Thus, although the range of cultural performances expands with increasing cultural capacity, cultural evolution is not always linearly progressive. The development of cultural capacity is a systemic process involving the co-evolution of the three dimensions outlined above and their interaction with the specific functional environment (resource space, ecological niche). We stress that we perceive the evolution of cultural capacity as a continuous and ongoing process, yet we define eight main grades in the process of cultural expansion, the first four of which can also be found in several animal species.

A model of cultural evolution

A model of cultural evolution has to explore and explain the course of changes in cultural capacities. Multiple factors that affect the

development of individual and social aspects of cultural behavior can be identified, including learning and social transmission of information (Csibra & Gergely, 2011), memory (Bjorklund & Sellers, 2014), group conformity (Claidière *et al.*, 2014; van Leeuwen & Haun, 2014), and cooperation (Tomasello *et al.*, 2012). Each of these and other factors are important, but it is difficult to link them to a historical sequence. We attempt here to give a framework for the expansion of cultural capacities, based on the extensions of types of socially transmitted information. This model can be used as a scaffold to attach and combine the different factors in the course of cultural development and human evolution.

Tracing the evolution and expansion of cultural capacities

The available data sets are a challenge for efforts to build a model of the evolution of cultural capacity that integrates the different levels of pre-cultural, proto-cultural and cultural behavior, as identified in extant animals and cultural expansions in human evolution. Thus far, attempts have been based on ethological data (Tennie *et al.*, 2009; Tomasello, 1999; Whiten & van Schaik, 2007), focusing on the mechanisms of the social transmission of information. While Whiten and van Schaik (2007) concentrated on the evolution of animal culture with minor reference to hominin development, Tomasello (1999) and Tennie *et al.* (2009) compared mechanisms of cooperation and learning in chimpanzees and modern humans to describe the unique character of human cumulative culture – process-oriented copying in the human case, versus product-oriented copying in chimpanzees. In humans this process is aided by cooperation-based factors – active teaching, social motivation for conformity, and normative sanctions against non-conformity. Together, these result in an accumulation of cultural traits over time, the so-called ratchet effect. However, the developmental aspect of the evolutionary process in hominins, from the non-human foundations to current human cultural behavior is lacking in both approaches, due to limitations of the included data. Whilst useful

to begin to differentiate animal from modern human (*Homo sapiens*) cultural behavior, these ethologically-based approaches cannot detect possible preceding or successive capacities underlying cultural evolution.

We argue that tracing such wider developments must be based on the data which most directly open up the black box of hominin cultural evolution – the archaeological record. This provides the only evidence, although fragmented and indirect (cf. Haidle, 2014), of past hominin behavior. The questions that can be posed based on artifacts and fossils go beyond those derived from ethological data. Aspects of the cognitive background, the mechanisms of social transmission of information and the population level patterning of cultural behavior can only be partially inferred from archaeological finds. The type of socially transmitted information, however, could be accessible in prehistoric as well as in modern material remains, but is often neglected.

As an integrative structure for a systematic comparability of different archaeological remains and ethological data, we characterize the type of socially transmitted information by analyzing the ‘problem-solution distance’. The problem-solution distance (PSD) represents the behavioral route from perceiving a problem or need to its solution or satisfaction including possible loops or sidetracks. The PSD was first mentioned in Wolfgang Köhler’s (1926) comparative studies of chimpanzee behavior, where an extended PSD was suggested to be identifiable in tool behavior. In tool use, a goal is not approached directly (as when a hungry zebra starts to eat grass), but by moving away from the target object (e.g., a nut) to reach satisfaction (feeding) via an intercalated tool (e.g., a hammer). Haidle extended the concept of PSD and developed a model to systematically assess levels of complexity by coding them in cognigrams (Haidle, 2012, 2014; Lombard & Haidle, 2012). Using this method, PSDs of tool behaviors in living animals, ancient hominins, and recent humans can be compared directly (Haidle, 2009, 2010, 2012; Haidle & Bräuer, 2011; Hodgskiss, 2014; Hunt *et al.*, 2013). Differences can be found in the number of active and passive

attention foci necessary to solve a problem, and in the number of actions taken to satisfy a need. However, most significant for an evolutionary analysis of types of socially transmitted information and the expansion of cultural capacities are the different effective concepts through which attention foci are linked to each other.

Individual tool behaviors, and the PSD underlying them, comprise the tool-behavior performances of organisms and groups, which are part of their behavioral performances as a whole. The manufacture and use of tools of fossil hominins can be construed from the fragmentary material remains of the performances preserved in the archaeological record (cf. Haidle, 2014). Based on these data, we can deduce superordinate cultural capacities, defined by types of socially transmitted information, from the range of tool-behavior performances represented in ethological and archaeological assemblages. Rather than focusing narrowly on a particular artifact and the possibility of its invention by a single individual, our approach, similar to that of Whiten and colleagues (1999), aims to consider the entire accessible cultural repertoire of a group. In contrast to systematic differentiations of modes in stone technology (Clarke, 1969; Shea, 2013), PSD underlies all artefact types and technologies, and it shows a necessary developmental sequence. Additionally, an extended PSD is not exclusive to tool behavior, but is inherent also in social behavior and in the fulfilment of tasks needing self-control (MacLean *et al.*, 2014). Thus, the problem-solution capacities identified in tool behavior represent a minimum cultural capacity available to perform different types of cultural behavior. Assessing or reconstructing the different effective concepts, arising through the analysis of PSD in tool behavior, is one possibility to create a model of expansions of cultural capacities. The approach taken here is not a quantitative one, but distinguishes qualitative extensions of behavioral options. It provides the possibility to integrate animal, fossil hominin and modern human data within a unitary evolutionary model and the possibility to link different developmental factors to this scaffold. The empirical validation

and respectively falsification of this model will be subsequently given by developmental evidence of factors connected to cultural evolution supporting, contradicting, or altering the integrative model presented in the following.

A model for the evolution and expansion of cultural capacities (the EECC-model)

Changes in biological, historical-social and/or individual factors do not produce ‘culture’ in a single creative event. If chimpanzees possess a capacity for culture, it does not imply that theirs exists in the same form as ours. Rather, a range of factors generate different cultural capacities with specific requirements and possibilities of expression. The concept of different and developing “cultural capacities” is more appropriate for studying the evolution in cultural behavior than simply assessing the presence or absence of “culture” in certain living and extinct species. We offer a differentiated analysis of cultural evolution based on socially transmitted information, as observed in animals, such as other primates, in comparison with cultural remains from hominins. We also focus on the conditions associated with different grades of culture.

Our model for the evolution and expansion of cultural capacities (EECC model) comprises eight grades (Fig. 3). The model does not imply a progressive ladder, the climbing of which leaves the lower steps behind (cf. Lombard 2012; in press), but focuses on expansion of cultural capacities that extends the behavioral options and repertoire while retaining the possibilities of earlier states. To streamline our exposition, we present and discuss only the evolutionary-biological and historical-social dimensions (c.f. Figs. 1 and 2), placing the individual dimension on hold. Initially, the biological dimension dominates the development of cultural capacities, while the role of the historical-social dimension is minimal. In the course of expansion of cultural capacities, there was a marked increase in the biological dimension. An even larger, non-linear increase is suggested in the historical-social dimension, exponential through developmental self-enhancement and the interdependencies with alterations of the

specific functional environment induced by cultural behavior. The historical-social dimension dominates the development of cultural capacity in current human societies.

The first four grades can be observed in some extant animal species and partially correspond to Whiten and van Schaik’s (2007) ‘pyramid’ model of cultural evolution. The focus in the EECC model, however, is changed from mechanisms of social transmission of information and population-level patterning, as in Whiten & van Schaik (2007), to the type of information that is socially transmitted. As foundational capacities even simpler than socially learned information, more basic types of social information are proposed. Further grades of socially learned information (in Whiten & van Schaik [2007] the process of social learning) and tradition are derived from the Whiten-van Schaik pyramid model, but adjusted to the EECC model. For example, we extend the original “culture” step of the pyramid model, beginning with a grade labeled “basic culture”. Then, based on conceptual differences in the PSD represented in material culture (see above), four grades are distinguished based on the prehistoric record. These grades replace the single extension towards “cumulative culture” as presented in the Whiten-van Schaik model. Our newly suggested expressions include modular, composite, complementary, and notional cultural capacities. Below we discuss the eight grades of expansion within our proposed model.

1 – Socially facilitated information capacity.

