Hum Nat (2014) 25:161–179
DOI 10.1007/s12110-014-9192-5

Imitation Is Necessary for Cumulative Cultural Evolution in an Unfamiliar, Opaque Task

Helen Wasielewski

Published online: 12 February 2014

Abstract Imitation, the replication of observed behaviors, has been proposed as the crucial social learning mechanism for the generation of humanlike cultural complexity. To date, the single published experimental microsociety study that tested this hypothesis found no advantage for imitation. In contrast, the current paper reports data in support of the imitation hypothesis. Participants in "microsociety" groups built weight-bearing devices from reed and clay. Each group was assigned to one of four conditions: three social learning conditions and one asocial learning control condition. Groups able to observe other participants building their devices, in contrast to groups that saw only completed devices, show evidence of successive improvement. These results are consistent with the hypothesis that imitation is required for cumulative cultural evolution. This study adds crucial data for understanding why imitation is needed for cultural accumulation, a central defining feature of our species.

Keywords Social learning · Cultural transmission · Imitation · Experimental microsocieties · Cultural evolution

Socially learned information can be an important source of adaptive behavior for animals in many taxa (Galef and Laland 2005). Humans have especially complex shared behavioral traditions, or *culture*, which have allowed extensive modification of the natural environment and consequently expansion into a wide variety of habitats (Boyd and Richerson 1995; Mithen 1996; Tomasello 1999). Human cultural complexity is enabled by an additive process of individual innovation coupled with transfer of this information to others in the population via social learning. This additive process is termed *Cumulative Cultural Evolution* (CCE) (Boyd and Richerson 1996), or the cultural ratchet effect (Tomasello et al. 1993).

Electronic supplementary material The online version of this article (doi:10.1007/s12110-014-9192-5) contains supplementary material, which is available to authorized users.

H. Wasielewski (✉)
Department of Anthropology, 131 George Street, RAB 306, New Brunswick, NJ 08901, USA
e-mail: helen.wasielewski@rutgers.edu

Among animal species, humans have uniquely complex culture. As a result of the additive nature of human cultural traditions, the socially learned body of information that humans acquire vastly exceeds what any individual could invent in his or her lifetime. In other animal species, the degree to which socially learned information exhibits this additive quality seems relatively limited, and the difference between what can be acquired by individual and social learning is less pronounced. One hypothesis is that imitation is required for humanlike cultural complexity (Boyd and Richerson 1985, 1996; Tomasello 1999; Tomasello et al. 1993). Imitation, which is defined as behavioral replication in an observer following witnessing of that behavior in a demonstrator, is proposed to be especially important for the accumulation of cultural information because it allows high-fidelity information transfer between individuals. This hypothesis suggests that in the absence of a high-fidelity transmission mechanism, information is likely to be lost; individual modifications will not be socially acquired and therefore not be subject to the additional modification that enables cultural complexity (see Galef 1988; Heyes 1993 for alternative views).

Modeling efforts have provided results consistent with the idea that transmission fidelity is important for cultural ratcheting. Using a mathematical model, Nakahashi (2013) found that highly accurate social learning is essential for cultural improvement, and Enquist et al. (2010) report that small increases in fidelity can result in longer-lived traditions. Trait longevity is important for cumulative cultural evolution because accumulation occurs through individual modification of existing practices, and loss of culture traits exempts them from this process. Building on the work Enquist et al. (2010), Lewis and Laland (2012) explicitly modeled the effect of transmission fidelity on cumulative cultural evolution by manipulating rates of trait loss. Their analysis suggests that even small increases in fidelity can lead to cumulative culture. Although these results are consistent with the idea that high-fidelity transmission is important for CCE, whether imitation produces higher-fidelity information transfer than other social learning mechanisms remains an open question (Laland and Hoppitt 2003).

Social learning mechanisms can be arrayed on a hierarchy that describes varying degrees of information exchanged between individuals (for a review see Whiten et al. 2009). In a process referred to as *stimulus enhancement* (Spence 1937), for example, observers learn from having their attention drawn to an element of the environment by another individual; in contrast to imitation, the manipulations of the observed individual increase the observer's attention to the item in question, but particular behaviors are not transmitted. Even in a low-resolution process such as stimulus enhancement, however, cognitive constraints or the physical limitations of the task may in some cases result in matching behavior—a necessary prerequisite for cumulative cultural evolution according to the imitation hypothesis for CCE described above (see Franz and Matthews 2010; Matthews et al. 2010 for a discussion of traditions arising from low-level social learning). Acerbi et al. (2012) have demonstrated in an evolutionary, agent-based model that limiting the number of alternative behaviors can result in shared behaviors at the group level even when transmission fidelity is low. In addition to manipulating the number of possible behaviors, Acerbi et al. (2011, 2012) examined the effects of social learning on agents who exist in search spaces that are defined by different payoff gradients. In "smooth" spaces, behaviors that are closer to the optimal behavior provide higher payoff and thus enable agents to adjust their strategies to reach the ideal behavior for the space. In "peaked" spaces, in contrast, only a single, best behavior provides a payoff, which means that agents are unable to orient their searches to reach this peak. Under the assumption that social learning imposes costs, high-fidelity social learning evolved in this model only in populations that had large behavioral repertoires, and little information that individuals might use in determining the optimal behavior (Acerbi et al. 2012). Acerbi et al. (2011, 2012) argue that many human artifacts have these two characteristics: there is relatively little built-in constraint for the behaviors that might be used in the creation of any complex item of human material culture, and often creating an item that is not identical will result in something nonfunctional, rather than a slightly less efficient version.

Low-resolution processes such as stimulus enhancement can generate culture when behaviors are limited by constraints on behavioral alternatives, or guided by feedback information for nonoptimal solutions. Increased fidelity of social learning enables the possibility of behavioral homogeneity even in the absence of these constraining mechanisms. In a social learning process called *emulation*, observers learn from the environmental effect of actions, rather than from actions directly. There are several sub-categories of emulative learning. Copying completed products, but not the actions used to create them, is referred to as *end-state emulation* (Whiten et al. 2004). *Object movement reenactment* involves copying the movements of a manipulated object, rather than the actions of the observed individual (Custance et al. 1999). In *affordance learning*, social learners acquire information about the properties of products or of the environment (Gibson 1979). In the current article, following Call and Carpenter (2002), the subtypes of emulative learning are collectively referred to as results-oriented copying, whereas imitation is referred to as action-oriented copying.

