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Stone handling, an object play behaviour in macaques: welfare and neurological health implications of a bio-culturally driven tradition

Charmalie A.D. Nahallage^a, Jean-Baptiste Leca^b and Michael A. Huffman^{c,*}

^a Department of Sociology and Anthropology, University of Sri Jayawardenepura,
Nugegoda, Sri Lanka

^b Department of Psychology, University of Lethbridge, 4401 University Drive W,
Lethbridge, AB, Canada T1K 6T5

^c Department of Ecology and Social Behavior, Primate Research Institute, Kyoto University,
41-2 Kanrin, Inuyama, Aichi 484, Japan

* Corresponding author's e-mail address: huffman.michael.8n@kyoto-u.ac.jp

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Abstract

Object play in primates is viewed as generally having no immediate functional purpose, limited for the most part to immature individuals. At the proximate level, the occurrence of object play in immatures is regarded as being intrinsically self-rewarding, with the ultimate function of supporting motoneuronal development and the acquisition of skills necessary to prepare them for survival as adults. Stone handling (SH), a solitary object play behaviour occurs, and has been studied, in multiple free-ranging and captive troops of provisioned Japanese macaques, as well as rhesus and long-tailed macaques for over 35 years now. A review of our combined findings from these observations reveal that infants acquire SH in the first 3-4 months of life and exhibit increasingly more complex and varied behavioural patterns with age. The longitudinal data shows that many individuals maintain this activity throughout life, practicing it under relaxed ecological and social conditions. The ultimate function may be bimodal, promoting motor development in young and neural maintenance and regeneration in adult and aging individuals.

Keywords

object play, *Macaca*, behavioural tradition, self-rewarding, health, welfare, neural regeneration hypothesis.

“We don’t stop playing because we grow old;
we grow old because we stop playing.”

G. Stanley Hall, 1904

1. Introduction

Early research on play behaviour mainly explored the evolutionary origins and pathways of this seemingly functionless activity by comparing the frequency, form and context of object, social, and locomotor play across a wide range of animal taxa (Groos, 1898, 1901; Smith, 1978; Bekoff & Byers, 1981; Burghardt, 2005). Since then, studies of animal play in all its forms, conducted in the wild and in captivity, in both natural social settings and experimental conditions, have provided substantial insights into the developmental, physiological, as well as social and physical environmental correlates of the acquisition, occurrence and expression of play behaviour (e.g., Biben, 1982; Bateson et al., 1990; Bekoff, 1995; Nunes et al., 1999; Mitchell, 2002; Burghardt, 2005; Nahallage & Huffman, 2007a). As a result, research on play behaviour has branched out into several new directions, including the ontogenetic processes underlying the early expression of play during infancy and its maintenance into adulthood (Fairbanks, 2000; Göncü & Gaskins, 2007; Leca et al., 2007a, 2011; Nahallage & Huffman, 2007a; Vig, 2007), mechanisms of the brain mediating motivation to engage in play activities (Siviy, 1998; Lewis & Barton, 2006; Bell et al., 2009; Pellis et al., 2010) and the testing of a series of hypotheses pertaining to the adaptive value of play (Barber, 1991; Byers & Walker, 1995; Špinka et al., 2001; Burghardt, 2005). In this line of research, one of the most recent trends is to investigate the benefits of play activities for psychological wellbeing and neurological health (Boissy et al., 2007; Held & Špinka, 2011).

In wild animals, play behaviour is mainly limited to the young and sub-adult classes, and even among them, it does not occur as frequently as it does in domestic and captive animals (Hall, 1998). In addition to the stress induced by the presence of predators (Siviy, 2010), the relatively low levels of play in wild animals could be due to the fact that they have to spend a considerable amount of their active time foraging and moving to meet their daily subsistence needs, leaving little time for young to play, except when adult group members are stationary and resting. In support of this view, it is acknowledged that play is more common in domestic pets and

captive animals because they have plenty of free time. Since their caretakers fulfill their two most important demands, food and protection, threats to their survival are relatively low, and as a result, animals living in captive settings tend to allocate this extra time to play and other sedentary social activities (e.g., Lawrence, 1987; Pellis, 1991; Fraser & Duncan, 1998; Špinka et al., 2001; Palagi et al., 2004; Dawkins, 2006; Held & Špinka, 2011).

Any species' behavioural repertoire can be greatly influenced by the environment it inhabits (e.g., Burghardt, 2005; Jaman & Huffman, 2008; Nahallage & Huffman, 2008a). In order to overcome gradual or sudden environmental changes and to adapt successfully to new environments, animals can innovate and generate new behavioural variants within the range of their behavioural predispositions (Kummer & Goodall, 1985; Thierry, 1994; Huffman & Hirata, 2003). This new information can then be disseminated within the group through social networks (Scheurer & Thierry, 1985; Hauser, 1988), between groups through migrating individuals (McGrew & Collins, 1985) or through the fission of groups (Burton & Bick, 1972). The rate, speed, and pattern of diffusion of behavioural innovations depend upon ecological, demographic, social and behavioural factors, and may result in group-specific behavioural traditions that are maintained over generations (e.g., Huffman & Hirata, 2003).

