



Stone-throwing by Japanese macaques: form and functional aspects of a group-specific behavioral tradition

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ABSTRACT

Throwing is a major behavioral component of hominid evolution. Comparison of this behavior across a broad range of non-human primate species is needed to elucidate the phylogenetic constraints on throwing behavior. In this study of stone-throwing in Japanese macaques, we present a systematic multi-group comparison of the frequency and prevalence of this behavior as well as detailed descriptions and quantitative data on the form, context, and possible social transmission of stone-throwing. Stone-throws were mainly underarm, performed from a tripod posture, and often accompanied by repeated vertical leaps. We found marked individual hand preferences for throwing, but no consistent group-level handedness. Our results support the hypotheses relating body posture, throwing style, and handedness in throwing by primates. Based on the analysis of the contexts that may elicit the behavior, we postulate that unaimed stone-throwing in Japanese macaques may serve to augment the effect of agonistic displays, and accordingly, can be regarded as spontaneous tool-use. Our findings are consistent with the comparative data using modern non-human primate species to model the structural processes and functional aspects of throwing evolution in early hominids. This study supports the view that tool-use evolves from initially non-functional behaviors, such as stone handling, which is a form of object play. Stone-throwing by Japanese macaques meets several criteria of a behavioral tradition, including group-specificity. This first report of a stone-tool-use tradition in Japanese macaques is of direct relevance to the question of the evolution of stone technology in hominids.

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Introduction

Throwing is considered a major behavioral component of human evolution. There is little doubt that the emergence of throwing behavior had important socio-ecological and neuro-cognitive effects during all stages of hominid evolution (Darlington, 1975). First, the ability to project objects with force, velocity, and accuracy probably provided our prehistoric primate ancestors with numerous advantages, such as greater hunting and offensive success, better defense against predators and rivals, and the possibility to cooperate through food-sharing by transferring food items thrown within and between social groups (Dennell, 1997; Westergaard et al., 1998; Watson, 2001). Second, throwing is predominantly a one-handed sequential-movement operation exposed to selection pressures in the natural environment of early hominids. Throwing constraints may have contributed to the pre-adaptation of their growing brain and changing body to a variety of traits,

including handedness, bipedalism, and complex language processing (Calvin, 1983; Fifer, 1987; Hopkins et al., 1993; Churchill and Schmitt, 2002; Schmitt et al., 2003).

Due to their physical properties and ubiquity, stones are likely to have been the first effective and ready-to-use missile-weapons for our primate ancestors (Fifer, 1987; Isaac, 1987). Unfortunately, archeological evidence for the evolution of stone-throwing behavior in hominids is rare: fossil forelimb bones are rare and unlike most other stone-tools, thrown stones were presumably scattered away from body parts (Darlington, 1975; but see Leakey, 1948). Although the cognitive processes which underlay the throwing behavior in humans are more complex than those which underlay the throwing behavior in monkeys and apes, models of early hominid throwing behavior can be tested by a comparative approach using modern non-human primate species (Calvin, 1983; Westergaard and Suomi, 1995; Cleveland et al., 2003).

From the structural viewpoint, several hypotheses have been proposed to relate skeletal modifications, body posture, throwing style, and handedness in throwing (Calvin, 1983; Fifer, 1987; Knüsel, 1992; Hopkins et al., 2005). As opposed to monkeys that exhibit underarm throwing from a tripod posture, the ability for chimpanzees, bonobos, and humans to perform overarm throws by

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maintaining a bipedal stance may be due to similar structures of hip and shoulder joints (Beck, 1980; Calvin, 1983; Savage-Rumbaugh et al., 2001). This distinction in throwing style and posture plays a crucial role in the explanation of the prevalence of right-handedness observed in human populations (Annett, 2002), whereas chimpanzees and capuchin monkeys did not show clear hand preference for throwing at the group level (Westergaard et al., 2000; McGrew and Marchant, 2001; but see Hopkins et al., 2005). Regarding functional aspects, Calvin (1993) hypothesized that predatory or defensive-aimed stone-throwing by early hominids (defined as the goal-directed projection of stones toward an identifiable target: Westergaard and Suomi, 1994) emerged from unaimed or non-directional throwing of objects, similar to that which has been observed in non-human primates as part of agonistic displays (Beck, 1980).

Therefore, research examining the form, context, and learning of stone-throwing in various non-human primate species, including throwing posture, handedness, direction, and distance, description of the thrown stones, and assessment of the situations that may elicit the performance and social transmission of throwing, can provide vital insight into the biological basis and evolution of stone-throwing in humans (Fifer, 1987; Westergaard et al., 2000; Hopkins et al., 2005). A variety of monkeys and apes living in natural and captive conditions, particularly capuchins (*Cebus* spp.), baboons (*Papio* spp.), macaques (*Macaca* spp.), and chimpanzees (*Pan* spp.), were reported to perform aimed and unaimed stone-throwing, either spontaneously or in problem-solving tasks (e.g., Goodall, 1964; Hamilton et al., 1975; Tokida et al., 1994; Westergaard et al., 2000).