The contention that action-oriented copying is producing the conditions necessary for accumulation is corroborated by the lack of evidence for cumulative culture in wild nonhuman populations, among which no clear evidence of imitative learning of traditions has been collected to date, in part owing to the difficulty of testing particular social learning mechanisms under field conditions (Whiten 2011). Interestingly, however, cultural transmission studies with chimpanzees have provided evidence of diffusion of experimentally seeded behaviors across several individuals (Bonnie et al. 2007; Horner et al. 2006; Whiten et al. 2005, 2007), complicating the argument that differences in transmission fidelity are responsible for the relative lack of complexity in nonhuman cultural behaviors. Of particular relevance to the current study is the diffusion chain research conducted by Horner et al. (2006). In this study, a single chimpanzee in each of two groups was trained to open an artificial fruit using one of two techniques. One individual was then allowed to observe the model, and after acquiring the behavior the observer individual served as a demonstrator for another observing individual, who in turn acted as a demonstrator for an additional individual. Horner et al. (2006) report that the alternative demonstrated techniques were reliably transmitted across two chains several generations of individuals long, suggesting that chimpanzees are capable of some degree of transmission fidelity. Claidière and Sperber (2010), however, question the degree of stability exhibited by this and other chimpanzee transmission chain studies, raising the idea that socially learned preferences appear stable only when animals' access to the experimental device is restricted (e.g., Whiten et al. 2005). Further, Claidière and Sperber (2010) argue that the degree of transmission fidelity demonstrated by chimpanzees in laboratory experiments is insufficient for the maintenance of cultural traditions that are observed in the wild. Although the data provided by Horner et al. (2006) are consistent with social learning of behaviors, their naturalistic study design was also not intended to identify the social learning mechanisms underlying the transmission events.

Among studies designed to discover the social learning mechanisms used by chimpanzees, findings for imitation are mixed, with the central debate surrounding the differentiation of action-oriented copying from results-oriented copying. Chimpanzees have been found to be capable of emulation (e.g., Hopper et al. 2008; Nagell et al. 1993; Tennie et al. 2010a), and some have argued that results-oriented copying, rather than action-oriented copying, is the primary ape social learning mode (Call and Carpenter 2002; Call et al. 2005; Tennie et al. 2006, 2009, 2012; Tomasello 1999). Consistent with the imitation hypothesis, Dean et al. (2012) found that children's performance in solving a puzzlebox equipped with sequential challenges covaried with a suite of abilities that included imitative behavior. Capuchins and chimpanzees, in contrast, showed little evidence of utilizing these social skills in solving the task, and they underperformed relative to children. Comparative research with children suggests that when apes do learn from actions, they do not exhibit the degree of bodily action matching that characterizes human imitation (Horner and Whiten 2005; Nagell et al. 1993; Tennie et al. 2010b).

In order for imitative learning to be positively identified, the possibility that the performance resulted from results-oriented copying must be eliminated. This requirement has necessitated the use of creative methods, most notably the experimental "ghost control" (for a review of such studies see Hopper 2010). Experimental "ghost controls" are intended to parse the effects of imitation and object movement reenactment by moving apparatuses or tools without a visible actor (e.g., by fishing line). A demonstration that copying requires the observation of actions would support the idea that imitation, rather than object movement reenactment, is responsible for copying when actions are observed. In the ghost control condition of a comparative study of chimpanzees and children, for example, Hopper et al. (2008) used fishing line to slide the door of an acrylic test box to the left or right. Both children and chimpanzees demonstrated copying of the direction of door movement when a model was observed receiving a reward after the door was opened, supporting the hypothesis that chimpanzees are capable of results-oriented copying. Other studies employing ghost controls, however, have not found evidence for emulative learning in chimpanzees (Hopper et al. 2007; Tennie et al. 2006). Hopper et al. (2007) report that chimpanzees demonstrated learning from the actions of a model but failed to do so in a ghost control condition, a finding that is seemingly in conflict with the idea that chimpanzees are exclusively results-oriented copiers. Yet these results, as with other negative results, are difficult to interpret, and they rely on the unsubstantiated assumption that chimpanzees are attending to ghostly manipulations in the same way as they do a conspecific (Byrne 2002; Tennie et al. 2009). In addition, Whiten et al. (2004, 2009) have questioned whether there is an essential difference between the process of copying object movements and the process of copying the actions of a model on those objects. To remove the complication of differentiating between action- and results-oriented copying, Tennie et al. (2012) eliminated the affordance or object movement information that might be used for learning in any action demonstration that includes manipulated objects. In this study, chimpanzees were trained to provide action demonstrations to observer individuals. When these actions were familiar, only a single individual replicated the observed action, whereas when the actions were novel, none of the chimpanzees succeeded in replicating the target action. In sum, the data from experimental research suggest that chimpanzees are capable of transmission fidelity at least at the level required to generate shared behaviors recognizable at the population level, but that they seem to focus primarily on results-oriented copying and do not demonstrate the sort of high-fidelity behavioral replication thought to be required to sustain cultural practices and enable progressive evolution of culture.

To date, the only published report to explicitly test the imitation hypothesis for CCE using a physical task with adult subjects, Caldwell and Millen's (2009) experimental microsociety study, surprisingly found no evidence of a superior effect of imitation over related social learning mechanisms in generating CCE. The current study was designed to elaborate on Caldwell and Millen's (2009) work, using the same basic experimental microsociety design with a novel task. Experimental microsocieties approximate cultural dynamics in a laboratory setting by examining the flow of information in groups of participants as they complete an experimental task (see Mesoudi and Whiten 2008 for a review). The addition and removal of group members is intended to simulate cultural generations. After validating their microsociety design in an earlier study (2008), Caldwell and Millen (2009) asked participants to build and fly paper airplanes as part of a transmission chain. In their design, each member of the group had a start time that was slightly staggered relative to others', allowing for some overlap in cultural generations and therefore opportunity for social learning. Each group of participants was randomly assigned to one of seven experimental conditions, each with various degrees of social information access. Groups in the actions conditions were allowed to observe other group members building airplanes, enabling learning via imitation. Groups in the results conditions were able to examine completed planes and their flight distances, providing opportunity for results-oriented copying. Caldwell and Millen found evidence of cultural accumulation in all seven conditions tested, and they found no superiority in performance of groups with access to action information compared with those without access to action information. Caldwell and Millen interpret these results to mean that imitation is not required for CCE.