Animals of many social species, both vertebrate and invertebrate, are attracted to the vicinity of others based on cues correlated with successful exploitation of resources, such as foraging patches (Giraldeau, 2008). Such attraction does not necessarily require learning; instead it may merely constitute a basic capacity to respond to a set of social cues. However, it can result in homogeneity of behavior between the individual and others in the group. Since such homogeneity is the result of social influence, rather than genetic inheritance or direct environmental shaping, it represents the most basic biological foundation

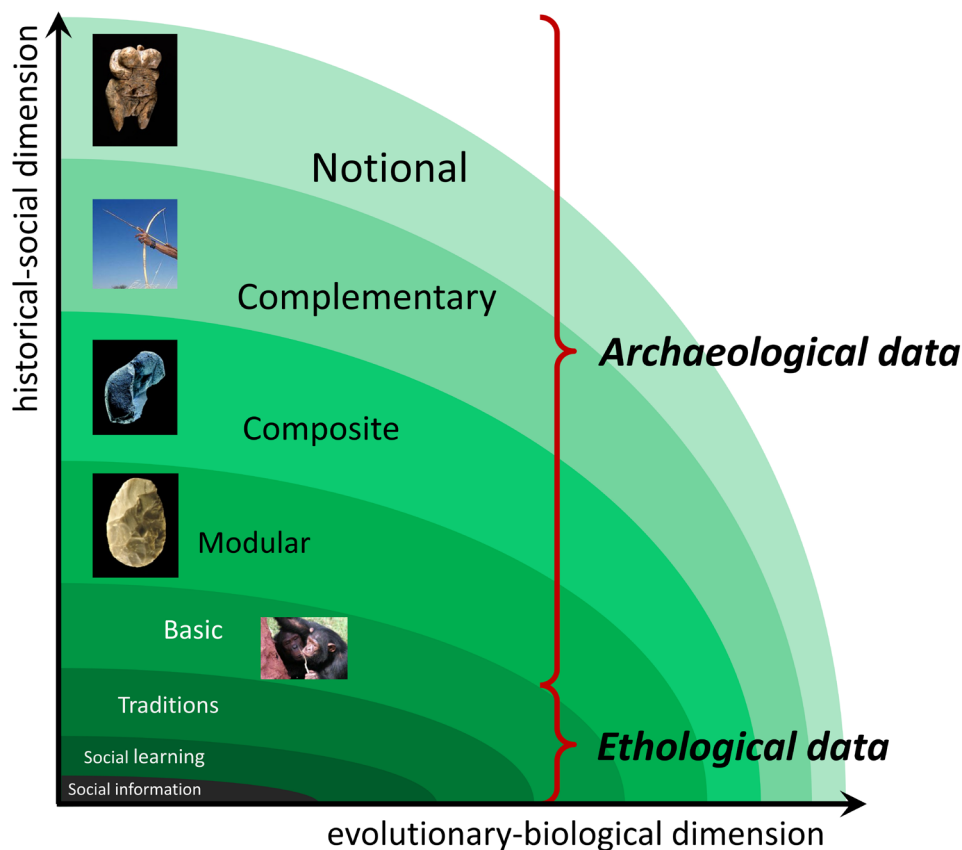


Fig. 3 - The expansion of cultural capacity in eight grades. The basic four grades ('social information' to 'basic') have been documented in some animal species, while the subsequent four ('modular' to 'notional') have, thus far, only been identified in the course of human evolution. With expanding cultural capacities the prominence of the historical-social dimension increases relative to the biological dimension. The colour version of this figure is available at the JASs website.

to culture. Thus, socially-derived homogeneity is arguably the most fundamental characteristic of 'culture'. Examples other than joining foraging groupings include attraction to nest sites in colonially nesting birds ('habitat copying'), and to the mate choices of others ('mate choice copying'). These phenomena are often referred to as 'public information use' or the exploitation of 'inadvertent social information' (Danchin, 2008). Decision-making may extend beyond basic attraction to capacities like discrimination and preferences for such additional cues such as the rate of observed foraging success (Giraldeau,

2008). Of course, since an ability to learn might be evident in the species concerned, individual-level learning may follow the initial attraction. For example, birds attracted to a foraging patch may learn its characteristics and return to it later. However, the basic attraction process need not involve learning, and many examples may be short lived. Such attraction can, however, give rise to long-term, and even trans-generational effects. For example, when birds are attracted to certain breeding colonies, and their offspring express the same preference, whether the cross-generation stability of the breeding colony could

be considered a tradition becomes a moot question, even if not dependent on social learning. Most definitions of traditions and culture (see below) require social learning as a key criterion.

2 – Socially learned information capacity. When the acquisition of information via others has durable effects in an animal's memory systems, a capacity for social learning is apparent. For example, an animal witnessing another's successful foraging may learn things that shape its future behavior. Exactly what is learned covers an extensive range, from the mere location or items involved (local and stimulus enhancement, respectively) to imitation (copying the form of actions in others) and emulation (learning about significant results of others' actions). The many different forms and processes involved in animal social learning have been dissected, both theoretically and empirically, over the last few decades (Hoppitt & Laland, 2008; Whiten & Ham, 1992; Whiten *et al.*, 2004). Social learning can generate faster and safer adaptive behavioral modifications than either individual learning or selection on underlying genetics. Recent work has even begun to address the rules animals apply for when to favor social over individual learning, and under what circumstances different cues and kinds of learning are preferred (Laland, 2004). For example, male vervet monkeys migrating to new groups have been found to readily abandon their natal food preferences for different ones expressed in the groups they join – a potent effect of social learning (van de Waal *et al.*, 2013). However, much of what is learned from others may be relatively transient. It may be useful for a chimpanzee to learn from observing others what is a good fruiting tree to visit, but this may be relevant for only a few days. Only when the effects are much more durable do we see progression towards the next grade of cultural capacity – the creation of behavioral traditions.

3 – Tradition capacity. Traditions are created when behavioral entities are transmitted through repeated social learning by individuals to become durable characteristics of an identifiable

grouping of individuals. A capacity to sustain such traditions has been identified in a diversity of vertebrate taxa, including fish, birds, primates and other mammals (Galef, 2004; Whiten *et al.*, 2012). The type of socially transmitted information, culminating in traditions, depends on the kind of social learning involved, including mechanisms as imitation and emulation. For example, the transmission of birdsong dialects involves copying of the form of the songs themselves, rather than their results, whereas the transmission of tool use in chimpanzees, such as used in nut-cracking, appears to be focused more on emulative learning of the results of such actions (Biro *et al.*, 2006; Tennie *et al.*, 2009). Similar to other forms of social information, traditions may be transmitted vertically, from parent to offspring, or (unlike genetic inheritance) horizontally between peers, or diagonally from older individuals other than parents. Horizontal transmission has been rigorously identified in 'diffusion experiments', in which alternative foraging techniques have been seeded in different groups of birds and mammals, within which they were later shown to spread (Whiten & Mesoudi, 2008). Recent studies in chimpanzees show that group-specific traditions could be observed over 25 years. The immigrating females adapted their original behavior to the form commonly used in the incorporating group (Luncz & Boesch, 2014). This evidence suggests that group conformity is not only a main trigger to adopt innovations as has been documented in experimental studies with birds (Aplin *et al.*, 2015). Moreover, information about group conformity may become an independent socially transmitted feature in addition to the information about the manner in which a problem can be solved (see also Haun *et al.*, 2014; van de Waal *et al.*, 2013; van Leeuwen & Haun, 2014).

4 – Basic cultural capacity. Many writers in the biological sciences treat the terms 'tradition' and 'culture' essentially as synonyms. For others, however, the latter term requires additional criteria, such as modes of social transmission that are assumed to be particularly critical in

human culture, notably imitation and teaching (Galef, 1992); or the appreciation of prescriptive social norms, about how one 'should' behave in one's local culture (Perry, 2009). A criterion proposed by Whiten and van Schaik (2007) is that 'cultures' be recognized as constituted by multiple traditions that incorporate a diversity of behavioral forms. This criterion is evidenced most richly among non-human species in great apes such as chimpanzees and orangutans, where variations extend to scores of behaviors spanning food processing, tool use, and aspects of social and sexual behavior. An important inference from the existence of these diverse and multiple-tradition cultures in the living great apes, including humans, is that our common ancestor of approximately 14-million years ago would have displayed such characteristics as stem cultural phenomena, as would their immediate hominin descendants (Whiten, 2011). However, there is also evidence of significant, if less rich, multiple-tradition cultures in other primates, including capuchins and macaques (Whiten, 2012), and through evolutionary convergence in cetaceans such as dolphins and humpback whales (Allen *et al.*, 2013; Rendell & Whitehead, 2001; Whitehead & Rendell, 2015). A special feature of basic cultural capacity documented in chimpanzees and humans, but not orangutans, are nested structures in cultural assemblages "if cultures with a small repertoire of traits tend to comprise a proper subset of those traits present in more complex cultures. This nesting will occur if some traits are sequentially gained or lost" (Kamilar & Atkinson, 2014, p. 111).

Possible expressions of traditions and basic cultural capacities are behavioral performances using tools. In contrast to direct behavior between subject and object, each tool-use event represents an extension of the PSD: instead of approaching a goal directly, at this level of tool behavior, attention has to be switched from the main goal (e.g., a nut) to a means to reach the goal (e.g., a hammerstone). The basic form of tool behavior has been documented in a variety of animal species (Haidle, 2012). Chimpanzees show an additional extension of the problem-solution

distance by using sets of different primary tools employed in sequence to a common end, such as an initial tool to excavate followed by a finer tool to probe within, to gather ants (Sanz *et al.*, 2009), to extract termites (Sanz *et al.*, 2004), or to collect honey (Boesch *et al.*, 2009; Brewer & McGrew, 1990; Sanz & Morgan, 2009). Even though tool use and production is well known in different animal species in the context of traditions and basic cultural capacity, it is limited to the ability to use unmodified objects or objects only altered by the animal's own bodily facilities (as distinct from using a tool to modify a tool). In these grades the tools are generally bound to a result-specific context.