In order for a behavioural innovation to emerge and become fixed in the repertoire of a group, the risks associated with the performance of the new behaviour should be lower than the incurred benefits in terms of social prestige, survival rate, or reproductive success. Many behavioural innovations reported in animals to date have been related to subsistence (e.g., acquisition of novel food sources, or food processing techniques; Huffman & Hirata, 2003). While the benefits of other behavioural traditions may not seem obvious (e.g., object play culture: Huffman, 1984; non-conceptive sex culture: Leca et al., 2014), they are nonetheless sometimes incorporated into the behavioural repertoire of a group (Leca, 2015).

In ethology, perhaps one of the most easily recognizable yet difficult behaviours to explain is object play. Object play can be defined as a divertive interaction with an inanimate object that includes exploratory manipulation (Hall, 1998). Whereas social play is most likely to occur when individuals appear to be relaxed and free from social stress, hence the use of social play as an indicator of animal welfare (see Burghardt, 2005), it is still unclear whether object play can also be used as a behavioural measure to assess

an individual's psychological well-being. Does object play have short-term benefits, like the reduction of stress? Are their possible long-term biological benefits to object play behaviour that could explain why, in some species, individuals continue this practice well into old age, far past the time play behaviour in most species other than humans cease to be performed? Following the work by Held & Špinka (2011) on play and welfare, we address these questions by reviewing the results of our combined 35 years of research on stone handling (SH) behaviour, focusing on (1) the developmental processes underlying its acquisition, (2) the environmental correlates of its expression, (3) its social transmission and persistence into old age and (4) the potential biological benefits of this solitary object play behaviour in macaques and its value in helping to predict the individual state of well-being.

2. Stone handling behaviour across macaque species and age classes

SH is defined as the repetitive non-instrumental manipulation of stones in different ways (e.g., Gather, Pick up, Scatter, etc.), by young and adult macaques and in that sense, is considered as a form of object play. SH by provisioned free-ranging Japanese macaques (*Macaca fuscata*) was first briefly reported in the Takagoyama troop by Hiraiwa (1975). It was later described in detail in the Arashiyama and Takasakiyama populations and defined by Huffman (1984) as object play behaviour with no immediate functional outcome. Since then, SH has been found in some but not all captive and provisioned free-ranging troops, but has never been observed in non-provisioned wild troops of Japanese macaques (Huffman, 1996; Leca et al., 2007b; Nahallage & Huffman, 2007b; Figure 1). Interestingly, SH behaviour is not limited to Japanese macaques. It has also been reported in a captive population of rhesus macaques (*M. mulatta*; Nahallage & Huffman, 2008b, 2012), it has been observed in provisioned free-ranging Balinese long-tailed macaques (*M. fascicularis*; authors' personal observations), and preliminary evidence suggests it might also occur in captive Taiwanese macaques (*Macaca cyclopis*; H. Su & Huffman, unpublished data). All of these species belong to the *fascicularis* lineage, a taxonomic sub-group of macaques known to share a number of basic behavioural and physiological traits (Thierry, 2007). Therefore, the co-occurrence of SH behaviour across macaque species in this lineage is indicative of the phylogenetic underpinnings of this object play tradition. SH has not been observed yet in macaques outside of this taxonomic group or in any other nonhuman primate species.