In light of the accumulating evidence that imitation is essential for cumulative cultural evolution, Caldwell and Millen's (2009) result is puzzling. Although Caldwell and Millen do not explore the idea in detail, they do acknowledge that the nature of the task may not be appropriate for generalization to the transmission processes for other cultural behaviors, which, owing to their complexity, may require imitation to generate accumulation (2009:1482). One possible explanation is that high-fidelity information transmission is not needed for cumulative cultural evolution (Caldwell et al. 2012), although this explanation would contradict the empirical work that supports a strong relationship between transmission fidelity and accumulation (e.g., Enquist et al. 2010; Lewis and Laland 2012; Nakahashi 2013). A second possibility is that results-oriented copying enables high-fidelity information transmission (Caldwell et al. 2012). Such an explanation is consistent with the hypothesis that chimpanzees lack cumulative cultural evolution because their social learning mechanisms, whether focused on actions or results, are low in fidelity (although Caldwell et al. 2012 do not hold this view). To test these possibilities, Caldwell et al. (2012) evaluated the degree of transmission fidelity for results-oriented copying using a task that had been shown in an earlier study to generate accumulation (Caldwell and Millen 2008). In each of these studies, participants built towers from uncooked spaghetti and clay, with the goal of building the tower as tall as possible. To evaluate the effects of results-oriented copying on fidelity, participants were shown either a completed tower or a photo of a completed tower, in one of two designs. Caldwell et al. (2012) report that participants built towers with design features that were highly similar to the design that was displayed, even though they were not told directly to copy the design that they saw. Caldwell et al. (2012) argue that these results support the idea that high-fidelity transmission can be supported by results-oriented copying, contrary to the imitation hypothesis for CCE.

Considered alongside their earlier results (Caldwell and Millen 2009), the findings of Caldwell et al. (2012) invite broader questions about the relationship between end-states and actions that warrant further discussion. Actions required to recreate an observed artifact are considered "cognitively opaque" when viewing the completed end product is insufficient to understand how to recreate it (Gergely and Csibra 2005). In contrast, the experimental task employed by Caldwell and Millen (2009) is highly transparent—in other words, inferring the actions needed to modify an observed paper airplane is comparatively easy. A completed paper airplane differs in this way from a complex, more cognitively opaque tool, such as an Acheulian hand axe, which would be more difficult to effectively create and modify without additional information about required actions (see Shipton 2010 for a discussion of imitation and the Acheulian). In adults, little has been done to directly test the effect of end-product opacity on the ability to match target actions, although the use of action-oriented copying has been previously associated with increasing task difficulty in both chimpanzees (Horner and Whiten 2005; Tennie et al. 2010b) and children (Tennie et al. 2010b). The one existing study to compare action and results conditions using a cognitively opaque virtual task found an advantage for groups that were able to view actions (Derex et al. 2013), consistent with the idea that imitation is required to generate CCE for such tasks. The current research was designed to test the hypothesis that a more cognitively opaque and novel task might require the use of action-oriented copying to generate CCE.

In the current study, participants were assigned to microsociety groups and asked to build devices from a length of weaving reed and a portion of modeling clay. Research staff assessed the success of these devices by measuring the number of weights held by each device while it was suspended from a wooden stand. Visual access to actions (building behaviors) and end products (completed devices) was manipulated to test the idea that imitation is required for CCE when the task is cognitively opaque. This task was expected to be more opaque than the paper airplane task in several important ways and therefore to show ratcheting only when action information was available.

The first aspect of transparency for a paper plane, as for a spaghetti and clay tower, is that recreating (and tweaking) its various characteristics is relatively easy, even without being able to observe the building process. This is the case because the design attributes that contribute to the flying ability of the plane are visible. Although observers may not be entirely certain which element of the plane was responsible for increasing its loft, for example, the various folds and creases in the plane are observable. In contrast, a clay and reed device was thought to be more likely to have design attributes that are hidden to someone unable to witness the device-creation process. For example, kneading the clay may result in increasing its elasticity and therefore its weight-bearing capability, but kneading does not leave an obvious visible trace on the finished device. When these characteristics are important for the functioning of the device, observers were predicted to be unable to recreate a device with improved performance. Caldwell et al. (2012) report high-fidelity replication of spaghetti tower device designs, with equal or improved performance relative to the demonstration designs, suggesting that the important functional characteristics of these towers are visible to observers. However, one possibility is that the two spaghetti tower device designs that Caldwell et al. (2012) created as models may have been especially transparent in terms of their functional features. Caldwell and Millen (2008) reported that the spaghetti tower task can generate ratcheted performance, but since that study did not control access to social information it is unknown whether other design variants are equally well transmitted through end-state emulation.

End-product copiers are also challenged with the need to determine which actions will lead to effecting a similar result. Visible, functionally important traits of artifacts vary in terms of how clear the actions required to create them are to observers. For a paper airplane, inferring the likely processes used to create its various characteristics is relatively easy. For example, a crease indicates that the paper has been folded. The various design attributes of the artifact map clearly onto their behavioral precursors, making it easy to reverse-engineer. For the most important and visible design attributes of clay and reed devices and the spaghetti towers, as well, reverse-engineering is probably relatively easy. The reverse-engineering capacity of these tasks contrasts with artifacts that are more cognitively opaque: a complex knot's functional qualities are visible, but recreating a knot is comparatively more difficult because it also requires understanding the sequence in which the required steps must be executed (see Derex et al. 2013).

A third element of paper plane building that is important in explaining the results of Caldwell and Millen (2009) is past experience, or skill, with the task. The development of skill is valuable because it reduces uncertainty about the actions that might be used to create a similar, or better, end product. To an experienced stone tool maker seeking to recreate an observed flake, for example, the range of possible actions, as well as their sequence, is constrained by past experience. Making a paper plane is a relatively transparent task for the U.K. participants tested by Caldwell and Millen (2009) because it is highly familiar, and it consists of a small number of proscribed steps executed in a predictable order. To an experienced builder of paper airplanes, the attributes of a completed plane are even more readily interpreted in terms of actions needed to recreate them than by someone who is unfamiliar with paper plane creation. Prior to observing the completed planes, participants would already have an idea of the actions required to make their own planes and would only need to add modifications to their existing behavioral template. The task used in the current study, in contrast, was designed to be novel for participants: building a weight-bearing device from weaving reed and modeling clay is not a task with which many of the participants in the current study would have been familiar, and certainly there is no agreed-upon series of steps that could be mentally accessed to solve the problem. This means that a demonstration of ratcheting in the clay and reed device task used in the current study would require that participants mentally work backwards from the form of a completed device, itself novel, to the steps needed to make their own, slightly better version. The spaghetti-tower performance results reported by Caldwell et al. (2012) are expected to be far less affected by past experience than those using their paper airplane task, and therefore visible functional features and reverse-engineering are likely to be especially important for the high-fidelity replication of spaghetti tower end products.

The paper plane building task therefore is high on three measures of transparency: it is easy to reverse-engineer because the end product displays the process used in its creation, the traits important for functioning are visible, and the possible steps are constrained for participants familiar with paper plane making. These characteristics of the task mean that in the results condition of Caldwell and Millen's study (2009), improvement of end products proceeded without direct access to actions, through results-oriented copying. The clay and reed device task used for the current study, in contrast, is much more cognitively opaque. Participants were expected to be unfamiliar with the task and unable to ascertain some of the functionally important features of completed end products.