However, with respect to spontaneous stone-throwing in non-human primates, we lack detailed descriptions and quantitative data on the form, context, and learning of the behavior, systematically collected and based on long-term observations of multiple social groups of various species across the primate order. There are at least four reasons for this lack of information: 1) most reports on this behavior are based on interviews of primate keepers in zoos or anecdotal accounts relayed from anonymous travelers encountering wild primates (Hall, 1963; Kortlandt and Kooij, 1963; Beck, 1980); 2) the performance of stone-throwing in non-human primates is uncommon (Torigoe, 1985); 3) throwing behavior is generally exhibited by one individual or at the most a few group members, depending on their age/sex class or social status, mostly dominant adult males, although this is more inferred from incomplete evidence than significant correlations (e.g., Schaller, 1963; Goodall, 1964; Struhsaker, 1975; Nishida et al., 1999); and 4) stone-throwing has been reported most frequently in primate species that use tools in other contexts, namely capuchins and chimpanzees (Beck, 1980; Torigoe, 1985).

The genus *Macaca* is the most widely distributed of non-human primates. Its 20 extant species feature a broad diversity of social relationships, and present a variety of morphological and behavioral adaptations to different environments that make this taxon of particular interest for research on evolutionary biology and ecology (Fa and Lindburg, 1996; Thierry et al., 2004). However, macaques are not frequent tool-users and are not considered frequent stone-throwers (Beck, 1980; Torigoe, 1985). More data are needed to provide a broader inter-species comparison and to elucidate the phylogenetic constraints on throwing behavior. Any further information on stone-throwing (or lack thereof) in macaques is of interest to the debate surrounding the evolution of this behavior in humans.

Stone-throwing in Japanese macaques has recently been listed as one of the numerous behavioral patterns of the stone handling (SH) repertoire of this species (Leca et al., 2007a,b; Nahallage and Huffman, 2007a). Defined as seemingly-playful stone-directed manipulative actions, SH is considered a traditional behavior, socially

transmitted between same-age partners, such as peer playmates and across generations from mother to offspring (Huffman, 1984, 1996; Huffman and Quiatt, 1986; Nahallage and Huffman, 2007b). We found major inter-group differences in the frequency of occurrence and the prevalence of SH patterns, with local variants being customary in some troops, and rare or even absent in others, performed by a majority of individuals in some troops, and only idiosyncratically in others (Leca et al., 2007a,b).

Although showing inter-group differences is not sufficient evidence for culture, the “group-contrast” method has often been used as a first step to identify candidates for cultural behaviors, particularly in primate stone-tool cultures (e.g., Whiten et al., 1999). However, data on the rate and form of stone-throwing behavior in different troops within the same monkey species have not been reported in the literature so far (but see Leca et al., 2007a for general data). From a functional viewpoint, the current SH patterns observed in Japanese macaques are regarded as a non-instrumental manipulation of stones with no obvious survival value (Huffman, 1984, but see Nahallage and Huffman, 2007a for a possible ultimate function of SH). However, Huffman (1996) suggested that if SH persists sufficiently in a given troop, direct material benefits may be acquired in the future, provided some modifications of the behavioral patterns or the direct integration of SH with foraging activities (e.g., stone-tool-use) or social interactions (e.g., agonistic display) (Huffman and Quiatt, 1986; Huffman and Hirata, 2003; Leca et al., 2008a). Since stone-throwing is considered tool-use according to Beck's (1980) definition, this particular SH pattern is a strong candidate for such transformations. From this perspective, Japanese macaques could be used as a non-human primate model for processes that contributed to the evolution of stone-throwing in early hominids.

In an effort to encourage the compilation of relevant data on stone-throwing in non-human primate species and stimulate general interest in the evolution of hominid throwing behavior, this paper will address the following questions: When Japanese macaques throw stones, do they perform an overarm action? Do they stand bipedally? Do they show hand preference? Do they throw from an elevated position? How far do they throw? Do they select particular stones? Do they aim or do they throw at random as part of a display sequence? Does stone-throwing occur in all troops or is it a group-specific behavioral practice? Is there evidence for social transmission of this behavior among group members? Can stone-throwing in Japanese macaques be referred to as a behavioral tradition?

In this study of stone-throwing in Japanese macaques, we aim to: 1) present a systematic multi-group comparison of the frequency and prevalence of this behavior; 2) provide further descriptive and quantitative data on the form of stone-throwing, including motor patterns, postures, handedness, throwing location, direction, and distance, as well as the number and size of stones thrown; 3) document the contexts of occurrence of stone-throwing events and propose functional explanations for this behavior; and 4) investigate the channels and modes of intra-group diffusion of stone-throwing with regards to age, sex, and dominance classes.

Materials and methods

Subjects and study conditions

We observed a total of 10 troops of Japanese macaques (*Macaca fuscata*) at six geographically isolated sites in Japan (Table 1). Captive troops were supplied with commercial primate pellets, vegetables, or fruits. Free-ranging troop members gathered regularly around feeding sites where they were artificially provisioned with cereal grains by the staff technicians of the Koshima Field Station, Kyoto University (Kosh.) or by the staff members and managers of monkey

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