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Social Learning Cast in Stones

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ABSTRACT—Sixty years ago, the notion that animals could have culture was unthinkable to most behavioral scientists. Today, evidence for innovation, transmission, acquisition, long-term maintenance, and intergroup variation of behavior exists throughout the animal kingdom. What can the longitudinal and comparative study of monkeys handling stones tell us about how culture evolved in humans? Now in its 30th year, the systematic study of stone-handling behavior in multiple troops of Japanese macaques has shown that socially mediated learning is essential to explain the spread, persistence, and transformation of individual behavioral innovations among group members. The integrative research paradigm presented here can be applied to the study of various candidate behavioral traditions in other species.

KEYWORDS—solitary object play; socially biased learning; development; behavioral tradition; cultural zones

The concept of culture (also referred to as behavioral tradition) in animals was first proposed in 1952 by the founder of primatology in Japan, Kinji Imanishi, who predicted that culture should be present in all socially living animals. The first evidence for culture in primates came shortly thereafter from field research on Japanese macaques. The innovation by the juvenile female "Imo," for washing sandy sweet potatoes in seawater, and the behavior's subsequent transmission widely within the group (Kawai, 1965), is now a frequently cited example for social learning and culture in animals.

Evidence now exists for socially mediated learning and culture in many species including the great apes, New World monkeys, rats, cetaceans, birds, and fish (see Fragaszy & Perry, 2003). All of these studies have looked at determinants of cultural behavior, including innovation, transmission, acquisition, developmental constraints thereof, long-term maintenance, and intergroup variation. However, none have considered the role of all of these factors within an integrated framework of social learning.

There are two basic approaches to the study of social learning. The first focuses on underlying mechanisms—that is, *how* the information is transferred between two individuals. In a controlled experimental setting, a naïve subject, faced with a problem-solving task, is given the opportunity to observe an experienced subject and learn from its behavioral strategies (Custance, Whiten, & Fredman, 1999). The second approach focuses on the pathway of behavioral diffusion under natural conditions in a stable social group—that is, *from whom* the information is transferred (Biro, Inoue-Nakamura, Yamakoshi, Sousa, & Matsuzawa, 2003). Interindividual tolerance allowing spatial proximity, frequency of the behavior performed, and the attention paid to the behavior are essential factors to predict the speed of diffusion of a novel behavior and pathway of transmission (Coussi-Korbel & Fragaszy, 1995; Huffman & Hirata, 2003; van Schaik, Fox, & Fechtman, 2003). However, not only social, but also environmental, demographic, and developmental constraints can affect the efficiency and speed of acquisition and diffusion of a particular behavior (Huffman & Hirata, 2003). Only the study of stone handling (SH) in Japanese macaques has embraced all of these determinants into the understanding of a single cultural behavior. Our long-term study supports the idea of SH culture and provides insights into the nature of social learning, its role in the spread of behavioral innovations, and the importance of culture in the process of behavioral evolution.

SH is a seemingly nonadaptive, solitary object-play activity (Huffman, 1984,

1996; but see Nahallage & Huffman, 2007a). SH consists of manipulation of stones in various ways, including rubbing or clacking them together; pounding them onto other hard surfaces; picking up and rolling them together in the hands; and cuddling, carrying, pushing, or throwing them (Fig. 1; Box 1). Currently, 45 different behavioral patterns are documented in Japanese macaques (Leca, Gunst, & Huffman, 2007a).

SH occurs in four captive troops and six provisioned free-ranging troops across Japan. This behavior has been followed for 30 years across multiple generations in the Arashiyama troop, Kyoto, Japan, beginning from its innovation in 1979 by a juvenile female named "Glance 6476" (Huffman, 1984; Huffman, 1996). Unlike potato washing, SH was first transmitted horizontally among playmates. Transmission began to occur vertically from elder to younger individuals around 1984. Since then, SH has been acquired by every infant in the group, but it was never acquired by individuals over 5 years of age in the years right after the behavioral innovation.

ACCESS TO DEMONSTRATORS BY NAÏVE INDIVIDUALS AND THE ACQUISITION OF BEHAVIORS

This long-term study at Arashiyama allows us to understand the pathways of diffusion of SH. Mothers were presumed to be the primary source of an infant's early exposure to SH (Huffman, 1984, 1996). Through controlled captive conditions, we were able to systematically evaluate the effect of pivotal individuals as demonstrators on the initial acquisition and development of SH behavior by focusing on interindividual interactions, particularly mother–infant pairs. We (Nahallage & Huffman, 2007b) studied a group of 48 Japanese macaques at the Primate Research Institute, Kyoto University, for 24 months spanning two breeding seasons over a 3-year period, during which 14 infants were born. In these 14 mother–infant pairs, all but one infant started SH within the first 6 months after birth. There was great variability among them in the age SH was first displayed (6–31 weeks). During their first 3 months of life, infants spent 75% of the time within 1 meter of their mother, significantly more time than they spent with other individuals. This high level of proximity to the mother had a significant impact on the age at which SH was acquired. Infants of mothers with higher SH frequencies exhibited the behavior earlier than did infants of less frequent SH mothers. Two infants born in consecutive years to the same non-SH mother were the last to acquire the behavior. These results suggest that the acquisition of SH behavior in infants was strongly influenced by the amount of time spent in proximity to a stone handler and the frequency of the behavior displayed by that model. Infants of frequent SH mothers spent twice as much time (83%)