Conditions

Participant groups were assigned to one of three social conditions or one non-social control condition.

Non-social Control Condition

In the non-social control condition, participants saw neither the completed devices of others, nor their actions.

End-product Condition

In the end-product condition, participants had visual access to completed devices others on their team had created, but they were not able to view their building behaviors.

Action Condition

In the action condition, participants were able to see the building behaviors used to create devices. They were not able to view the completed devices of others.

End-product and Action Condition

In the end-product and action condition, participants were able to view both the completed devices of others as well as their building process.

Imitation requires observation of the actions of another individual. Therefore, if imitation is required to generate accumulation in this task, accumulation is predicted to occur only in two conditions: the action condition and the end-product and action condition. In the end-product condition, participants would not have been able to imitate. Instead, these participants could only have relied on results-oriented copying. Because of the opacity and unfamiliarity of this task, participants in the end-product condition are predicted to be less efficient in the conservation of information compared with participants in the action conditions, and therefore are predicted to fail to exhibit ratcheting.

Methods

Participants

Participants were recruited from the local community and the campus of Rutgers University. 604 subjects (349 females and 255 males) took part in the study. The mean age for subjects was 21 years (SD=4.80, range=18–60). The testing took place in central New Jersey between October 2010 and April 2011. All applicable human subjects protection protocols were followed, and permission to do the study was granted by Rutgers University Institutional Review Board.

Materials

Each subject was provided a 160-cm length of 6.35-mm (¼-in) flat weaving reed and 75 g of modeling clay. Participants also had access to a wooden stand with a 12.5-cm-diameter hole (Fig. 1). These materials were distributed to each team at the beginning of the task, but participants were instructed that they were not allowed to touch the materials until instructed to begin building their devices. All instructions were given to participants both orally and in writing.

Fig. 1 The wooden stand, reed, and clay that participants used in creating their weight-bearing devices

Procedure

Once seated, participants were told that they were part of a team trying to build devices to hold as much weight as possible. During this instructional period, participants were shown the weights and the weight-adding process: a research staff member showed participants an example weight and, using a stand and a weight, repeatedly demonstrated the weight-adding process by dropping weights through the center of the hole in the stand. This demonstration was made to every two participants in the row to ensure all participants were able to view it, and research staff assessed attention to the demonstration by observing eye contact with the stand. If any participants appeared not to be paying attention, the group was reminded to watch the demonstration, until all participants had been observed to gaze at the stand.

In all conditions, participants were instructed that at some points in time they might be able to watch what others were doing, or see the completed devices of others. Participants were instructed that looking at others or at their completed devices was permitted, but that talking to one another was not permitted, and no participant was observed talking to any other individual. Following Caldwell and Millen (2008), building start times for each participant were staggered. In every condition, the third participant waited an additional 5 min to begin building his device following the start time of the second participant. By waiting, the third participant in the end-product condition had access to the completed device of the second participant 5 min earlier. Thus, the third participant in the end-product condition was not unduly disadvantaged relative to the third participant in the action condition. Each participant spent a period of time waiting to begin building, and 15 min building. Participants were provided with a timer showing two times simultaneously counting down and were instructed that the number on top was the “waiting time” while the bottom number was the “building time.” Each timer was programmed to ring twice, to indicate the start and end of the building period. Participants were told that they could begin building as soon as they heard the timer chime initially.

While waiting, participants were unable to see others building devices, or their completed devices. During the waiting period participants were not permitted to wear headphones, to use cell phones for any purpose, or to use a computer. These activities were prohibited because of their potential to disturb other participants or distract participants from beginning the task on time. Waiting times were equal across the conditions for a given position in the chain because participants may have used the available time to strategize how to complete their devices. The asocial control condition was included to control for the possibility that individuals later in the chain were better able to make devices because of the longer time spent planning. See Fig. 2 for group composition.

Following completion of the device or expiration of the 15-minute build time, 50.6 g weights were added to the device by a research assistant, one at a time, until a weight slipped off the stand or the device fell or broke. If a weight slipped off the stand but the device did not fall or break, the weights were added again in order to control for variation in the adding process. If weights were added again, the higher number was recorded as the number of weights held. The higher number, rather than the mean, was chosen as the measure of success because bias in the adding process is more likely to negatively affect the number of weights than to artificially increase the number of weights held, given the physical limitations of the clay and reed devices. Therefore, the