The principal limitation in capacity, implied by these most complex forms of culture in non-humans, lies in the absence of all but the most limited signs of cumulative culture, in which yet more complex forms are built on what went before. Chimpanzees may have accumulated many different traditions over time, but with a few possible, minimal exceptions, these 'traditions' do not appear to go beyond what was likely the original innovation (Tennie *et al.*, 2009). Marked conservatism displayed in their cultural repertoires (Gruber *et al.*, 2011; Marshall-Pescini & Whiten, 2008) might be a possible reason for this limitation, but the degree of the behavioral conservatism of chimpanzees is debated (Manrique *et al.*, 2012). Chimpanzees apply many different tools for many different purposes, but their tool behavior is deconstructive, for example, removing the leaves on a stem to be used for fishing. Thus far, they have not shown key aspects of 'cumulative culture' such as making and using one tool to shape a second tool or of constructive tool manufacture as represented in the hominin record. We encounter these aspects in the next expression of cultural capacity where modular and composite technologies are evidenced in the archaeological record.

5 – Modular cultural capacity. This capacity is characterized by the development and use of a set of independent cultural units which can be used as behavioral modules, combined in different

ways and put in an effective sequence by acting on and modifying each other. The socially transmitted information extends to behavioral units that are not exclusively bound to specific and acute problems. Instead, the elements of behavioral units (stimulus, concept of solution, goal) are increasingly abstracted and thus become applicable in different contexts. Traces of modular cultural capacity can be found in early hominin stone tool production (see below), the cognitive and cultural peculiarity of which has long been discussed (Davidson & McGrew, 2005).

An extension of the PSD is represented by the use of one tool to manufacture another, evident already in the oldest known flaked stone tools of about 2.6 Ma (Semaw *et al.*, 2003). The use of the hammerstone is not directly linked to butchering a carcass to gain food, but it is an effective element in the process of flaking with the products (flakes) used for different cutting tasks, for example, to dissect a carcass to feed on. The primary focus regarding a tool therefore shifts from applying it to a specific purpose to its general properties or functional options, such as 'cutting' or 'hammering'. Without the direct link of tool and final goal, tools can be used for several purposes and their effects can be chained in different ways. Although the initial development of secondary tool use (Kitahara-Frisch, 1993) in hominins may likely have happened without the initiators realizing the consequent options, the modular affordances of decoupling of tools from specific purposes, and chaining effects in different forms and contexts, were increasingly exploited in the following millennia.

Spontaneous secondary tool manufacture has thus far been observed only in a hominin context, although a capacity for stone knapping (and thus secondary tool use) has been shown by bonobos once they were taught the technique by humans (Roffman *et al.*, 2012; Toth & Schick, 2009). Whether the emergence of hominin behavioral novelty is based on cognitive changes (Haidle, 2010, 2012), or is part of a gradual increase of cultural behavior "due to variation in sociability, and hence opportunities for social learning" (Pradhan *et al.*, 2012, p. 180),

is open to debate (Toth & Schick, 2009; Wynn *et al.*, 2011). Associated with the occurrence of knapped stone tools, before and after 2 Ma, is the advanced exhaustion of cores (Delagnes & Roche, 2005), and a marked increase in transport distance of raw materials (Wynn *et al.*, 2011). The extensive exhaustion of cores, with more than 70 flakes detached, indicates the production of cutting tools independent from an acute need, as does raw material transport over several kilometers (Haidle, 2012, pp. 237-240). Both of these changes point to an increase in the decoupling of problem and solution in socially transmitted information. Evidence from the archaeological record surpasses basic culture's relatively immediate response to problems, as observed in animal species today. Handaxes, the production of fire, or simple wooden spears, are literally unthinkable without modular cultural capacity. The production of the 300-ka-old throwing and thrusting spears from Schöningen, Germany (Thieme, 1997, 1999) required several tools with different qualities – tools that had to be produced using other tools (Haidle, 2009, 2010). The expansion of modular behavior is associated with an extension of time depth between perception of a problem and its final solution. Hammerstones, raw materials, and specialized tools were not only procured when immediately needed, but were also transported over relatively long distances with a purpose in mind. As a consequence of the development of modular cultural capacities, freedom of action did not only broaden in a behavioral sense, but also spatially and temporally.

6 – Composite cultural capacity. This capacity is defined by the development and use of a set of cultural modules with specific qualities which are fused to form composites, with new qualities. The socially transmitted information exceeds that of modular cultural capacities through combining separate information on the basic elements of the composite "that may be obtained at different times and in different places" (Ambrose, 2010, p. S139), with information on the newly created functional unit which may be assembled much later (*ibid.*). Hafted tools and compound

adhesives are typical material examples of such composites. This technological augmentation is seen as a critical cognitive development (ibid.; Barham 2013; Lombard & Haidle 2012; Wadley, 2010; Wynn *et al.*, 2009), and we argue that it also represents an important expansion of cultural capacity. Composite tools and materials expand cultural capacities by welding independently existing ideas and solutions into new concepts. Hafting of stone tools, for example, combines the cutting qualities of a stone tool with qualities of the “handle”, (e.g. leverage, smooth grip, or the delivery system of a spear), and different fixing qualities of binding materials and adhesives. The resulting product possesses new qualities that go beyond the qualities of the parts. A hafted knife can be used with more power than a bare blade, a spear with a bone or stone point penetrates the prey differently than a simple wooden one. In compound adhesives used in Southern Africa at least since 70 ka, the different components of resin, ochre powder, and potentially beeswax, each with different properties, merge into a new and inseparable material with specific qualities – the adhesive (Wadley, 2013; Wadley *et al.*, 2009). Early evidence of composite cultural capacity reaches back at least 200 ka: At the site 8-B-11 on the Sudanese Nile Island Sai, core axes show micro-wear traces of wooden hafts (Rots & Van Peer, 2006). At the nearly contemporaneous Campitello quarry near Bucine in Central Italy (Mazza *et al.*, 2006), Late Acheulean stone tools were hafted in birch tar. Four pieces of fir wood from the Schöningen site, Germany, with cut notches at one or both ends and probably used as hafts for stone inserts, are thought to be more than 100 ka older (Thieme, 1999). If the dates for stone points from Kathu Pan, South Africa, interpreted as having been hafted in spears, can be replicated, they would push evidence of composite cultural capacity back to around 500 ka (Wilkins *et al.*, 2012).

7 – Complementary cultural capacity. Here we see the development and use of a set of cultural modules as an acting entity with two or more interdependent and exchangeable parts,

like bow-and-arrow, needle-and-thread, screw-and-screwdriver, key-and-lock etc. (Lombard & Haidle, 2012; Williams *et al.*, 2014). Direct material evidence of complementary cultural capacities can be found in complementary tool sets of two or more elements which act with each other in a symbiotic way such as a bow on a violin. In part, the sets are composed of expendable elements like arrows and thread, which function in relation to respective enhancing/controlling elements like bows (for arrows) and needles (for thread). The symbiotic elements must be developed and used in complementary correspondence with each other. The socially transmitted information thus expands. Not only does information about the components involved have to be transmitted, but also key formal information about the whole system is required. Because the individual is not acting directly on the item which is finally affecting the goal (e.g., an arrow killing the prey, or a violin producing a melody), but on a controlling/enhancing element which operates the finally goal-effective element (bow operates arrow or violin), formal information about the comprehensive system is needed to understand how the different components can be used together. Additionally, formal information is required to exchange some components with formally similar ones (e.g., arrows formally fitting to a certain bow, but with different tips – blunt, composite with stone or bone points, poisoned etc.). Evidence of complementary cultural capacity currently reaches back at least 64 ka in southern Africa where some Howieson’s Poort backed tools were used to tip arrows (Lombard, 2011; Lombard & Phillipson, 2010; see Williams *et al.*, 2014 for neuroarchaeological implications). Eyed needles have been known from the Upper Paleolithic in Europe, and the Caucasus region up to China (Bar-Yosef *et al.*, 2011; Gasparyan *et al.*, 2014; Huang *et al.*, 1986).