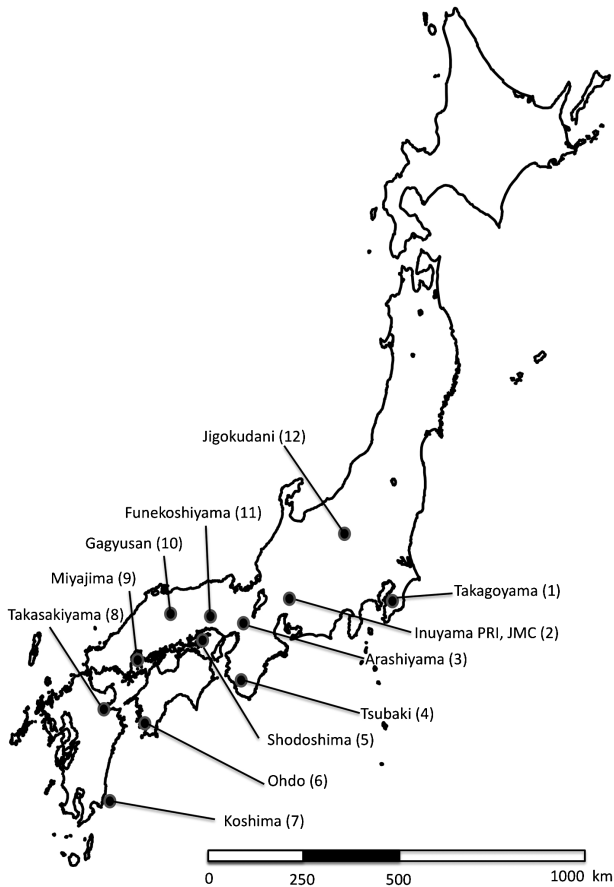


Figure 1. Stone handling troop site map in Japan. Site 2 holds a captive troop of Japanese macaques whereas provisioned free-ranging troops live at the other sites. Sources: sites 1, 3, 8, 10–12, Huffman & Hirata (2003); site 2, Nahallage & Huffman (2007a); site 4, Leca (2012); sites 5 and 7, Leca et al. (2007b); sites 6 and 9, Kunio Watanabe (personal communication).

Currently, 45 SH patterns have been identified in captive and free-ranging Japanese macaques (Leca et al., 2007b; Nahallage & Huffman, 2007b; Table 1) and 31 patterns in captive rhesus macaques (Nahallage & Huffman, 2008b, 2010). The number and type of SH behavioural patterns exhibited by different age classes vary substantially. There is a gradual increase in the number of patterns displayed from infants to juveniles, which then begins to decrease again with advanced age (Nahallage & Huffman, 2007a, b; Table 2). Most young individuals display investigative, locomotory or collecting and

Table 1.

Stone handing patterns recorded in Japanese macaques and grouped by behavioural categories.

Investigative activities	Sound producing activities
Pi (Pick)	ROS (Rub On Surface)
H (Hold)	RIH (Roll In Hand)
B (Bite)	RT (Rub Together)
L (Lick)	SC (Scatter)
SN (Sniff)	CL (Clack)
CD (Cuddle)	RWH (Rub With Hand)
PIM (Put In Mouth)	POS (Pound On Surface)
MIM (Move In Mouth)	SL (Slap)
	RWM (Rub With Mouth)
Collecting/gathering activities	RIM (Rub In Mouth)
GA (Gathering)	TIM (Tap In Mouth)
PU (Pick Up)	FL (Flint)
PUS (Pick Up a Small stone)	FP (Flip)
PUD (Pick Up and Drop)	FLM (Flint In Mouth)
GH (Grasp Hand)	
	Complex manipulative activities
Locomotor activities	WIL (Wrap In Leaf)
MP (Move and Push)	COO (Combine with Other Objects)
GW (Grasp Walk)	TH (Throw)
CA (Carry)	SGR (Stone Grooming)
CIM (Carry In Mouth)	SIH (Shake In Hand)
TW (Toss Walk)	ROF (Rub On Fur)
	W (Wash)
	PIW (Put In Water)
	SP (Spin)
	SW (Swipe)
	THS (Throw and Sway)
	TJ (Throw and Jump)
	TR (Throw and Run)

gathering patterns, which involves vigorous body movements and locomotion, typical of young developing primates (Leca et al., 2007b; Nahallage & Huffman, 2007b). Adults however mainly display sound producing patterns and other complex manipulative patterns which are mostly performed while stationary and involve complex manipulation of stones with their independent digit movements, reflecting this age group's relatively enhanced dexterity and complex sensory-motor skills (Leca et al., 2007b; Nahallage & Huffman, 2007b).

Table 2.

Summary of stone handling behavior in different age–sex categories.

	Average number of bouts/individual (SD)	Average SH bout duration (s)	Average number of patterns/individual (SD)
Young (0–4 years; $N = 24$)	15.92 (7.76)	82.29	16 (4.74)
Young adults (5–15 years; $N = 14$)	8.81 (6.50)	136.16	12 (4.60)
Older adults (16–30 years; $N = 7$)	9.57 (10.43)	273.68	10 (5.36)

As seen in other types of play (reviewed in Graham & Burghardt, 2010), the frequency of SH greatly decreases or stops all together under unfavourable environmental conditions and in periods of high social stress, resuming to normal levels again only after these conditions return to a more relaxed state (Nahallage & Huffman, 2008a, 2012). These points are consistent with the assumption that SH is influenced by developmental and other underlying biological processes, and is not a form of stereotypy.