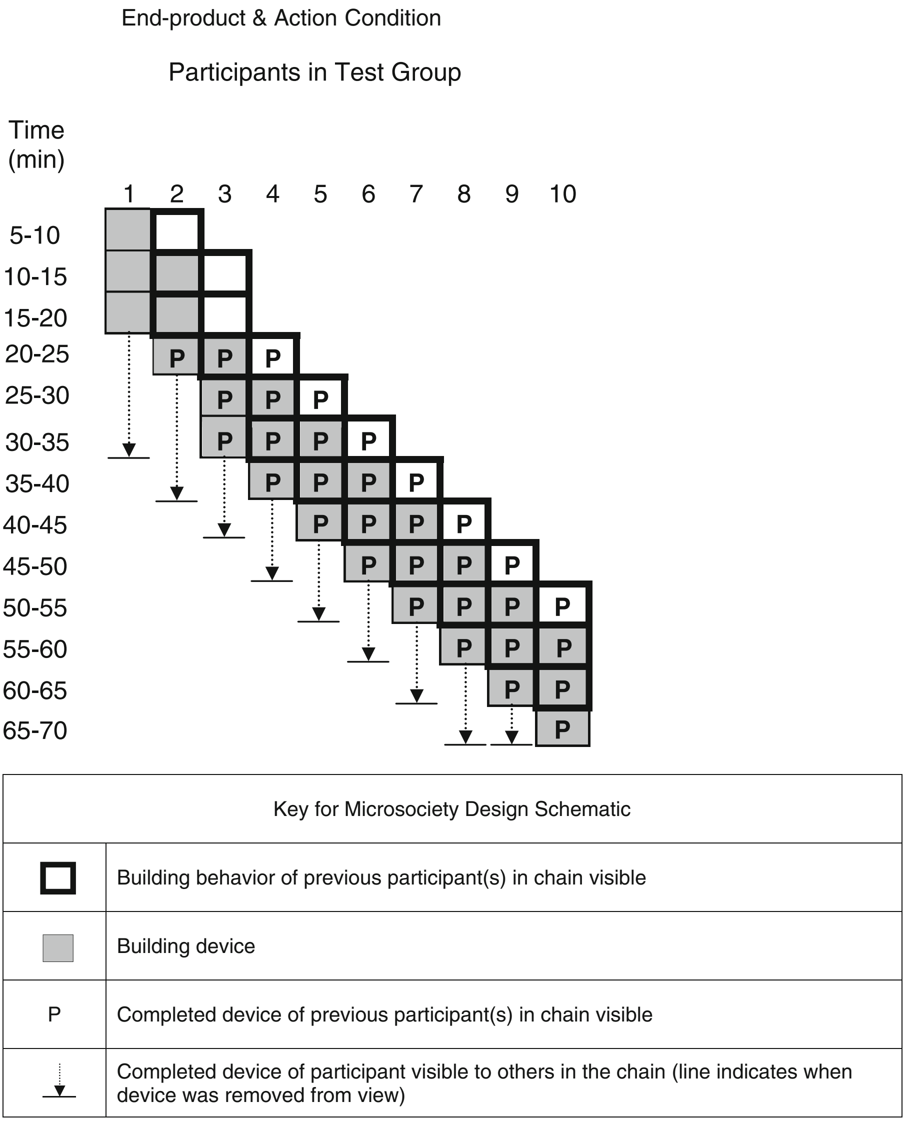

Fig. 2 Microsociety design schematic (following Caldwell and Millen 2008). This schematic indicates the role of each participant during any one trial for the end-product and action condition. In the end-product condition, no action information was available. In the action condition, no device information was available. In the asocial condition, no end-product or action information was available

higher number was conceived of as more accurately representing the true capability of the device than the mean of a higher and lower score.

Information about the success of devices was not provided to observers in any condition. The success of team members was not made available to mimic conditions of uncertainty in the real world: frequently, directly ascertaining the payoff of observed behaviors or end products is not possible, in particular during the initial period of observation for a novel behavior. When social learners do not have direct access to information about the success of a strategy, other available content and context cues are expected to inform decisions about when and whom to copy (Laland 2004; Rendell et al. 2011). Participants were not rewarded for performance. Following the weight-adding process, participants left the testing area.

Visual access to participants and their devices was manipulated by adding and removing lightweight barriers between participants. In conditions for which device information was available (end-product condition, and end-product and action condition), completed devices were placed on a display table 1.25 m in front of the line of participants, and this display table was shifted to give visual access to successive groups of participants. Barriers between participants and a barrier on the right-hand side of the display table prevented visual access to participants farther down the transmission chain. A maximum of two devices was placed on the display table at a time. As each participant completed his or her device, it was placed on the left portion of the display table, and any device(s) currently on the display table were shifted to the right. At this time, the right-most device on the display table was removed from the participants' view. The display table was shifted toward the end of the chain of participants every 5 min by aligning the barrier of the display table with the right-hand barrier of the next participant in the chain (see Fig. 2 for details). The display table began each trial with its barrier aligned with the right-hand barrier of participant 4. In order to maintain experimental control over the devices in view, participants were asked not to stand up in an attempt to view the devices, and no one was observed doing so. See Fig. 3 for details of the experimental setup at minutes 30–35.

Results

The mean number of weights held by a device in any condition was 6.68 (SD=9.11), and number of weights held ranged from 0 to 66. Figure 4 shows the mean number of weights held per device in positions 1–6, for groups of six or more (k=61, n=366). The group size has been restricted to groups of the same size because of variation as a result of no-show participants. Full results from every chain of the study are provided in ESM-1. The ESM also includes descriptive statistics for the performance of conditions based on various chain lengths (ESM-2), and photos of selected devices (ESM-3).

Cultural accumulation would predict successive improvement in each experimental generation such that each position does better than the one preceding it (10>9>8, etc.). Page's L trend test (Page 1963) was used to test this explicitly. Page's L trend test is a repeated-measures ranking test similar to Friedman's test that is used when the analysis requires a specific hypothesized rank order. Because of variation in group sizes from no-show participants, the results reported here are for participants in groups of at least six participants, truncating the group at position six (k=61, n=366). The L in both action conditions reached the critical value for significance ($p<0.05$), indicating a significant trend of improvement in both action conditions (action condition and end-product and action condition). No trend of improvement in the end-product condition or the asocial control condition was detected (Table 1).

In order to examine the effect of truncating the group size at six participants, the Page's L values were also determined for chains of size 3–10 (truncating at the third through the tenth participant, respectively). These truncation points create nested data (i.e., a group of five or more contains five-participant chains, as well as chains with