8 – Notional cultural capacity. This grade represents the last Paleolithic expansion of cultural capacities that can be detected on the basis of an extension of the PSD. It is characterized by the development of notional concepts as cultural

modules. Notional concepts are mentally constructed and socially shared entities and relationships that can be represented in a) the signification of objects/signs (e.g. cross, crescent, and Star of David as symbols of religions), b) systems of ideas (e.g. myths, religious beliefs, philosophical questions, constitutions of states), c) normative definitions (e.g. metric and value systems), or d) virtual beings (e.g. angels) and characters (e.g. protecting capacities of an amulet). The socially transmitted information exceeds that of all former capacities. It is now based on non-physical concepts, which can be manipulated only in the mind or through imagination, and their effects on real or other notional modules. Notional concepts can stand alone without an immediate link to a physical object, acting as independent operational foci such as ideas about 'justice', 'reincarnation', or the 'devil'. They can, however, also be combined with a physical object to form a composite with new functional qualities emerging out of the basic physical qualities and a certain meaning (e.g., a specific natural monument like a rock or a huge tree to be combined with a certain signification to form a sanctuary). Material evidence of notional cultural capacity and the possibility of preservation is bound to such composite artefacts.

Different from purely physical modules, notional modules unfold their main potential only in social use (cf. Porr, 2010; Schebesch, 2013). While even a complex bow-and-arrow set can be used individually without losing any major effect, the full potential of symbols, norms, and systems of ideas is bound to sharing within a group. Notional tools serve as devices for the communication of set, pre-determined or agreed-upon concepts. The composites of physical objects and notions are information carriers – artifacts such as balancing weights, cuneiform inscriptions or, in recent times, a banknote, a wedding ring or a token which gain their proper function only in association with exclusively virtual elements. Notional cultural capacity can increase the individual scope of competences, for example by using notational marks as mnemonic device (yet not every use of marks as mnemonic

device is necessarily notional). However, notional cultural capacity becomes increasingly visible and powerful when the notional elements are not only socially transmitted, but are also socially applied within a complementary group. A piece of art remains bare ornamental craftsmanship when there is no further meaning linked to it, but its stimulating power is enhanced when its meaning is understood by other individuals. Money is worthless without a shared concept of value, and writing not based on a socially accepted symbolic system remains scrawl.

Due to the virtual nature of notional modules it is often difficult to detect undoubted evidence of notional cultural capacity within the archaeological record. Pigments and cut marks on different raw materials are often claimed to implicate symbolic content (d'Errico & Henshilwood, 2011; d'Errico *et al.*, 2012; Mania & Mania, 1988), a fact which can hardly be proven without other unambiguous hints from the archaeological context (cf. Garofoli & Haidle, 2014). Recently, ca. 500 ka old shells from Trinil on Java, Indonesia have been reported as showing engravings in a geometrical pattern (Joordens *et al.*, 2014). However, it is not clear that the engravings are deliberate, let alone evidence of *Homo erectus* having attempted to signify something. Eagle claws from 130 ka old layers at Krapina suggest at least a Neandertal affection for special objects (Radović *et al.*, 2015); if possible ornaments as such are a proof of symbolism is debated (Garofoli, 2014). It is only around 40 ka ago that undisputable elements of figurative art occur in the archaeological record, which are accepted by most archaeologists as carriers of notional information (but see Malafouris, 2007 for an alternative conception of cave paintings). From that time, ivory sculptures depicting animals and females have been discovered from several cave sites of the Swabian Jura in Southern Germany (Conard, 2003, 2009; Higham *et al.*, 2012). As early evidence of notional concepts artistic representations of probably supernatural beings are counted like the ca 40 ka lion-man from the Hohlestein-Stadel cave in South Germany (cf. Kind *et al.*, 2014; Wynn *et al.*, 2009), the

'adorant' from the Geißenklösterle cave nearby (Hahn, 1994), and the small figurine interpreted as a lion-man from Hohle Fels cave (Conard, 2003). A stone figurine from Stratzing in Austria (Neugebauer-Maresch, 1989), paintings on rock fragments from Fumane Cave in Northern Italy (Broglio *et al.*, 2005), and the paintings from Grotte Chauvet in France (Clottes, 2001) are of roughly comparable age. The oldest cave paintings, so far, have been dated in Northern Spain back to more than 40.8 ka (Pike *et al.*, 2012). Outside Europe, the oldest evidence for figurative depictions was found in the Maros caves on Sulawesi, Indonesia dating back to more than 35 ka (Aubert *et al.*, 2014) and in 27.5 ka old layers at Apollo 11 Cave in Namibia (Vogelsang, 1998).

Conclusions

The development of cultural capacities can be studied on a variety of levels. We propose three dimensions of development – evolutionary-biological, historical-social, and ontogenetic-individual – that create the scaffold within which multiple factors form cultural performances. Each of the factors developed on its own path in interdependence with other factors, and within the context of ever-changing specific environments/ecological niches. Such an integrated concept of cultural performances and their evolution, as presented in this paper, offers a combination of aspects and concepts dealing with evolution. More specifically it encompasses: notions of cultural evolution such as the dual-inheritance theory (Richerson & Boyd, 1978) that raised attention on cultural developmental processes beyond genetics and on gene-culture coevolution (see also Aoki, 2001; Feldman & Laland, 1996); the comparison of biological and cultural transmission of traits (Cavalli-Sforza & Feldman, 1981); the emphasis put on the evolution of psychological mechanisms (as factors of the evolutionary-biological dimension), and the population dynamics of cultural systems (as factors of the historical-social dimension) (Henrich & McElreath, 2003); epigenetic processes as part

of an ontogenetic-individual dimension in evolution (Jablonka & Lamb, 2007); the developmental interrelation between cultural performances and neurobiological and psychological processes (Kim & Sasaki, 2014); or the interaction of environmental factors and cultural performances in the construction of niches/specific functional environments (Kendal *et al.*, 2011; Laland & O'Brien, 2011). The emphasis of the EECC model for cultural performances lies in the integration of an increasingly comprehensive, cross-disciplinary set of factors and processes affecting the development of cultural performances. Such an integrated approach gives special attention to interdependencies of factors and processes within and between the three developmental dimensions and the specific functional environment (resource space, ecological niche).

We also attempted to interconnect models and data on cultural basics in animal behavior with developments in hominin behavior, as deduced from archaeological remains, in order to create a scaffold to which observations on specific factors and the development of (sets of) single performances can be fixed. There is not a single cultural capacity representing a "set of genetically based cognitive abilities that, collectively, make human culture possible" (Lind *et al.*, 2013, p. 1), but several grades of cultural capacity expansion in non-human animals and hominins (Tab. 1). The grades of cultural capacity evolution in the EECC model presented above have been identified on the basis of expansions in the PSD observable in tool behavior. There might be other possible classifications of cultural development, but the later grades defined within our model can be detected in the archaeological record and can be combined with ethological data. It is assumed that each grade is accompanied by an expansion in the evolutionary-biological dimension such as gene expressions in the brain, the biological basis of natural pedagogy, or the different physical and mental properties necessary to perceive and produce language, completed by historical-social extensions. Due to the enormous number of factors involved in the three developmental dimensions, and the

Tab. 1 - Summary of the eight grades of expansion of cultural capacity identified on the basis of the extension of the problem-solution distance.

CULTURAL CAPACITY	TYPE OF SOCIALLY TRANSMITTED INFORMATION	PROBLEM-SOLUTION DISTANCE ON CULTURAL LEVEL	MATERIAL EXPRESSION - EMPIRICAL
1 Socially facilitated information	Immediate response to social stimulus	A → B	
2 Social learning	Durable response to social stimulus	A → B	
3 Tradition	Durable transgenerational transmission of single independent behavioral units (stimulus, rough concept of solution, goal)	A → B	(simple tools)
4 Basic	Durable transgenerational transmission of sets of independent behavioral units (specific stimuli, rough concepts of solutions, specific goals)	A → B	(simple tools)
5 Modular	Durable transgenerational transmission of sets of independent cultural units which can be used as modules and combined in different ways in an effective sequence	A → B → C	secondary tools (tools to make tools)
6 Composite	Durable transgenerational transmission of sets of cultural modules which can be fused to form composites with new qualities	A ⊕ → C B	composite tools (e.g. spear with hafted tip, compound adhesive)
7 Complementary	Durable transgenerational transmission of sets of cultural modules as acting entity with interdependent parts (complementary set)	A } → C B	complementary tools (e.g. bow-and arrow, needle-and-thread, ornamental systems)
8 Notional	Durable transgenerational transmission of notional concepts as cultural modules	A } → C B	Notional tools (e.g. figurative art)

specific functional environment with its own developmental paths, due to the multiple interdependencies between these factors, and due to the varying combinations of factors in different performances, the identified grades of the evolution and/or expansion of cultural capacities can only be analytic approximations, as opposed to being selective categories. The emergence of a new qualitative grade of cultural capacity does not replace all the preceding or plesiomorphic grades (as presented in our model, not necessarily in time), but is integrated with them, creating a completely new cultural system of

relationships. Importantly, cultural performances in each of the grades do not stop evolving. Thus, it is possible, for example, that archaic hominin groups who never developed, say, notional culture could have reached cultural performances in one or more of the other grades of cultural capacity that go beyond those found in groups exhibiting notional culture. The more inclusive grades of cultural capacity are not necessarily “better” than those with seemingly less complexity. They could have increased Darwinian fitness only in relation to contingent situations. If the conditions change, it is perfectly possible that notional

Tab. 2 - Grades of expansion of cultural capacities in hominins.