3. Social transmission of SH

SH is arguably one of the best and longest studied behavioural traditions in non-human primates. At Arashiyama, SH behaviour initially arose from the innovation by a 3.5-year-old female, named Glance 6476. SH was then systematically recorded as it spread to similar age playmates and older immature individuals belonging to the Glance matriline (Huffman, 1984). As these individuals aged, the behaviour was transmitted to younger sibs and then their own infants when some of these female stone handlers became mothers (Huffman & Quiatt, 1986; Figure 2). Prior to 1979, and in spite of over 29 years of continuous research at Arashiyama, SH had not been observed (Huffman, 1991). Since then, SH has never been newly acquired by individuals over the age of 5 years, which is probably the critical period for the acquisition of this behaviour. The critical period of acquisition could not be confirmed in our nine other SH study sites, since SH was already wide spread across all age classes in these troops when our observations of them began. At Arashiyama as of the 2008 survey, SH was found to have spread to 93% of the troop (Leca et al., 2012). A 10-troop comparison of the SH

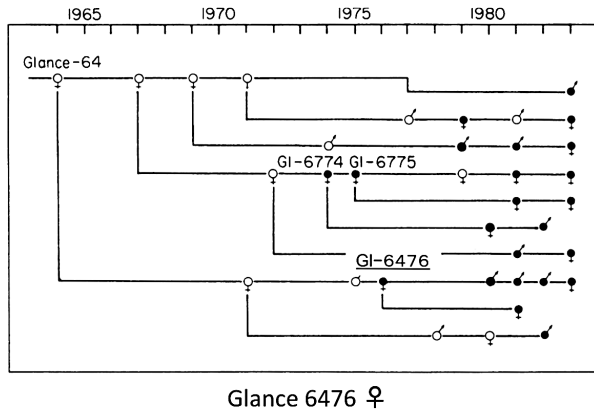


Figure 2. Initial transmission of SH behaviour from key innovator, 3.5 year-old female Glance 6476 to other kin-group members.

behaviours confirmed that SH was practiced into old age in some of these troops as well (Leca et al., 2007b), however due to management practices of the captive SH troops under study, it is not possible to introduce non-SH individuals into a SH troop to see whether or not it is possible to acquire the behaviour as adults.

Data from Arashiyama also showed that once the social diffusion of SH was established, all infants acquired SH behaviour within the first six months of life (Huffman, 1996). It was proposed that mothers were the primary route of transmission for their young during the subsequent ‘tradition phase’. Later, the process of acquisition of SH behaviour was systematically investigated in the captive Takahama troop of Japanese macaques. Acquisition of SH was demonstrated to occur between 6 weeks and 6 months after birth (Nahallage & Huffman, 2007a). With regards to the mode of acquisition of the behaviour by these young individuals, our data supported the ‘social stim-

Table 3.

Social influence of mothers on the offspring's acquisition of SH behavior.

	Mothers with high SH frequency	Mothers with low SH frequency
Average SH time/bout (s)	133 ± 57.25	73 ± 72.95
Infant watching mothers (%)	83	42
Tried to take stones (%)	75	33

uli' hypothesis, which holds that infants acquire SH by means of exposure to SH models and that thus the behaviour is socially transmitted. Our data did not support the 'environmental stimuli' hypothesis, which holds that SH acquisition is determined only by the local availability of stones and the amount of contact with them (Nahallage & Huffman, 2007a).

This study also demonstrated that proximity to an available model and the frequency of the behaviour displayed by that model played an important role in determining when SH behaviour was first exhibited by infants (Nahallage & Huffman, 2007a; Tables 3 and 4). The typical SH model for an infant was its mother, since the infant is constantly exposed to her behaviours during the critical period of its early development (Nahallage & Huffman, 2007a). This motivation for wanting to do what the mother does can be described as an 'education by master-apprenticeship relationship' (Matsuzawa et al., 2001). For example, infant chimpanzees are driven to copy their mothers' tool-assisted foraging behaviour less because they are motivated by the food to be obtained but more because it is intrinsically rewarding to copy an

Table 4.

Mother's frequency of SH and the infant's age at first observed stone handling bout.

Mother's frequency of SH bouts/h	Infant's age when SH was first performed (weeks)
0	31
0.28	18
0.47	22
0.65	12
1.3	6
2.23	6

individual with whom one shares strong affectionate bonds (see also the ‘Bonding and Identification-based Observational Learning’ model: de Waal, 2001). Perhaps in a similar way, SH is not associated with any specific goals that must be mastered, and the monkeys are eager to engage in the behaviour. When a mother displays SH behaviour frequently and for a long period of time, her infant has more opportunity to observe her than an infant whose mother does not display the behaviour as often and for a shorter period of time, or not at all (Huffman & Nahallage, 2007a). This process stems from two forms of social learning: stimulus enhancement and response facilitation.