watching their mothers when she engaged in that behavior than did infants whose mother showed low SH frequency (42%). The former tried to take stones away from their mothers in 75% of the SH bouts whereas the latter tried to do so in only 33% of these bouts, resulting in a difference in the amount of time an infant took part in its mother's activity. Differences in mothers' SH frequency could affect their infants' exposure to SH, opportunities of handling stones, and practice of SH. We interpret this as evidence of learning by stimulus enhancement (when attention is drawn to a specific object via the actions of others).

FACTORS RESPONSIBLE FOR INTERGROUP VARIATION

To better understand how the SH culture in Japanese macaques may appear, spread, and be maintained within a group over generations, we (Leca, Gunst, & Huffman, 2007a) investigated the roles of social and demographic factors in explaining intergroup similarities and differences in SH. We conducted a systematic comparison of SH in 10 troops of Japanese macaques, including two troops studied over a long period of time at Arashiyama and Takasakiyama. The analysis of 1,950 hours of observation revealed substantial variability in the frequency and form of SH between the troops. Most of the 45 SH patterns we documented were customary in some troops and rare or even absent in others even though they were ecologically possible (Leca, Gunst, & Huffman, 2008).

When we only considered the 33 SH patterns that were not observed in all 10 troops studied, we found cultural similarity to be significantly related to geographic proximity. Neighboring troops living at the same site, with overlapping home ranges and coming into occasional contact around the provisioning site—where SH activity most often occurs—tended to share similar SH patterns. The numbers of patterns showing the same occurrence in the two troops at Shodoshima and in the two troops at Takasakiyama were 26 and 25, out of 33, respectively. We propose the phenomenon of cultural zones, based on intertroop observation and possibly males transferring SH patterns when migrating from one troop to another. When such intertroop social influences do not exist (e.g., troops separated by substantial geographic distance in natural situations or by artificial barriers like concrete walls in captive conditions), the troops showed more differences in their SH repertoires: Their mean number of behaviors showing the same frequency of occurrence was only 12.1 ± 7.3.

To test the hypothesis that SH will be more prevalent in more cohesive groups, we calculated, for the 10 study troops, a group-level index of social tolerance, defined as the mean percentage of group members within 1 meter of each other, and recorded every 15

minutes by the observer visually or physically moving from one side of the troop to the other, in a set direction. Group level social tolerance was not significantly correlated with the frequency and rate of diffusion of SH (Leca, unpublished data). In other words, the troops showing higher levels of positive social interactions (e.g., grooming and playing) were not necessarily the troops with more frequent episodes of SH and higher percentages of stone handlers. Instead, group size and group spatial cohesion after food provisioning was positively correlated with the prevalence of SH. Larger troops characterized by closer physical proximity among individuals feeding on provisioned food also showed higher percentages of troop members exhibiting SH simultaneously, which may reveal the contagious nature of play (Leca, Gunst, & Huffman, 2007b).

Another demographic factor, age structure of the group, may also affect the diffusion and maintenance of SH. Troops with abnormal age structure (e.g., missing age classes) showed a lower proportion of stone handlers and a lower frequency of SH than did more normally age-structured groups (Leca, Gunst, & Huffman, 2007b). These findings are consistent with long-term observations at Arashiyama suggesting that (a) after initial innovation by youngsters, SH behavior first spreads among young individuals, probably peer playmates; (b) there is a critical period after which SH cannot be acquired by an individual (> 5 years); and (c) when a behavioral practice is restricted to a particular class of group members, its propagation should be slow and its maintenance may be jeopardized (Huffman, 1996).

At Arashiyama and Takasakiyama, the SH culture has at least a 30-year history. By using similar methods of data collection in these troops, 13 and 15 years apart, respectively, we found that the size of the SH repertoire almost doubled in both troops. The SH patterns not recorded before involved complex manipulative actions, such as combining stones with other objects and grooming with a stone (Leca, Gunst, & Huffman, 2007a). These longitudinal data suggest a "ratchet effect," defined as an increase in the diversity and complexity of SH patterns compared to earlier generations of stone handlers. As the duration of a group's experience with SH increases, so does the variety of patterns displayed, possibly as a product of an increase in the number of "individual contributions" to the group's behavioral repertoire, which gradually diffuse through the group (e.g., shake-in-hands and stone-throwing patterns in the Takahama group).

Our comparative approach revealed that intergroup variability in SH may be best explained by demographic factors, opportunities for observational learning, and behavioral coordination at the group level.