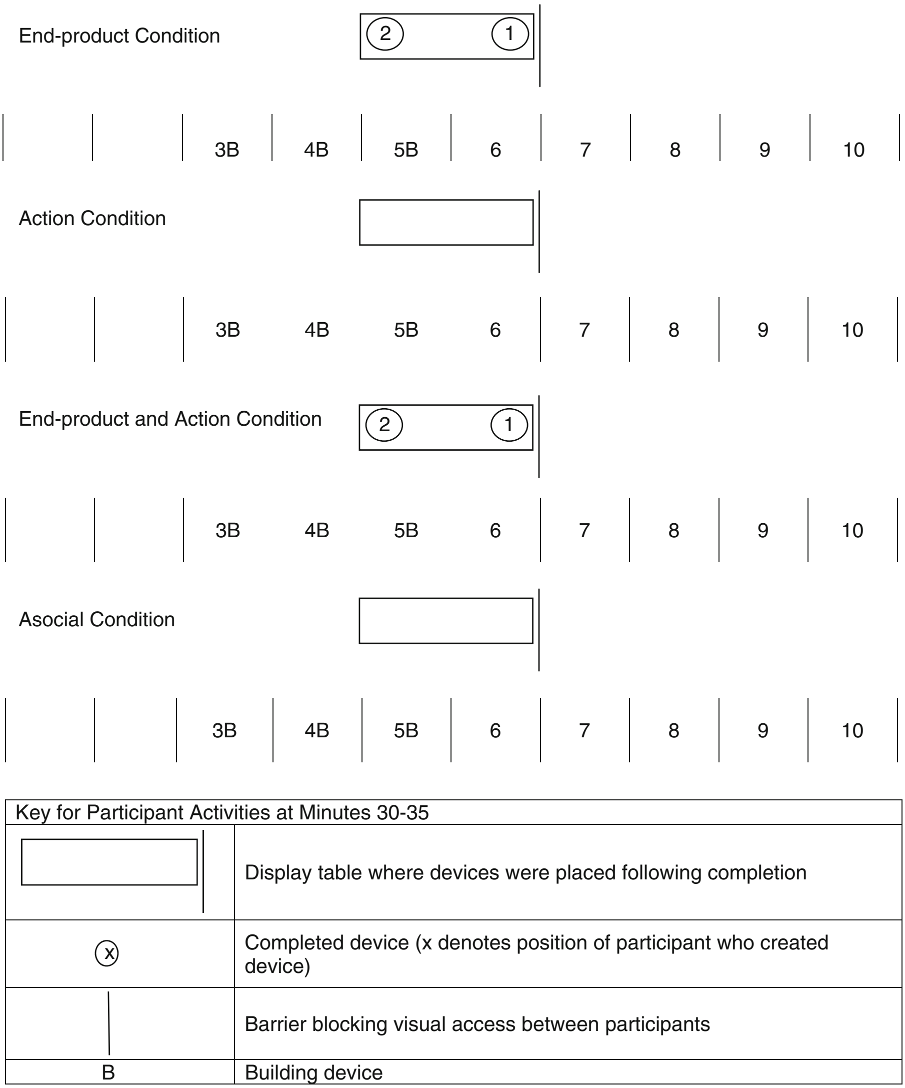

Fig. 3 Participant activities at minutes 30–35. At minute 30, participants 1 and 2 have left the testing area. Participants 6–10 are waiting to begin building. Participants 3–5 are building. In the results conditions (end-product and end-product and action), participants in positions 3–6 are able to view completed devices of participants 1 and 2. In the action conditions (action and end-product and action) participants 3–6 are able to watch one another building the devices

original lengths of 6–10 that have been truncated at position five). The overall pattern of Page's L scores from the full data set for chains of at least three participants mirrors the findings of the six-person chains: no chain length in the asocial or end-product condition reached the critical L, so no evidence for accumulation was found for groups not allowed access to actions, regardless of truncation point. In contrast, of the action-condition truncation points (chains of 3–10), 11 of 16 reached the critical L. Two additional groups were within one or two points of reaching critical L status. The full set of trend test results for groups of size 3–10 can be found in ESM-4.

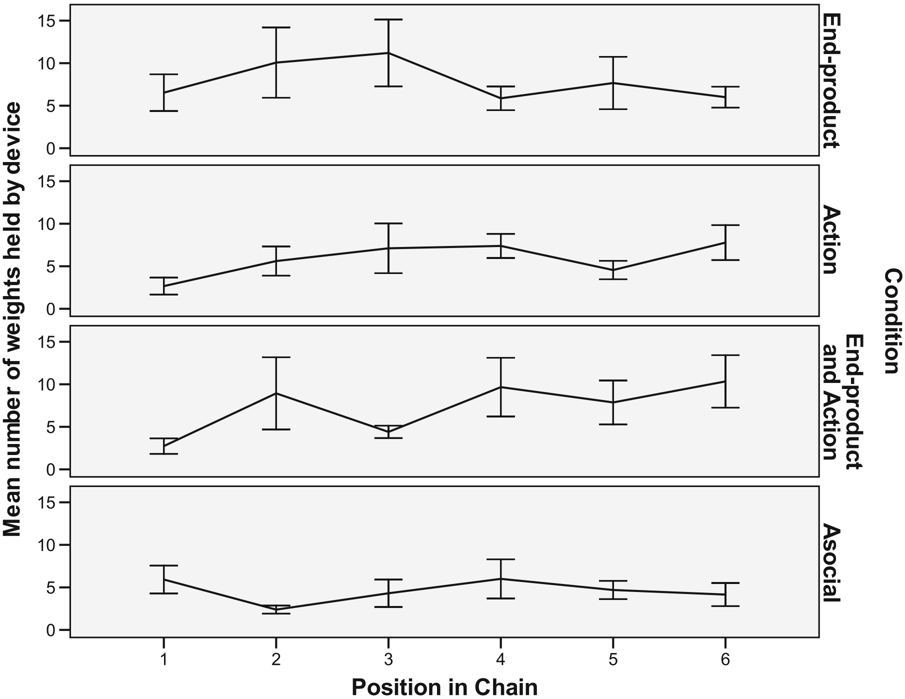

Fig. 4 Measures of success of clay and reed devices over generations, for groups of six or more. Error bars indicate SEM

The Page's *L* trend test reveals whether there is a trend of improvement along the transmission chains for each condition, but it does not allow explicit comparison between the conditions. To make this comparison, a two-way ANOVA was performed using Spearman correlation coefficients that were derived per chain (the correlation here is between the actual rank of scores and the predicted ordered rank). The correlation coefficients were then transformed using Fisher's *z*-transformation to make the distribution approximately normal. See Table 2 for details of the correlation results. To determine whether there was a significant difference in performance between the conditions depending on the presence of behavior, a two-way ANOVA was calculated on the Fisher's *z*-transformed correlation coefficients for action conditions (action and end product, and action) and non-action conditions (end product and asocial). This analysis included chains of at least six participants (k=61, n=466). The ANOVA results revealed a significant main effect of actions ($F_{1,57}$=10.563, p=0.002), but not of end product ($F_{1,57}$=0.001, p=0.973), and there was no interaction effect ($F_{1,57}$=0.835, p=

Table 1 Summary of cultural accumulation results: page's *L* trend test. Rows in **bold** are significant

Condition	*L*	*p*
End-product (k=15, n=6)	1106	.454
Action (k=18, n=6)	**1395**	**.015**
End-product and Action (k=15, n=6)	**1167**	**.017**
Asocial (k=13, n=6)	962	.409

Table 2 Correlation coefficient results (z-transformed means)

Condition	*r* (z-transformed values)
End-product (k=15, $n\geq6$)	−0.164
Action (k=18, $n\geq6$)	0.197
End-product and action (k=15, $n\geq6$)	0.284
Asocial (k=13, $n\geq6$)	−0.054

0.365). The action conditions therefore show superior cumulative effects relative to the non-action conditions. When the asocial condition was removed from the analysis so the action conditions could be compared against the end-product condition alone, this ANOVA also showed a significant main effect of actions ($F_{1,57}$=9.616, p=0.003).

Since no evidence of cultural accumulation was found in the end-product condition, perhaps participants in this condition were not learning socially at all. In order to test this hypothesis, a comparison of the zero scores in each condition was conducted (Table 3). Zero scores indicate that the participant's device held no weight at all. Since those in the first position in the chain would be expected to have randomly distributed scores, position one scores have been excluded for this analysis. A Pearson's chi-square test showed a significant difference between the number of zero scores in each condition ($\chi^2_{(3,\ n=305)}$=8.72, p=0.033). In addition, comparison of the zero scores in the end-product condition and the asocial condition were significantly different, suggesting that those in the end-product condition were learning socially ($\chi^2_{(1,\ n=140)}$= 6.57, p=0.010).