4. Stone handling as a self-rewarding object play behaviour

While the acquisition process, as described above, is strongly influenced by others, for both Japanese and rhesus macaques, the continued practice of SH appears to be intrinsically self-rewarding. When an individual performs SH, it concentrates intensely on the stones being manipulated and often ignores conspecifics’ solicitations to engage in other activities (Nahallage & Huffman, 2012). For example, a young individual may decline an invitation for social play and adult females have been seen pushing their infants away when they disturb their SH behaviour by trying to take stones away or to suckle (Nahallage, Huffman, personal observations). On rare occasions, young adult males performing SH may even ignore sexual solicitations by oestrous females (Huffman, 1984; Leca, personal observations).

Such circumstantial evidence suggests that SH is rewarding to the individual who performs it. In this sense, SH meets Burghardt’s (2005) criteria for the definition of play. SH has no definite function and does not contribute to the immediate survival of the performer; it is not directly associated with feeding and does not appear to contribute directly to the reproductive fitness of the performer. Instead, SH appears to be an autotelic activity, i.e. ‘done for its own sake’ (Huffman, 1984).

The frequency of most play behaviours in Japanese macaques tend to decrease with age, and when the individuals enter adulthood, they usually disappear from the behavioural repertoire altogether. However, it was confirmed in at least five of our 10 study troops that SH behaviour continues to be practiced into adulthood and old age (30 years old or more) by individuals who acquired it early in life (Huffman & Quiatt, 1986; Huffman & Hirata,

2003; Nahallage & Huffman, 2007; Huffman et al., 2008, 2010; Leca et al., 2012). There are age differences in SH behaviour, and they are manifest in the frequency and duration of SH bouts. Adults perform the behaviour significantly less frequently than do younger individuals, but the mean duration of SH bouts is significantly longer than that of younger individuals (Table 2). In the free-ranging Arashiyama, Takasakiyama and captive Takahama troops of Japanese macaques, adults usually tend to have their own preferred locations to perform SH (Quiatt & Huffman, 1993; Nahallage & Huffman, 2007b). If other group members temporarily occupy these particular places, the individual generally waits nearby holding on to their stones. As soon as the preferred SH spots is vacated, the waiting individual goes there to start SH. From this perspective too, SH by young individuals is different, as they do not seem to have preferred locations to perform SH, and typically engage in short bursts of activity anywhere (Nahallage & Huffman, 2007b).

5. Possible benefits related to the performance of SH behaviour

The fact that SH is a form of solitary object play, acquired at a very early age and maintained throughout life, begs for an explanation of the possible age-dependent and context-dependent motivations, proximate mechanisms and ultimate functions of such a behaviour.

Currently, there are two main hypotheses to explain the performance of object play behaviour in animals, namely the ‘misdirected foraging’ hypothesis and the ‘motor training’ hypothesis. The ‘misdirected foraging’ hypothesis holds that animals perform object-oriented play behavioural patterns in anticipation of acquiring food. For example, the arousal level in captive oriental small-clawed otters, *Anonyx cinerea*, increases when feeding time approaches, and as a result, their frequency of object play increases (as a ‘pseudo feeding behaviour’) more than their frequency of social play (Pellis, 1991).

The ‘motor training’ hypothesis states that play activities in immature individuals allow for the practice, and thus faster development, of sensorimotor skills that are critical for survival in adulthood (Byers & Walker, 1995). For example, the fact that domestic cats (*Felis catus*) play with objects that resemble their main prey (mice) could be explained in terms of immediate or long-term effects on the development of such skills related to specific foraging behaviour in this species. A correlate of the ‘motor training’ hypothesis

is that object play provides opportunities to explore and acquire knowledge about the properties of new objects and environments, thereby facilitating affordance learning of possible tool use, while overcoming neophobia (Parker & Gibson, 1977; Lockman, 2000). Similarly, the ‘behavioural flexibility’ hypothesis holds that object play allows for the emergence and expression of novel behavioural patterns that could lead to functional actions (e.g., tool use), thus making individuals more likely to adapt to rapidly changing environmental situations (Fagen, 1981; see also Huffman & Quiatt, 1986 for a discussion on this in relation to SH).

The recent discovery of stone tool-assisted foraging by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*; Gumert et al., 2007; Gumert & Malaivijitnond, 2012), is consistent with the idea that the phylogenetic propensity for stone manipulation in the fascicularis macaque taxonomic group can lead to functional adaptations. This connection between SH and stone tool use in macaques could indicate cumulative culture (Huffman & Quiatt, 1986; Leca et al., 2012; but see Dean et al., 2014).

Even though many theories have been proposed to account for the functional consequences of play behaviour (Smith, 1978; Graham & Burghardt, 2010), no single one can be applied across the board to all play behaviours in all species. Indeed, within the same species, play activities may widely vary under different environmental conditions (e.g., Ramsey & McGrew, 2005). SH is no exception, as evidenced by the differences in the frequency, form, and context of expression of this object play behaviour between free-ranging and captive troops, and across age classes within the same troop (Leca et al., 2007a, b, 2008a, b; Nahallage & Huffman, 2007b).