CULTURAL CAPACITY	ARTIFACT MARKERS	EARLIEST EVIDENCE CURRENTLY WIDELY ACCEPTED	CURRENTLY ASSOCIATED SPECIES
4 Basic	basic tools	(> 2.6 Ma)	Chimpanzees, orangutans, bonobos, whales and dolphins, New Caledonian crows
5 Modular	modular tools	< 2.6 Ma	early <i>Homo</i> + <i>H. erectus</i>
6 Composite	composite tools	< 300 ka	<i>H. sapiens</i> + late archaics
7 Complementary	complementary tools	< 100 ka	<i>H. sapiens</i>
8 Notional	notional tools	< 40 ka	<i>H. sapiens</i>

cultural performances become detrimental for human survival. Increase in complexity of behavioral network is not “better” in absolute terms. It is simply more complex.

In general, the cultural performances do not exhaust the potential capacities. It is, however, a characteristic of cultural behavior that individuals can socially learn, or be taught, parts of the cultural system or its operation without fully understanding the concept/s on which it is based. The individual performances based on specific cultural capacities can be enormously variable. It could range from limited use of some expressions of a concept to the full understanding thereof, and of the potential of possible derivatives. Due to this cultural effect, chimpanzees and bonobos can learn (from modern humans) how to communicate using symbol charts, but they have not been able to develop such a symbolic system on their own. Although they are able to adopt free-hand, stone-to-stone percussion to create useful flakes for cutting to gain access to food resources (Whiten *et al.*, 2009), neither chimpanzees nor bonobos have yet been observed to show performances based on modular cultural capacities without human contact.

To facilitate the integration of newly identified developmental factors and the inclusion of new observational data and archaeological finds, the EECC model has been created as an open

model. No hominin species or periods are fixed to the grades of expansion. The examples provided reflect the current state of knowledge respectively, mainly accepted opinion, but the linkage to a species or time frame is floating, pending (new) finds and observations. Table 2 provides a sketch of the grades of evolution/expansion of cultural capacities in hominins with current information about the bearers and datings. These general grades of evolution in cultural capacity are associated with expansions of various specific features and abilities including the alteration and expansion of the specific functional environment/ecological niches, technological skill, planning depth, anticipation, problem perception, and different forms of play (Nowell, in press). Changes in life history, like the extension of childhood (Bock & Sellen, 2002) and of the post-fertile phase (Bogin, 2009; O’Connell *et al.*, 1999), and consequent changes in social organization led to larger social groups, loose mother-offspring ties, increased pro-sociality among juveniles, and greater opportunities for social learning. Demographic parameters including population size, and the rate and scale of interactions, are important for the development of cultural capacity in general, and especially for new forms of collective action (Powell *et al.*, 2009; Shennan, 2001; but see also Read [2012], Collard *et al.* [2013], and French [2015] for limitations of the demographic model). They affect innovation

rates as well as the rates of extinction of cultural items. Which of the different factors and processes gained in importance in which grade, how they influenced each other, and how developments in the evolutionary-biological, the historical-social, and the ontogenetic-individual dimension and the specific functional environment specifically interacted in certain cultural performances, remains to be studied in detail. Further research is also necessary to clarify for each developmental grade the different forms and processes of transmission of information, and the set of problems that can be approached by the grade-specific form of socially transmitted information. The integrative concept of cultural performances respectively, capacities with three developmental dimensions embedded in the specific functional environment and the EECC model, based on the extension of the type of socially transmitted information, is simply an inclusive frame that now can be fleshed out with further data and details.

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References

- Allen J., Weinrich M., Hoppitt W. & Rendell L. 2013. Network-based diffusion analysis reveals cultural transmission of lobe-tail feeding in humpback whales. *Science*, 340: 485-488.
- Andersson C., Törnberg A. & Törnberg P. 2014. An evolutionary developmental approach to cultural evolution. *Curr. Anthropol.*, 55: 154-174.
- Ambrose S. 2010. Coevolution of composite-tool technology, constructive memory, and language. *Curr. Anthropol.*, 51: S135-S147.
- Aoki K. 2001. Theoretical and empirical aspects of gene-culture coevolution. *Theor. Popul. Biol.*, 59: 253-261.
- Aplin L.M., Farine D.R., Morand-Ferron J., Cockburn A., Thornton A. & Sheldon B.C. 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518: 538-541.
- Aubert M., Brumm A., Ramli M., Sutikna T., Saptomo E.W., Hakim B., Morwood M.J., van den Bergh G.D., Kinsley L. & Dosseto A. 2014. Pleistocene cave art from Sulawesi, Indonesia. *Nature*, 514: 223-228.
- Barham L. 2013. *From hand to handle: the first industrial revolution*. Oxford University Press, Oxford.
- Bar-Yosef O., Belfer-Cohen A., Mesheviliani T., Jakeli N., Bar-Oz G., Boaretto E., Goldberg P., Kvavadze E. & Matskevich Z. 2011. Dzudzuana: an Upper Palaeolithic cave site in the Caucasus foothills (Georgia). *Antiquity*, 85: 331-349.
- Biro D., Sousa C. & Matsuzawa T. 2006. Ontogeny and cultural propagation tool use by wild chimpanzees at Bossou, Guinea: Case studies in nut cracking and leaf folding. In Matsuzawa T., Tomonaga M. & Tanaka M. (eds): *Cognitive development in chimpanzees*, pp. 476-508. Springer, Tokyo.
- Bjorklund D.F. & Sellers P.D. II. 2014. Memory development in evolutionary perspective. In Bauer P.J., Fivush R. (eds): *The Wiley handbook on the development of children's memory*, 1, pp. 126-156. John Wiley & Sons, Hoboken.
- Bloch M. 1991. Language, anthropology and cognitive science. *Man*, 26: 183-198.
- Bluff L.A., Kacelnik A. & Rutz C. 2010. Vocal culture in New Caledonian crows *Corvus moneduloides*. *Biol. J. Linn. Soc.*, 101: 767-776.
- Bock J. & Sellen D.W. 2002. Childhood and the evolution of the human life course. *Hum. Nature*, 13: 153-159.

- Boesch C., Head J. & Robbins M.M. 2009. Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *J. Hum. Evol.*, 56: 560-569.
- Bogin B. 2009. Childhood, adolescence, and longevity: a multilevel model of the evolution of reserve capacity in human life history. *Am. J. Hum. Biol.*, 21: 567-577.
- Brewer S.M. & McGrew W.C. 1990. Chimpanzee use of a tool set to get honey. *Folia Primatol.*, 54: 100-104.
- Broglio A., Cremaschi M., Peresani M., De Stefani M., Bertola S., Gurioli F., Marini D. & Di Anastasio G. 2005. Le pietre dipinte dell'Aurignaziano. In Broglio A. & Dalmeri G. (eds): *Pitture Paleolitiche nelle Prealpi Venete. Grotta di Fumane e Riparo Dalmeri*, pp. 38-43. Museo Civico di Storia Naturale di Verona, Verona.
- Brooke J.L. & Larsen C.S. 2014. The nurture of nature: genetics, epigenetics, and environment in human biohistory. *Amer. Hist. Rev.*, 119: 1500-1513.
- Byrne R.W., Barnard P.J., Davidson I., Janik V.M., McGrew W.C., Miklósi A. & Wiessner P. 2004. Understanding culture across species. *Trends Cogn. Sci.*, 8: 341-346.
- Cavalli-Sforza L. L. & Feldman M.W. 1981. *Cultural transmission and evolution: a quantitative approach*. Princeton University Press, Princeton.
- Claidière N., Bowler M., Brookes S., Brown R. & Whiten A. 2014. Frequency of behavior witnessed and conformity in an everyday social context. *PLoS One*, 9: e99874.
- Clark G. 1969. *World prehistory: A new synthesis*. Cambridge University Press, Cambridge.
- Clottes J. 2001 (ed). *La Grotte Chauvet: L'art des origines*. Seuil, Paris.
- Conard N.J. 2003. Palaeolithic ivory sculptures from southwestern Germany and the origin of figurative art. *Nature*, 426: 830-832.
- Collard M., Ruttie A., Buchanan B. & O'Brien M.J. 2013. Population size and cultural evolution in nonindustrial food-producing societies. *PLoS One*, 8: e72628.
- Conard N.J. 2009. A female figurine from the basal Aurignacian of Hohle Fels Cave in southwestern Germany. *Nature*, 459: 248-252.
- Coward F. & Grove M. 2012. Rethinking phylogeny and ontogeny in hominin brain evolution. *Human Origins*, 1: 65-91.
- Cross I. 2001. Music, cognition, culture, and evolution. *Ann. New York Acad. Sci.*, 930: 28-42.
- Csibra G. & Gergely G. 2011. Natural pedagogy as evolutionary adaptation. *Philos. Trans. R. Soc. B*, 366: 1149-1157.
- Danchin É. 2008. Cultural evolution. In Danchin É., Giraldeau L.-A. & Cézilly F. (eds): *Behavioural ecology: an evolutionary perspective on behaviour*, pp. 693-726. Oxford University Press, Oxford.
- Davidson I. & McGrew W.C. 2005. Stone tools and the uniqueness of human culture. *J. Roy. Anthropol. Inst. (N.S.)*, 11: 793-817.
- Delagnes A. & Roche H. 2005. Late Pliocene hominid knapping skills: The case of Lokalalei 2C, West Turkana, Kenya. *J. Hum. Evol.*, 48: 435-472.
- d'Errico F., García Moreno R. & Rifkin R.F. 2012. Technological, elemental and colorimetric analysis of an engraved ochre fragment from the Middle Stone Age levels of Klasies River Cave 1, South Africa. *J. Archaeol. Sci.*, 39: 942-952.
- D'Errico F. & Henshilwood C.S. 2011. The origin of symbolically mediated behaviour: from antagonistic scenarios to a unified research strategy. In Henshilwood C.S. & d'Errico F. (eds): *Homo symbolicus. The dawn of language, imagination and spirituality*, pp. 49-74. John Benjamins, Amsterdam, Philadelphia.
- El Mouden C., André J.-B., Morin O. & Nettle D. 2014. Cultural transmission and the evolution of human behaviour: a general approach based on the Price equation. *J. Evol. Biol.*, 27: 231-241.
- Enquist M., Ghirlanda S., Jarrick A. & Wachtmeister C.A. 2008. Why does human culture increase exponentially? *Theor. Popul. Biol.*, 74: 46-55.
- Feldman M.W. & Laland K.N. 1996. Gene-culture coevolutionary theory. *Trends Ecol. Evol.*, 11: 453-457.
- Fisher S.E. & Ridley M. 2013. Culture, genes, and the human revolution. *Science*, 340: 929-930.
- French J.C. 2015. Demography and the Palaeolithic archaeological record. *J. Archaeol.*