Discussion

When they were able to view members of their team creating devices, participants demonstrated evidence of cumulative culture, improving their device performance for each participant in the chain. Comparison of performance between action and non-actions conditions indicates that observation of actions is required to generate CCE in this task. This result is in accordance with the hypothesis that imitation is required for cumulative cultural evolution. The distribution of completely unsuccessful devices between conditions suggests the null result in the end-product condition is not due to failure to attend to the completed devices (or other experimental contingencies). That is, while participants in the end-product condition seem to be gaining some information from observation of completed devices in this condition, they were unable to improve

Table 3 Zero scores distribution

	End-product	Action	End-product and action	Asocial
Observed count	5	9	7	14
Expected count	8.6	10.3	8.6	7.5
Std. residual	−1.2	−0.4	−0.5	2.4
% within condition	6.7	10	9.3	21.5

their device designs. This lack of improvement in the end-product condition, in contrast to the improvement demonstrated in the action conditions, implies that participants extracted (and improved on) some specific information about building techniques from the observed demonstrations. Apparently the information contained in completed devices was insufficient to convey how to improve one's device. Although they were unable to improve their devices after observing completed devices, it is unclear whether participants in the current study were also unable to ascertain the actions used to create the devices. It would seem that replication of the building behaviors, or at least the capability to reproduce these actions, would be a minimal component of technique improvement. These two possibilities might be distinguished in future studies by asking participants explicitly to recreate the actions used to create an observed device. This question is also interesting because one implication of the imitation hypothesis for CCE is that improvement is possible when behavioral techniques are replicated, yet action information could provide additional information that allows for improvement of devices which simple replication does not. One extra-imitative advantage of behavior is that it provides information about whom to copy: observers of actions are able to assess the skill of models, whereas observers of end products have no additional information about the qualifications of the device creator. Those in the end-product condition may have been particularly unsure about whom to copy because participants in this study were not apprised of the success of other members of their team. Indeed, comparison of the rate of copying of successful and unsuccessful device designs suggests that in action conditions, but not in non-action conditions, participants were able to discriminate between successful and unsuccessful team members. These data support the conclusion that model-based biases may have contributed to the performance improvement noted in the action conditions.

In contrast to Caldwell and Millen (2009), evidence for CCE was not found for the end-product condition of the current study. One explanation for these conflicting results is a difference in the degree of cognitive opacity of these products: whereas performance on Caldwell and Millen's task was enhanced via results-oriented copying alone, participants in the current study needed the additional information provided by actions in order to improve their device designs. The creation of complex artifacts in human evolutionary history likely involved a similar problem in terms of opacity of the relationship between end product and actions, which Gergely and Csibra (2005) have argued selected for enhanced imitative abilities in the human lineage. The ability to imitate releases our species from the inefficiencies of trial-and-error learning by enabling the transmission of particular techniques, some of which are imperfectly communicated by artifact forms. Individuals who are adapted to attain information from others through imitation not only are able to build their innovations on accumulated advances of past generations: they are also able to acquire information that may have been quite difficult to learn individually, specifically because the relationship between ends and their behavioral means is difficult or impossible to detect (Gergely and Csibra 2006; Tennie et al. 2012). In addition to their enhanced imitative abilities, humans likely have enhanced emulative abilities, as demonstrated by their ability to replicate some end products with high fidelity (e.g., Caldwell et al. 2012). Tennie et al. (2012) discuss the advantage of having a social learning system for culture that provides redundancy: by being able to learn from actions as well as results, the possibility of error is reduced, and efficiency is increased.

The current study provided a cognitively opaque task that mirrors the conditions that led to the development of enhanced imitative abilities in our species. The clay-and-reed devices are difficult to reverse-engineer, have functional features that are hidden in the final form, and the participants would not have been able to draw on existing knowledge about behaviors needed for this particular task. Future research efforts might be directed toward understanding the threshold at which artifacts become too opaque to reproduce via results-oriented copying alone. End-product learning might be imagined as existing on a continuum that would be revealed by explicitly requesting that research subjects replicate both the results and the actions that were used to create those results. Highly opaque end products are those that are impossible to recreate without action information because of either limited reverse-engineering capacity or absent functional features. Some of the devices created in the current study appear to be highly opaque because their functional features are not visible (e.g., woven reed completely encompassed by layers of clay). Semi-opaque end products are those that contain sufficient functional information for replication, but insufficient information for reverse-engineering. Although the attributes of the end product are apparent, understanding how to create them is not. An Acheulian stone tool is semi-opaque because its functional features (e.g., a sharp cutting edge) are visible, but the final form of the artifact does little to limit the possible actions that might be used by observers to recreate it (Jacquet et al. 2012). Finally, as Whiten and Ham (1992) suggest, when there are few behavioral options for creating a device with similar design features, it may be the case that behavioral replication can be produced even in the absence of observing behaviors. Transparent items are those that can be successfully replicated, using the same actions. Because of the highly constrained nature of the paper airplane building task, with its combination of familiarity, apparent features, and ease of reverse-engineering, it would likely fall into the transparent category. The imitation hypothesis specifies that details of behavior that allow improvement are lost in the absence of observation. If there is a behavioral script available to be activated, however, there is little reason to expect that learners would require observation of the details of a demonstration to produce improvements. It is also important to recognize that an end-product pathway for action transmission, even with transparent products, would not permit improvements to techniques, such as increases in efficiency, that do not leave an observable trace on end products. For cumulative cultural evolution based solely on behavior, as for the replication of highly opaque end products, imitation is required.

Acknowledgments This material is based on work supported by the National Science Foundation under Grant No. 096213. Several individuals provided helpful comments on earlier drafts: I am grateful for the help of Lee Cronk, Steve Buyske, Alex Mesoudi, Sarah Wise, and members of the Evolution, Psychology, and Culture group. Two anonymous reviewers also provided useful comments. Finally, I thank the research assistants and research participants for their help.

References

Acerbi, A., Tennie, C., & Nunn, C. L. (2011). Modeling imitation and emulation in constrained search spaces. *Learning & Behavior, 39*, 104–114.

Acerbi, A., Jacquet, P. O., & Tennie, C. (2012). Behavioral constraints and the evolution of faithful social learning. *Current Zoology, 58*, 307–318.

Bonnie, K. E., Horner, V., Whiten, A., & de Waal, F. B. (2007). Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proceedings of the Royal Society of London B: Biological Sciences, 274*, 367–372.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.

Boyd, R., & Richerson, P. J. (1995). Why does culture increase human adaptability? *Ethology and Sociobiology, 16*, 125–143.

Boyd, R., & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy, 88*, 77–93.

Byrne, R. W. (2002). Imitation of novel complex actions: what does the evidence from animals mean? *Advances in the Study of Behaviour, 31*, 77–105.