The functional components of play are expected to vary according to the form and context of the behaviour itself, due to potential motivational differences brought about by local variation in the social and ecological environments, and by species’ level propensities. For example, Hall (1998) describes object play in predatory species as boisterous and enjoyable. SH in Arashiyama Japanese macaques, on the other hand, occurs under low arousal conditions (Huffman, 1984, 1996). In captive settings, the expression of SH is not consistent with the ‘misdirected foraging’ hypothesis (Nahallage & Huffman, 2007b). In provisioned free-ranging troops of Japanese macaques, the fact that SH occurs predominantly after feeding, and not before (Huffman, 1996), does not support the anticipatory component of the ‘misdirected foraging’ hypothesis. However, in the latter situation, handling stones may

still be an extension of foraging-like behaviours, that is a continuation of manipulatory actions directed towards non-edible objects (stones), while chewing certain provisioned foods (hard cereal grains) that do not require further food-processing behaviours (Huffman & Quiatt, 1986; Huffman & Hirata, 2003; Leca et al., 2008b). However, in captive troops of SH Japanese and rhesus monkeys, that are fed commercial pellets, SH occurs at all times of the day and is not anchored to a window of time after feeding, since the troops are fed only once a day, in the morning (Nahallage & Huffman, 2008a, 2012).

Given the differences in frequency, form, and context of expression of SH across age classes, the possible motivations for performing the behaviour may be different for young and adults. This is of particular interest since only individuals younger than five years acquired this behaviour in the initial stages of its diffusion within the Arashiyama troop (Huffman, 1984, 1996). Therefore, unlike other play behaviours that disappear from the repertoire of most primates when they reach adulthood, presumably because they no longer serve a function, we argue that biological and cultural selective forces may be acting on individuals who have acquired SH, to maintain its practice throughout their lives. One possibility is that the behaviour is intrinsically pleasurable for both young and older individuals, and the physiological mechanisms underlying such a positive reinforcement remain active over the lifespan.

5.1. Benefits of SH for young individuals

Young individuals are naturally curious and readily explore new objects and environments (Hall, 1998). The immediate motivation for immature macaques to engage in SH is most likely related to the intrinsically enjoyable nature of this activity. Young Japanese macaques are also naturally curious about others' SH activity and are often attracted to the particular stones used by others to start SH themselves (Huffman, 1984; Leca et al., 2010a). At the functional level, playing with stones may further enhance interactive motor and perceptual skills supportive of physical and neurophysiological development. In macaques, a surge of synaptogenesis occurs roughly two months before birth and continues up to three years of age (Rakic et al., 1986; Bourgeois et al., 1994). The overall trend in the increasing diversity and complexity of SH behaviours performed over time from infancy to the juvenile period is consistent with this increase in neural-motor developmental activity (Nahallage & Huffman, 2007a).

During the first six months of life, the average number of patterns displayed by young Japanese macaques is 3.28 ± 1.72 , and the simple behavioural patterns exhibited at this very young age (i.e., Pickup, Cuddle, Bite and Hold) are performed while in a stationary position involving minimal manipulation (Nahallage & Huffman, 2007a). After six months, individuals start to engage in additional and more complex manipulative actions directed to stones, and the average number of patterns displayed by an individual between the age of seven and twelve months increases to 8.85 ± 2.26 . At this stage, the SH patterns performed include combining more than one stone in the same action (e.g., Clack, Rub Together and Rub on Surface). Also, individuals start to carry stones with their hands and/or feet, and push them with both hands while walking (Nahallage & Huffman, 2007a).

The average number of SH patterns displayed by an individual over 12 months of age is 11.71 ± 4.30 , and the most common one consists of combining stones with other objects (Nahallage & Huffman, 2007a). At this age, as individuals become more familiar with their environment they sometimes wrap leaves around stones, or strike stones against metallic and plastic objects. The number of behavioural patterns displayed by individuals gradually increases up to four years of age (e.g., Flint, Shake in Hand, Wash). Indeed, older juveniles exhibit the highest number of SH patterns among all age classes, but then, the number of patterns displayed tend to decrease into adulthood (Nahallage & Huffman, 2007a).