- Method Th.*, 2015: 1-50, DOI 10.1007/s10816-014-9237-4.
- Galef B.G. 1992. The question of animal culture. *Hum. Nature*, 3: 157-178.
- Galef B.G. 2004. Approaches to the study of traditional behaviors of free-living animals. *Learn. Behav.*, 32: 53–61.
- Garofoli D. 2014. Do early body ornaments prove cognitive modernity? A critical analysis from situated cognition. *Phenom. Cogn. Sci.*, 2014: 1-23, DOI 10.1007/s11097-014-9356-0.
- Garofoli D. & Haidle M.N. 2014. Epistemological problems in cognitive archaeology: an anti-relativistic proposal towards methodological uniformity. *J. Anthropol. Sci.*, 92: 7-41.
- Gasparyan B., Kandel A.W. & Montoya C. 2014. Living the high life: The Upper Paleolithic settlement of the Armenian Highlands. In Gasparyan B. & Montoya C. (eds): *Stone Age of Armenia. A guide-book to the Stone Age archaeology in the Republic of Armenia*, pp. 107-131. Center for Cultural Resource Studies, Kanazawa University, Kanazawa, Japan.
- Giraldeau L.A. 2008. Social foraging. In Danchin É., Giraldeau L.-A. & Cezilly F. (eds): *Behavioural ecology: an evolutionary perspective on behavior*, pp. 257-283. Oxford University Press, Oxford.
- Gruber T., Muller M.N., Reynolds V., Wrangham R. & Zuberbühler K. 2011. Community-specific evaluation of tool affordances in wild chimpanzees. *Sci. Rep.*, 1, DOI 10.1038/srep00128.
- Hahn J. 1994. Menschtier- und Phantasiewesen. In Ulmer Museum (ed): *Der Löwenmensch. Tier und Mensch in der Kunst der Eiszeit*, pp. 101-116. Jan Thorbecke Verlag, Sigmaringen.
- Haidle M.N. 2008a. Kognitive und Kulturelle Evolution. *Erwägen – Wissen – Ethik*, 19: 149-209.
- Haidle M.N. 2008b. Verschiedene Welten. Umweltwahrnehmung und Umweltgestaltung im Laufe der menschlichen Evolution. In Knopf T. (ed): *Umweltverhalten in Geschichte und Gegenwart. Vergleichende Ansätze*, pp. 30-41. Attempto, Tübingen.
- Haidle M.N. 2009. How to think a simple spear? In de Beaune S.A., Coolidge F.L. & Wynn T. (eds): *Cognitive archaeology and human evolution*, pp. 57-73. Cambridge University Press, New York.
- Haidle M.N. 2010. Working memory capacity and the evolution of modern cognitive capacities - implications from animal and early human tool use. *Curr. Anthropol.*, 51: S149-S166.
- Haidle M.N. 2012. *How to think tools? A comparison of cognitive aspects in tool behavior of animals and during human evolution*. Cognitive perspectives in tool behaviour Vol. 1. http://tobias-lib.uni-tuebingen.de/frontdoor.php?source_opus=6014.
- Haidle M.N. 2014. Building a bridge – an archaeologist's perspective on the evolution of causal cognition. *Frontiers in Psychology*, 5: 1-15, DOI 10.3389/fpsyg.2014.01472.
- Haidle M. N. & Bräuer J. 2011. Special issue: innovation and the evolution of human behavior. From brainwave to tradition – How to detect innovations in tool behaviour. *PaleoAnthropology*, 2011: 144-153.
- Haidle M.N. & Conard N.J. 2011. The Nature of Culture – Summary report on an interdisciplinary symposium held in Tübingen, Germany, 15-18 June 2011. *Mitt. Gesellschaft für Urgeschichte*, 20: 65-78.
- Hallpike R.C. 2008. *How we got here. From bows and arrows to the space age*. Authorhouse, Central Milton Keynes.
- Hammel L. 2007. Der Kulturbegriff im wissenschaftlichen Diskurs und seine Bedeutung für die Musikpädagogik. Versuch eines Literaturberichts. *Z. Kritische Musikpädagogik*, 2007: 1-21.
- Haun D.B.M., Rekers Y. & Tomasello M. 2014. Children conform to the behavior of peers; other great apes stick with what they know. *Psychol. Sci.*, 25: 2160-2167.
- Henrich J. & McElreath R. 2003. The evolution of cultural evolution. *Evol. Anthropol.*, 12: 123–135.
- Higham T., Basell L., Jacobi R., Wood R., Ramsey C.B. & Conard N.J. 2012. Testing models for the beginnings of the Aurignacian and the advent of figurative art and music: The radiocarbon chronology of Geißenklösterle. *J. Hum. Evol.*, 62: 664-676.