Caldwell, C. A., & Millen, A. E. (2008). Experimental models for testing hypotheses about cumulative cultural evolution. *Evolution and Human Behavior, 29*, 165–171.

Caldwell, C. A., & Millen, A. E. (2009). Social learning mechanisms and cumulative cultural evolution: is imitation necessary? *Psychological Science, 20*, 1478–1483.

Caldwell, C. A., Schillinger, K., Evans, C. L., & Hopper, L. M. (2012). End state copying by humans (*Homo sapiens*): implications for a comparative perspective on cumulative culture. *Journal of Comparative Psychology, 126*, 161–169.

Call, J., & Carpenter, M. (2002). Three sources of information in social learning. In C. L. Nehaniv & K. Dautenhahn (Eds.), *Imitation in animals and artifacts* (pp. 211–228). Cambridge: MIT Press.

Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Animal Cognition, 8*, 151–163.

Claidière, N., & Sperber, D. (2010). Imitation explains the propagation, not the stability of animal culture. *Proceedings of the Royal Society of London B: Biological Sciences, 277*, 651–659.

Custance, D. M., Whiten, A., & Fredman, T. (1999). Social learning of artificial fruit processing in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 113*, 13–23.

Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science, 335*, 1114–1118.

Derex, M., Godelle, B., & Raymond, M. (2013). Social learners require process information to outperform individual learners. *Evolution, 67*, 688–697.

Enquist, M., Strimling, P., Eriksson, K., Laland, K., & Sjostrand, J. (2010). One cultural parent makes no culture. *Animal Behaviour, 79*, 1353–1362.

Franz, M., & Matthews, L. J. (2010). Social enhancement can create adaptive, arbitrary and maladaptive cultural traditions. *Proceedings of the Royal Society B: Biological Sciences, 277*(1698), 3363–3372. doi: 10.1098/rspb.2010.0705.

Galef, B. G. (1988). Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In T. R. Zentall & B. G. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 3–28). Hillsdale: Lawrence Erlbaum Associates.

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: empirical studies and theoretical models. *Bioscience, 55*, 489–499.

Gergely, G., & Csibra, G. (2005). The social construction of the cultural mind: imitative learning as a mechanism of human pedagogy. *Interaction Studies, 6*, 463–481.

Gergely, G., & Csibra, G. (2006). Sylvia's recipe: The role of imitation and pedagogy in the transmission of cultural knowledge. In N. J. Enfield, & S. C. Levinson (Eds.), *Roots of human sociality: Culture, cognition and interaction* (pp 229–255). New York: Berg.

Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton Mifflin.

Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour, 46*, 999–1010.

Hopper, L. M. (2010). 'Ghost' experiments and the dissection of social learning in humans and animals. *Biological Reviews, 85*, 685–701.

Hopper, L. M., Spiteri, A., Lambeth, S. P., Schapiro, S. J., Horner, V., & Whiten, A. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour, 73*, 1021–1032.

Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2008). Observational learning in chimpanzees and children studied through 'ghost' conditions. *Proceedings of the Royal Society of London B: Biological Sciences, 275*, 835–840.

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition, 8*, 164–181.

Horner, V., Whiten, A., Flynn, E., & de Waal, F. B. M. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 13878–13883.

Jacquet, P. O., Tessari, A., Binkofski, F., & Borghi, A. M. (2012). Can object affordances impact on human social learning of tool use? *Behavioral and Brain Sciences, 35*, 227–228.
Laland, K. N. (2004). Social learning strategies. *Learning & Behavior, 32*, 4–14.
Laland, K. N., & Hoppitt, W. J. E. (2003). Do animals have culture? *Evolutionary Anthropology, 12*, 150–159.
Lewis, H. M., & Laland, K. N. (2012). Transmission fidelity is the key to the build-up of cumulative culture. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 367*, 2171–2180.
Matthews, L. J., Paukner, A., & Suomi, S. J. (2010). Can traditions emerge from the interaction of stimulus enhancement and reinforcement learning? An experimental model. *American Anthropologist, 112*, 257–269.
Mesoudi, A., & Whiten, A. (2008). Review. The multiple roles of cultural transmission experiments in understanding human cultural evolution. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 363*, 3489–3501.
Mithen, S. J. (1996). *The prehistory of the mind: A search for the origins of art, religion, and science*. London: Thames and Hudson.
Nagell, K., Olguin, R. S., & Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology, 107*, 174–186.
Nakahashi, W. (2013). Evolution of improvement and cumulative culture. *Theoretical Population Biology, 83*, 30–38.
Page, E. B. (1963). Ordered hypotheses for multiple treatments: a significance test for linear ranks. *Journal of the American Statistical Association, 58*, 216–230.
Rendell, L., Fogarty, L., Hoppitt, W. J., Morgan, T. J., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences, 15*, 68–76.
Shipton, C. (2010). Imitation and shared intentionality in the Acheulean. *Cambridge Archaeological Journal, 20*, 197–210.
Spence, K. W. (1937). Experimental studies of learning and higher mental processes in infra-human primates. *Psychological Bulletin, 34*, 806–850.
Tennie, C., Call, J., & Tomasello, M. (2006). Push or pull: imitation vs. emulation in great apes and human children. *Ethology, 112*, 1159–1169.
Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 364*, 2405–2415.
Tennie, C., Call, J., & Tomasello, M. (2010a). Evidence for emulation in chimpanzees in social settings using the floating peanut task. *PLoS One, 5*, e10544.
Tennie, C., Greve, K., Gretscher, H., & Call, J. (2010b). Two-year-old children copy more reliably and more often than nonhuman great apes in multiple observational learning tasks. *Primates, 51*, 337–351.
Tennie, C., Call, J., & Tomasello, M. (2012). Untrained chimpanzees (*Pan troglodytes schweinfurthii*) fail to imitate novel actions. *PLoS One, 7*, e41548.
Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge: Harvard University Press.
Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences, 16*, 495–552.
Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 366*, 997–1007.
Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In P. J. B. Slater, J. S. Rosenblatt, C. Beer, & M. Milinski (Eds.), *Advances in the study of behaviour* (pp. 239–283). New York: Academic.
Whiten, A., Horner, V., Litchfield, C. A., & Marshall-Pescini, S. (2004). How do apes ape? *Learning & Behavior, 32*, 36–52.
Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature, 437*, 737–740.
Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J., et al. (2007). Transmission of multiple traditions within and between chimpanzee groups. *Current Biology, 17*, 1038–1043.
Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 364*, 2417–2428.

Helen Wasielewski earned her doctorate in anthropology at Rutgers University in 2012. She is currently a visiting research scholar at Rutgers University in the Department of Anthropology. Her current interests include cultural transmission, research design, and biocultural approaches to health.