CONSTRAINTS OF NEUROMOTOR DEVELOPMENT ON THE EXPRESSION OF SH BEHAVIORS

Few longitudinal studies have been conducted on the ontogeny of specific cultural behaviors; most research has tended to deduce development from cross-sectional observations (Lonsdorf, 2005). Furthermore, neuromotor development has rarely been considered as a constraint in the expression of matched behavioral patterns between experienced and naïve individuals. Our study shows that, though mothers have a strong influence on infants' initial acquisition of SH behavior, infants do not perform the same behavioral patterns as adults, mainly because of developmental constraints in the kinds of behaviors they can perform (Nahallage & Huffman, 2007b). There is a gradual increase in the number and complexity of SH patterns displayed by infants, which reveals a neuromotor developmental phase of this behavior. The infants we studied acquired the basic SH behaviors at around 2 to 3 months. Common to other behavioral traits observed during the early stages of infant development in macaques, stone-manipulation patterns are simple actions—mainly, picking them up or cuddling, licking, or biting them. Such actions are typically short in duration. Infants do not perform any complex manipulative action with stones during this time. The average number of patterns performed by an individual up to 6 months of age was 3.75 ± 1.90. Around 6 months, individuals started to perform clacking or rubbing two stones together or on a substrate. On average, they displayed 8.85 ± 2.26 patterns from 6 to 12 months of age. The earliest sign of relative independent finger movement occurs at 2 to 3 months, with mature patterns occurring at 7 to 8 months (Bortoff & Strick, 1993). Galea and Darian-Smith (1995) reported that performance on a reach-and-grasp test by a group of young macaques approached adult levels by 6 months. This agrees with our study showing infants starting with only the very basic SH behaviors between 2 and 3 months and performing activities that requires firm grasp of the stones around 6 months. Though the motoneuronal projections responsible for finger movement develop rapidly in the first months after birth, they do not mature until the second year of life. This explains the increase in the number of SH patterns up to 3 to 4 years of age. Older juveniles displayed the highest number of patterns among all age classes (18.14 ± 5.38), whereas the number of patterns displayed decreased into adulthood, which may reveal the appearance of individual preferences or behavioral routines over the years (Nahallage & Huffman, 2007b).

We concluded that at the time of acquisition, infants acquire a rudimentary form of SH but are constrained from matching specific behaviors due to their level of

neuromotor development. Our findings support juvenile-primate developmental theories (Pereira & Fairbanks, 1993). Later on, however, this kind of matching does appear to occur, and is noticeable particularly in rare behaviors displayed by the mother, which are now being seen to diffuse among offspring and others.

FUTURE DIRECTIONS

SH is one of the longest-studied cultural behaviors in animals to date. Research on this behavior in both captive and free-ranging groups of monkeys has opened up new ways of addressing the complexities of learning in socially living animals through a deeper understanding of the dynamics of behavioral transmission. In order to understand the mechanisms associated with socially biased learning, future studies need to integrate this methodology with controlled experimentation on captive groups. This will allow us to more clearly address behavioral innovation and the underlying mechanism of diffusion within social groups.

Object manipulation provides a pool of behavioral variants that, if fortuitously reinforced, can become tool-use patterns. Long-term observations and documentation of the transformation of behavioral patterns are important to fully appreciate the potential transformation of noninstrumental use of objects into their instrumental use as tools. Longitudinal studies of SH already suggest that this could happen. The recent emergence of a unique behavior, stone-throwing, may serve to augment the effect of intimidation displays. Research on such transformations may shed light on the evolution of stone-tool use in early hominids.

Recommended Reading

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Huffman, M.A. (1984). (See References). The first detailed published account of SH in Japanese macaques.

Moscovice, L.R., & Snowdon, C.T. (2006). The role of social context and individual experience in novel task acquisition in cottontop tamarins, *Saguinus oedipus*. *Animal Behaviour*, *71*, 933–943. Recent research article detailing the role of social attention in the acquisition of behaviors, of interest to those contemplating social-learning studies.

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Fig. 1. Four stone-handling behaviors: (a) carry, (b) clacking, (c) rub on surface, and (d) rub together.

Box 1.

Representative Stone-Handling Behaviors

MP (Move and Push): Push/pull a stone forward/backward with one or both hands while working

GW (Grasp Walk): Walk with one stone or more in the palm of one or both hands

CA (Carry): Carry a stone cuddled in one's hand from one place to another

GA (Gathering): Gather stones into a pile in front of oneself

ROS (Rub on Surface): Rub or roll a stone on a surface

RT (Rub Together): Rub stones together

RWH (Rub with Hands): Hold a stone in one hand and rub it with the other

SC (Scatter): Scatter stones about, on a substrate, in front of oneself

CL (Clacking): Clack stones together (both hands moving in a clapping gesture)

FL (Flinting): Strike a stone against another held stationary

POS (Pound on a surface): Pound a stone on a substrate