- Hill J.H. & Hill K.C. 1970. A note on Uto-Aztec color terminologies. *Anthropol. Linguist.*, 12: 231-238.
- Hill K. 2009. Animal "culture"? In Laland K.N. & Galef B.G. Jr. (eds): *The question of animal culture*, pp. 269-287. Harvard University Press, Cambridge, MA.
- Hodgskiss T. 2014. Cognitive requirements for ochre use in the Middle Stone Age at Sibudu, South Africa. *Camb. Archaeol. J.*, 24: 405-428.
- Hohmann G. & Fruth B. 2003. Culture in Bonobos? Between-species and within-species variation on behavior. *Curr. Anthropol.*, 44: 563-571.
- Hoppitt W. & Laland K.N. 2008. Social processes influencing learning in animals: a review of the evidence. *Adv. Stud. Behav.*, 38: 105-165.
- Huang W., Zhang Z.F.R., Chen B.L.J. & Zhu M.W.H. 1986. Bone artifacts and ornaments from Xiaogushan site of Haicheng, Liaoning Province. *Acta Anthropol. Sinica*, 5: 259-266.
- Hunt G.R., Gray R.D. & Taylor A.H. 2013. Why is tool use rare in animals? In Sanz C., Call J. & Boesch C. (eds): *Tool use in animals: cognition and ecology*, pp. 89-118. Cambridge University Press, Cambridge, MA.
- Jablonka E. & Lamb M. J. 2007. Evolution in four dimensions. *Behav. Brain Sci.*, 30: 353-392
- Jäncke L. 2009. The plastic human brain. *Restor. Neurol. Neuros.*, 27: 521-538.
- Joordens J. C., d'Errico F., Wesselingh F. P., Munro S., de Vos J., Wallinga J., Ankjærgaard C., Reimann T., Wijbrans J.R., Kuiper K.F., Mûcher H.J., Coqueugniot H., Prié V., Joosten I., van Os B., Schulp A.S., Panuel M., van der Haas V., Lustenhouwer W., Reijmer J.J.G. & Roebroeks W. 2014. *Homo erectus* at Trinil on Java used shells for tool production and engraving. *Nature*, 518: 228-231.
- Kamilar J.M. & Atkinson Q.D. 2014. Cultural assemblages show nested structure in humans and chimpanzees but not in orangutans. *Proc. Natl. Acad. Sci. U.S.A.*, 111: 111-115.
- Kay P., Berlin B. & Merrifield W. 1991. Biocultural implications of systems of color naming. *J. Linguist. Anthropol.*, 1: 12-25.
- Kendal J., Tehrani J.J. & Odling-Smee J. 2011. Human niche construction in interdisciplinary focus. *Philos. Trans. R. Soc. B*, 366: 785-793.
- Kim H. S. & Sasaki J. Y. 2014. Cultural neuroscience: biology of the mind in cultural contexts. *Ann. Rev. Psychol.*, 65: 487-514.
- Kind C.-J., Ebinger-Rist N., Wolf S., Beutelspacher T. & Wehrberger K. 2014. The smile of the Lion Man. Recent excavations in Stadel Cave (Baden-Württemberg, southwestern Germany) and the restoration of the famous Upper Palaeolithic figurine. *Quartär*, 61: 129-145.
- Kitahara-Frisch J. 1993. The origin of secondary tools. In Berthelet A. & Chavaillon J. (eds): *The use of tools by human and non-human primates. A Fyssen Foundation Symposium*, pp. 239-246. Clarendon Press, Oxford.
- Köhler W. 1926. *The mentality of apes*. Harcourt Brace, New York.
- Kroeber A.L. & Kluckhohn C. 1952. *Culture: A critical review of concepts and definitions*. Vintage books, New York.
- Laland K.N. 2004. Social learning strategies. *Learn. Behav.*, 32: 4-14.
- Laland K.N. & Galef B.G. Jr. 2009 (eds). *The question of animal culture*. Harvard University Press, Cambridge, MA.
- Laland K.N. & Janik V.M. 2006. The animal cultures debate. *Trends Ecol. Evol.*, 21: 542-547.
- Laland K.N. & O'Brien M.J. 2011. Cultural niche construction: an introduction. *Biol. Theory*, 6: 191-202.
- Laland K.N. & Sterelny K. 2006. Perspective: seven reasons (not) to neglect niche construction. *Evolution*, 60: 1751-1762.
- Ledón-Rettig C.C., Richards C.L. & Martin L.B. 2013. Epigenetics for behavioral ecologists. *Behav. Ecol.*, 24: 311-324.
- Lind J., Lindenfors P., Ghirlanda S., Lidén K. & Enquist M. 2013. Dating human cultural capacity using phylogenetic principles. *Sci. Rep.*, 3: 1785, DOI 10.1038/srep01785.
- Lombard M. 2011. Quartz-tipped arrows older than 60 ka: further use-trace evidence from Sibudu, Kwazulu-Natal, South Africa. *J. Archaeol. Sci.*, 58: 1918-1930.
- Lombard M. 2012. Thinking through the Middle Stone Age of sub-Saharan Africa. *Quat. Intern.*, 270: 140-155.

- Lombard M. (in press). Mountaineering or ratcheting? Stone Age hunting weapons as proxy for the evolution of human technological, behavioral and cognitive flexibility. In Haidle M.N., Conard N.J. & Bolus M. (eds): *The Nature of Culture*. Springer, New York.
- Lombard M. & Haidle M.N. 2012. Thinking a bow-and-arrow: cognitive implications of Middle Stone Age bow and stone-tipped arrow technology. *Camb. Archaeol. J.*, 22: 237-264.
- Lombard M. & Parsons I. 2011. What happened to the human mind after the Howiesons Poort? *Antiquity*, 85: 1-11.
- Lombard M. & Phillipson L. 2010. Indications of bow and stone-tipped arrow use 64,000 years ago in KwaZulu-Natal, South Africa. *Antiquity*, 84: 635-48.
- Luncz L.V. & Boesch C. 2014. Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. *Am. J. Primatol.*, 76: 649-657.
- Lycett S.J., Collard M. & McGrew W.C. 2007. Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. *Proc. Natl. Acad. Sci. U.S.A.*, 104: 17588-17592.
- Lycett S.J., Collard M. & McGrew W.C. 2011. Correlations between genetic and behavioural dissimilarities in wild chimpanzees (*Pan troglodytes*) do not undermine the case for culture. *P. Roy. Soc. Lond. B Biol.*, 278: 2091-2093.
- MacLachy L.M., Desilva J., Sanders W.J. & Wood B. 2010. Hominini. In Wardelin L. & Sanders W.J. (eds): *Cenozoic mammals of Africa*, pp. 471-540. University of California Press, Berkeley.
- MacLean E.L., Hare B., Nunn C.L., Addessi E., Amici F., Anderson R.C., Aureli F., Baker J.M., Bania A.E., Barnard A.M., Boogert N.J., Brannon E.M., Bray E.E., Bray J., Brent L.J.N., Burkart J.M., Call J., Cantlon J.F., Cheke L.G., Clayton N.S., Delgado M.M., DiVincenzi L.J., Fujita K., Herrmann E., Hiramatsu C., Jacobs L.F., Jordan K.E., Laude J.R., Leimgruber K.L., Messer E.J.E., Moura A.C. de A., Ostojic L., Picard A., Platt M.L., Plotnik J.M., Range F., Reader S.M., Reddy R.B., Sandel A.A., Santos L.R., Schumann K., Seed A.M., Sewall K.B., Shaw R.C., Slocombe K.E., Su Y., Takimoto A., Tan J., Tao R., van Schaik C.P., Virányi Z., Visalberghi E., Wade J.C., Watanabe A., Widness J., Young J.K., Zentall T.R. & Zhao Y. 2014. The evolution of self-control. *Proc. Natl. Acad. Sci. U.S.A.*, 111: E2140-E2148.
- Malafouris L. 2007. Before and beyond representation: towards an enactive conception of the Palaeolithic image. In Renfrew C. & Morley I. (eds): *A global prehistory of figurative representation*, pp 289-302. McDonald Institute of Archaeological Research, Cambridge.
- Malafouris L. 2010. Metaplasticity and the human becoming: principles of neuroarchaeology. *J. Anthropol. Sci.*, 88: 49-72.
- Malafouris L. 2013. *How things shape the mind: a theory of material engagement*. MIT Press, Cambridge, Mass.
- Mania D. & Mania U. 1988. Deliberate engravings on bone artefacts of *Homo erectus*. *Rock Art Res.*, 5: 91-107.
- Manrique H.M., Völter C.J. & Call J. 2012. Repeated innovation in great apes. *Anim. Behav.*, 85: 195-202.
- Marino L., Connor R.C., Fordyce R.E., Herman L.M., Hof P.R., Lefebvre L., Lusseau D., McCowan B., Nimchinsky E.A., Pack A.A., Rendell L., Reidenberg J.S., Reiss D., Uhen M.D., Van der Gucht E. & Whitehead H. 2007. Cetaceans have complex brains for complex cognition. *PLoS Biology*, 5: e139.
- Marshall-Pescini S. & Whiten A. 2008. Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Anim. Cogn.*, 11: 449-456.
- Mazza P.P.A., Martini F., Sala B., Magi M., Colombini M.P., Giachi G., Landucci F., Lemorini C., Modugno F. & Ribechini E. 2006. A new Palaeolithic discovery: tar-hafted stone tools in a European Mid-Pleistocene bone-bearing bed. *J. Archaeol. Sci.*, 33: 1310-1318.
- McPherron S.P., Alemseged Z., Marean C.W., Wynn J.G., Reed D., Geraads D., Bobe R. & Béarat H.A. 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, 466: 857-860.