In general, immature primates undergo a relatively long maturation period, during which they master the tasks that require complex sensory-motor actions, including extractive foraging patterns (Pereira & Fairbanks, 1993). Among primates, the index of dexterity and the use of relatively independent finger movement (RIFM) is thought to reflect the degree to which motor neurons innervating the muscles acting on hand and fingers receive direct, monosynaptic projections from the cerebral cortex (Phillips, 1971; Kuypers, 1981; Borotoff & Strick, 1993). In macaques, the earliest signs of RIFM occur at 2–3 months, with mature patterns at 7–8 months (Lawrence & Hopkins, 1976; Olivier et al., 1997). Galea & Darian-Smith (1995) reported that the performance on a reach and grasp test by young macaques approached that of adults by 6 months of age. These results allow us to discuss the possible neurological underpinning of the development of SH behavioural patterns in Japanese macaques. Even though the cortico-motoneuronal projections, responsible for RIFM, develop rapidly in the first neonatal months,

they do not mature fully until the second year of life (Armand et al., 1996). This may partly explain the observed increase in the number of SH patterns up to 3–4 years of age. An increase with age in the number of SH patterns displayed and the level of dexterity required to perform them seems to be concomitant with a gradual refinement of sensorimotor skills over the first 18 months of an infant's life (Nahallage & Huffman, 2007a). Within the next two years of their development, juvenile Japanese macaques exhibit the greatest diversity in SH patterns, which corresponds to the growth stage when individuals are highly active and explorative, as well as physically capable of generating a wide range of actions. Taken together, these factors could contribute to the increase in the behavioural diversity and complexity of SH behaviour.

The above findings are consistent with Fairbanks' (2000) model describing the heightened frequency of object manipulation in correlation with synaptic development in juvenile vervets and rhesus macaques (see also Fragaszy & Adams-Curtis, 1991 in capuchin monkeys). We argue that this model currently provides the best functional explanation for the development of SH in Japanese macaques. In provisioned free-ranging and captive groups of this species, SH activity may substitute for, or possibly allow for better sensory-motor training than other forms of object manipulation spontaneously practiced by young wild Japanese macaques during development. This needs to be followed up with direct neurological investigations using non-SH groups as a control for comparison. The logistical difficulties of doing this kind of an investigation non-invasively on captive and free-ranging primates have been a major obstacle thus far, but this should not prevent us from proposing possible long-term benefits of this object play behaviour.

5.2. Benefits of SH for adults

Since adults have already acquired the sensory-motor skills needed for survival and reproduction earlier in their life, we propose that the ultimate function of SH in adults is different from that of younger individuals. However, adults may gain an equally important neurophysiological benefit from the continued practice of SH. As macaques grow older, a decline in memory, cognitive impairment and associated pathology (e.g., senile plaque, synapse loss) of the prefrontal cortex occurs (Hof & Duan, 2001). In humans, this process is also associated with cognitive decline, dementia and Alzheimer's disease (Hof & Duan, 2001). A number of clinical studies have shown that

those impairments are reduced or delayed in elderly humans who regularly engage in leisure activities that require the brain and the hands to focus on various specific actions such as reading, playing board games, cards and musical instruments (e.g., Verghese et al., 2003). The neurological mechanisms underlying these effects are not yet completely understood, but in simple layman's terms, you either use it or you lose it. That is, mental exercise associated with such leisure activities may stimulate neural growth around damaged parts of the brain caused by aging (Coyle, 2003). In fact, physical exercise has been associated with increases in brain-derived neurotrophic factor production and other growth factors that stimulate neurogenesis and improve learning and mental performance in the elderly (Laurin et al., 2001; Cotman & Berchtold, 2002). Given the close similarities in the behavioural, physiological and neurological aging process between human and non-human primates (Hof & Duan, 2001), we generalize the compensation for cognitive degeneration in older adult humans playing cards to senescent macaques maintaining their cultural practice of SH, thus prolonging the benefits associated with this object play activity. In line with this argument, we found that senescent females performed significantly more bimanual (i.e., complex) SH patterns than senescent males (Leca et al., 2011). This is consistent with similar sex differences found in the late deterioration of complex manual movements in other species, including rats, rhesus macaques, and humans (Joseph et al., 1989; Jennings et al., 1998; Kritzer & Kohama, 1998). These results indicate that a lifetime of oestrogen exposure had a neuroprotective effect on females' nigrostriatal system (an area of the brain involved in fine and coordinated motor function), and enhanced motor coordination in manual tasks in old females (Lacreuse et al., 2005).

Overall, a gradual shift in the effects of SH activity from (1) sensorimotor development in immature individuals, to (2) basic neural maintenance and possibly tool use in adults (see above discussion for Burmese long-tailed macaques), and to (3) regeneration of neurophysiological pathways in aging monkeys may be the prominent ultimate functions behind the sustained practice of this seemingly non-adaptive behaviour in macaques. The benefits outlined above by the 'neural maintenance and regeneration' hypothesis (Nahallage & Huffman, 2007b) could be partially tested by means of comparative behavioural, demographic and postmortem neuro-anatomical investigations of individuals in groups where SH is an established behavioural tradition and in non-SH control groups. Accordingly, we predict that faster behavioural

developmental rates, higher cognitive performances, slower sensorimotor decline, and higher longevity (associated with less deteriorated brain anatomy and physiology) may be present in individuals from SH groups, compared to their wild or provisioned non-SH counterparts. This is consistent with the three processes of play outlined by Burghardt (2005), i.e. the neural maintenance and regeneration processes are similar to the secondary play process and the culture and creative components are related to tertiary play.