- Mesoudi A., Whiten A. & Laland K.N. 2006. Towards a unified science of cultural evolution. *Behav. Brain Sci.*, 29: 329-383.
- Neugebauer-Maresch C. 1989. Zum Neufund einer weiblichen Statuette bei den Rettungsgrabungen an der Aurignacien-Station Stratzing, Krems/Rehberg, Niederösterreich. *Germania*, 67: 551-559.
- Norris K.S. 1966 (ed). *Whales, dolphins, and porpoises*. University of California Press, Berkeley, Los Angeles.
- Nowell A. (in press). Childhood, play and the evolution of cultural capacity in Neandertals and modern humans. In Haidle M.N., Conard N.J. & Bolus M. (eds): *The Nature of Culture*. New York, Springer.
- O'Connell J.F., Hawkes K. & Blurton-Jones N.G. 1999. Grandmothering and the evolution of *Homo erectus*. *J. Hum. Evol.*, 36: 461-85.
- Odling-Smee F. J., Erwin D., Palkovacs E.P., Feldman M.W. & Laland K.N. 2013. Niche construction theory: a practical guide for ecologists. *Quart. Rev. Biol.*, 88: 3-28.
- Odling-Smee F.J., Laland K.N. & Feldman M.W. 1996. Niche construction. *Am. Nat.*, 147: 641-648.
- Peretz I. 2006. The nature of music from a biological perspective. *Cognition*, 100: 1-32.
- Perry S. 2009. Are nonhuman primates likely to exhibit cultural capacities like those of humans? In Laland K.N. & Galef B.G. Jr. (eds): *The question of animal culture*, pp. 247-267. Harvard University Press, Cambridge, MA.
- Petanjek Z. & Kostović I. 2012: Epigenetic regulation of fetal brain development and neurocognitive outcome. *Proc. Natl. Acad. Sci. U.S.A.*, 109: 11062-11063.
- Pihlström S. 2003. On the concept of philosophical anthropology. *J. Philos. Res.*, 28: 259-285.
- Pike A.W.G., Hoffmann D.L., García-Diez M., Pettitt P.B., Alcolea J., De Balbín R., González-Sainz C., de las Heras C., Lasheras J.A., Montes R. & Zilhão J. 2012. U-Series dating of Palaeolithic art in 11 caves in Spain. *Science*, 336: 1409-1413.
- Porr M. 2010. Palaeolithic art as cultural memory: A case study of the Aurignacian art of Southwest Germany. *Camb. Archaeol. J.*, 20: 87-108.
- Powell A., Shennan S. & Thomas M.G. 2009. Late Pleistocene demography and the appearance of modern human behavior. *Science*, 324: 1298-1301.
- Pradhan G.R., Tennie C. & van Schaik C.P. 2012. Social organization and the evolution of cumulative technology in apes and hominins. *J. Hum. Evol.*, 63: 180-190.
- Radović D., Sršen A.O., Radović J. & Frayer D.W. 2015. Evidence for Neandertal jewelry: modified white-tailed eagle claws at Krapina. *PLoS ONE*, 10: e0119802.
- Ramsey G. 2013. Culture in humans and other animals. *Biol. Philos.*, 28: 457-479.
- Read D. 2012. *Population size does not predict artifact complexity: analysis of data from Tasmania, arctic hunter-gatherers, and Oceania fishing groups*. Retrieved from: <http://www.escholarship.org/uc/item/61n4303q>
- Rendell L. & Whitehead H. 2001. Culture in whales and dolphins. *Behav. Brain Sci.*, 24: 309-382.
- Richerson P.J. & Boyd R. 1978. A dual inheritance model of the human evolutionary process I: basic postulates and a simple model. *J. Soc. Biol. Struct.*, 1: 127-154.
- Roffman I., Savage-Rumbaugh S., Rubert-Pugh E., Ronen A. & Nevo E. 2012. Stone tool production and utilization by bonobo-chimpanzees (*Pan paniscus*). *Proc. Natl. Acad. Sci. U.S.A.*, 109: 14500-14503.
- Rots V. & Van Peer P. 2006. Early evidence of complexity in lithic economy: core-axe production, hafting and use at Late Middle Pleistocene site 8-B-11, Sai Island (Sudan). *J. Archaeol. Sci.*, 33: 360-371.
- Sanz C.M. & Morgan D.B. 2009. Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *Int. J. Primatol.*, 30: 411-427.
- Sanz C., Morgan D. & Gulick S. 2004. New insights into chimpanzees, tools, and termites from the Congo Basin. *Amer. Naturalist*, 164: 567-581.
- Sanz C.M., Schöning C. & Morgan D.B. 2009. Chimpanzees prey on army ants with specialized tool set. *Amer. J. Primat.*, 71: 1-8.

- Schebesch A. 2013. Five anthropomorphic figurines of the Upper Paleolithic: communication through body language. *Mitt. Gesellschaft für Urgeschichte*, 22: 61-100.
- Scott-Phillips, T. C., Laland, K. N., Shuker, D. M., Dickins, T. E., & West, S. A. 2014. The niche construction perspective: a critical appraisal. *Evolution*, 68: 1231-1243.
- Semaw S., Rogers M.J., Quade J., Renne P.R., Butler R.F., Dominguez-Rodrigo M., Stout D., Hart W.S., Pickering T. & Simpson S.W. 2003. 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *J. Hum. Evol.*, 45: 169-177.
- Shea J.J. 2013. Lithic modes A-I: a new framework for describing global-scale variation in stone tool technology illustrated with evidence from the East Mediterranean Levant. *J. Archaeol. Method Th.*, 20: 151-186.
- Shennan S. 2001. Demography and cultural innovation: a model and its implications for the emergence of modern human culture. *Camb. Archaeol. J.*, 11: 5-16.
- Sterelny K. 2012. *The evolved apprentice: how evolution made humans unique*. MIT Press, Cambridge, Mass.
- Tennie C., Call J. & Tomasello M. 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. *Philos. Trans. R. Soc. B*, 364: 2405-2415.
- Thieme H. 1997. Lower Palaeolithic hunting spears from Germany. *Nature*, 385: 807-810.
- Thieme H. 1999. Altpaläolithische Holzgeräte aus Schöningen, Lkr. Helmstedt. *Germania*, 77: 451-487.
- Tomasello M. 1999. *The cultural origins of human cognition*. Harvard University Press, Cambridge, MA.
- Tomasello M., Melis A. P., Tennie C., Wyman E. & Herrmann E. 2012. Two key steps in the evolution of human cooperation. *Curr. Anthropol.*, 53: 673-692.
- Toth N. & Schick K. 2009. The Oldowan: The tool making of early hominins and chimpanzees compared. *Ann. Rev. Anthropol.*, 38: 289-305.
- Tylor E.B. 1871. *Primitive culture: Researches into the development of mythology, philosophy, religion, art, and custom*. Cambridge University Press, Cambridge (2010).
- van de Waal E., Borgeaud C. & Whiten A. 2013. Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, 340: 483-485.
- van Leeuwen E.J. & Haun D.B. 2014. Conformity without majority? The case for demarcating social from majority influences. *Anim. Behav.*, 96: 187-194.
- van Schaik C.P., Ancrenaz M., Borgen G., Galdikas B., Knott C.D., Singleton I., Suzuki A., Utami S.S. & Merrill M. 2003. Orangutan cultures and the evolution of material culture. *Science*, 299: 102-105.
- Vogelsang R. 1998. *Middle-Stone-Age-Fundstellen in Südwest-Namibia*. Heinrich Barth Institut, Köln.
- Wadley L. 2010. Compound-adhesive manufacture as a behavioral proxy for complex cognition in the Middle Stone Age. *Curr. Anthropol.* 51: S111-119.
- Wadley L. 2013. Recognizing complex cognition through innovative technology in Stone Age and Palaeolithic sites. *Camb. Archaeol. J.*, 23: 163-183.
- Wadley L., Hodgskiss T. & Grant M. 2009. Implications for complex cognition from the hafting of tools with compound adhesives in the Middle Stone Age, South Africa. *Proc. Natl. Acad. Sci. U.S.A.*, 106: 9590-9594.
- White L. 1959. The concept of culture. *Am. Anthropol.*, 61: 227-251.
- Whitehead H. & Rendell L. 2015. *The cultural lives of whales and dolphins*. University of Chicago Press, Chicago.
- Whiten A. 2011. The scope of culture in chimpanzees, humans and ancestral apes. *Philos. Trans. R. Soc. B*, 366: 997-1007.
- Whiten A. 2012. Social learning, traditions and culture. In Mitani J., Call J., Kappeler P., Palombit R. & Silk J. (eds): *The evolution of primate societies*, pp. 681-699. University of Chicago Press, Chicago.
- Whiten A., Goodall J., McGrew W.C., Nishida T., Reynolds V., Sugiyama Y., Tutin C.E.G., Wrangham R.W. & Boesch C. 1999. Cultures in chimpanzees. *Nature*, 39: 682-685.

- Whiten A. & Ham R. 1992. On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. *Adv. Stud. Behav.*, 11: 239-283.
- Whiten A., Hinde R.A., Stringer C.B. & Laland K.N. 2011. Introduction. *Culture evolves. Philos. Trans. R. Soc. B*, 366: 938-948.
- Whiten A., Hinde R.A., Stringer C.B. & Laland K.N. 2012 (eds). *Culture evolves*. Oxford University Press, Oxford.
- Whiten A., Horner V., Litchfield C. & Marshall-Pescini S. 2004. How do apes ape? *Learn. Behav.*, 32: 36-52.
- 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. & van Schaik C.P. 2007. The evolution of animal 'cultures' and social intelligence. *Philos. Trans. R. Soc. B*, 362: 603-620.
- Whiten A., Schick K. & Toth N. 2009. The evolution and cultural transmission of percussive technology: integrating evidence from paleoanthropology and primatology. *J. Hum. Evol.*, 57: 420-435.
- Wilkins J., Schoville B.J., Brown K.S. & Chazan M. 2012. Evidence for early hafted hunting technology. *Science*, 338: 942-946.
- Williams V.M.E., Burke A. & Lombard M. 2014. Throwing spears and shooting arrows: preliminary results of a pilot neuroarchaeological study. *S. Afr. Archaeol. Bull.*, 69: 199-207.
- Woollett K. & Maguire E.A. 2011. Acquiring "the knowledge" of London's layout drives structural brain changes. *Curr. Biol.*, 21: 2109-2114.
- Wynn T., Coolidge F. & Bright M. 2009. Hohlenstein-Stadel and the evolution of human conceptual thought. *Camb. Archaeol. J.*, 19: 73-83.
- Wynn T., Hernandez-Aguilar R.A., Marchant L.F. & McGrew W.C. 2011. "An ape's view of the Oldowan" revisited. *Evol. Anthropol.*, 20: 181-197.

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