6. Implications of SH for welfare

6.1. Performance of SH and stress

The frequency of performance of any behaviour is influenced by environmental factors and individual social characteristics, such as age, sex and the level of stress caused by aggression among troop members (e.g., Fedigan, 1972; Baldwin & Baldwin, 1977; Poirier et al., 1978; Starin, 1990; Pellis, 1991; Hall, 1998; Burghardt, 2005). In a captive troop of Japanese macaques, we found clear associations between environmental and social stressors and SH frequency (Nahallage & Huffman, 2008a). SH frequency was relatively higher under milder climatic conditions (i.e., sunny and warm days versus cloudy/rainy and cold days) and less stressful social conditions (i.e., resting time for most group members, with low levels of intragroup aggressive interactions). It is also noteworthy that troop members completely ceased SH activity following the group's annual medical check-up, a time of heightened stress and assumedly anxiety for the monkeys when the entire troop is captured, sedated and examined. SH frequency returned to its baseline level only after several weeks (Nahallage & Huffman, 2008a). These findings are consistent with the view that SH (like other form of play activities) can be used as a behavioural indicator of individual psychological well-being and group welfare in captive macaques. In contrast, there is evidence indicating that only mild to moderate stress in some animals may promote *social* play and, in turn, this play behaviour may reduce stress (Darwish et al., 2001; Von Frijtag et al., 2002; Norscia & Palagi, 2011; Mustoe et al., 2014; Taylor et al., 2015). These examples lead us to suggest that different levels of stress may affect object play behaviour and social play behaviour differently. It appears that the relationships between stress and play are more complex than previously thought, and further research is needed to explore them. For example, MAH has initiated the use of non-invasive methods to measure stress

hormone levels in stone handlers under varying stressful environmental conditions.

6.2. The contagious nature of SH and environmental enrichment

Although SH in Japanese macaques is primarily a solitary activity, the social aspects involved in the occurrence of this behaviour should not be overlooked. First, there is no doubt that it is socially transmitted (Huffman, 1984; Nahallage & Huffman, 2007a; Leca et al., 2010a). Second, an inter-group comparative study showed that group size was correlated with the proportion of group members exhibiting SH simultaneously. The effect of troop size on the synchronised performance of SH may reveal the contagious nature of play (Leca et al., 2007a). In other words, the sight of nearby stone handlers and even the loud noise generated by percussive SH patterns may increase the probability for individuals ‘in the audience’ who already acquired SH to start performing this behaviour (Leca et al., 2007a). This stimulation effect may be amplified by an increasing number of troop members and eventually result in a form of ‘hysterical contagion’ (Kerckhoff, 2002). This may help explain the increase in the number of individuals simultaneously engaged in SH activity around food provisioning time at Arashiyama, as this is the only time when most troop members are all together in the same location (Leca et al., 2008b). Third, SH is occasionally integrated with social interactions such as play wrestling and allogrooming (Huffman, 1984; Leca et al., 2008b). Fourth, once particular stones are being manipulated during a solitary SH episode, they appear to trigger great interest from other individuals who sometimes try to snatch them away from the handler as if they were the only stones available (Huffman & Quiatt, 1986; Leca et al., 2010). Fifth, beyond this direct social influence on the performance of SH, field experiments have shown the role indirect social influences play in the maintenance of the SH tradition via the occurrence of behavioural artefacts (e.g., experimentally created stone assemblages (Leca et al., 2010) and natural accumulation of stones along travel routes from the provisioning grounds to the forest (Quiatt & Huffman, 1993)).

The day to day performance of SH in captive rhesus macaques also seemed to follow a similar group-level contagion process, even to the extent of the behavioural patterns being exhibited (Nahallage & Huffman, 2008b, 2012). In this group, the most popular SH pattern was Rub on Surface (Nahallage & Huffman, 2008b). Sixty-percent of the outdoor enclosure was

covered with wooden climbing structures and the wooden logs were jointed together using metal nuts and bolts. The monkeys' most frequently displayed SH pattern consisted of rubbing stones on the nuts and bolts. The sound produced by this also appears to facilitate the expression of SH across the group (Nahallage & Huffman, 2008b). We argued that SH could allow these monkeys to cope with the monotony of life in captive settings (Nahallage & Huffman, 2008b). Therefore, providing captive primates with stones and a variety of objects and substrates to combine with them could be viewed as a form of environmental enrichment, as part of a broader welfare management program.

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