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Indirect social influence in the maintenance of the stone-handling tradition in Japanese macaques, *Macaca fuscata*

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Comparative and longitudinal studies have shown that stone-handling (SH) behaviour, defined as the noninstrumental manipulation of stones by performing various behavioural patterns, is socially transmitted across generations as a cultural behaviour in Japanese macaques. We investigated experimentally how stimulus/local enhancement, a form of indirect social influence through the physical traces typically left in the environment by previous stone handlers, might trigger SH behaviour at the individual level, and thus could contribute to the maintenance of the SH tradition at the group level. Through the semicontrolled conditions of field experiments, conducted in the free-ranging provisioned Arashiyama E troop, in which the SH tradition has been well established for nearly three decades, our results supported the stimulus/local enhancement hypothesis. Most group members preferentially directed their SH behaviour towards typical physical traces of SH activity (piles of stones) over randomly scattered stones. Encountering SH artefacts enhanced the use of these particular stones for performing SH in that particular part of the environment. The common occurrence of such 'play stations' may favour the frequent reuse of the same stones over time and explain the transport of stones between and around SH artefacts. We provided evidence for the role of indirect social inputs on the long-term persistence of the SH tradition in Japanese macaques, through SH by-products, the stimulating effect of which can be delayed in time and separate in space from others. We discuss our findings from the perspective of socially mediated behaviours, conformity-enforcing responses and niche construction.

In the quest for cultural versus alternative explanations of behavioural variation within and between groups of the same animal species, there has been a heated conceptual and methodological debate among field and laboratory researchers. Before such behavioural variability can be regarded as cultural, it is acknowledged that the effects of genetic and ecological factors should be minimal. However, depending on the environmental conditions of the study, the species' attributes and the behavioural domain under investigation, the questions addressed and the methods used to answer them vary considerably. Three major approaches have been taken to assess whether intra- and intergroup behavioural diversity in a given species can be considered evidence for culture (often labelled 'behavioural tradition' by ethologists; reviewed in Caldwell & Whiten 2007).

First, the 'group contrast' approach (see Fragaszy & Perry 2003a) consists of examining variation in the frequency of behavioural variants between groups (often sampled from geographically separate populations; Whiten et al. 1999; Rendell & Whitehead 2001; Hunt & Gray 2003; Perry et al. 2003; Leca et al. 2007a). Second, the longitudinal approach relies on the social context of diffusion and maintenance over time of a novel behaviour within a group, as a way to assess whether social or individual learning is more likely to be involved (Coussi-Korbel & Fragaszy 1995; Lefebvre 1995).

However, from a conceptual viewpoint, the very notion of culture is debatable until there is empirical evidence that the transmission and maintenance of the novel behaviour within the group are socially mediated (Fragaszy & Perry 2003b; Galef 2004). Therefore, the third approach consists of conducting experimental studies to determine whether 'socially biased learning' processes (Fragaszy & Visalberghi 2001, 2004) could support the putative cultural behaviours observed in the wild. Social learning is any form of learning influenced by the presence of, observation of or interaction with another individual (typically a conspecific) or its products (Galef 1988). The various 'social influences supporting the learning of novel behaviours' (Fragaszy & Visalberghi 2004, page

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27) or the performance of species-specific behaviours can thus be divided into two broad categories, namely direct social influences and indirect social influences (Galef 1988; Tomasello et al. 1993; Whiten 2000; Visalberghi & Fragaszy 2002).

Among the forms of direct social influences, the probability of an individual performing a behaviour may increase in the presence of a conspecific performing the behaviour, which is already in the observer's behavioural repertoire (social facilitation), or in the mere presence of a conspecific resulting in a behavioural disinhibition by reduction of isolation-induced fear (social enhancement). An individual's behaviour may also be triggered by the synchronized performance of a similar behaviour by several conspecifics, as part of an amplification process (contagion). Finally, an individual may learn to copy some part of the form of the behaviour performed by a demonstrator or may learn from a model the goal to pursue (imitation/emulation). Most studies on social-learning processes have focused on direct social influence through the necessary presence of other group members (reviewed in Zentall & Galef 1988; Fragaszy & Perry 2003a).

By contrast, indirect social influence assumes that an individual's behaviour may result from directing its attention to a 'limited aspect of the total stimulus situation to which the response is to be made' (Spence 1937, page 821), without necessarily interacting directly with a conspecific. If stimulus/local enhancement is involved in the acquisition, transmission or maintenance of a habit, then individuals should tend to focus their attention on, or aim their responses towards, particular objects or places in the environment after observing conspecifics' actions in conjunction with those objects or at that place (Thorpe 1963; Byrne & Russon 1998). Through the stimulating effect of the physical traces (or artefacts) left behind by previous individuals, indirect social influences are delayed in time and separate in space from others. For example, residual olfactory cues left on foraging trails by ants and rodents affect the selection of feeding sites (Hölldobler & Wilson 1991; Galef & Buckley 1996). As opposed to some of the complex learning processes mentioned above, the role of stimulus/local enhancement offers a more parsimonious explanation for the acquisition of foraging techniques by immatures in various taxa such as birds, rodents and primates (Denny et al. 1988; Tomasello et al. 1993; Huber et al. 2001; Gunst et al. 2008). However, to date, indirect social influence on the acquisition, performance or long-term maintenance of behaviours has not received the formal attention it deserves.

One reason for this could be the lack of experimental data obtained from the spontaneous behaviours in free-ranging and socially living groups of animals. Most experimental studies of social learning have used artificial tasks and were conducted in the unnatural social conditions of laboratory settings (reviewed in Galef & Laland 2005). Recent criticisms about the ecological validity of these studies has led to recommendations for field experiments using biologically relevant tasks and allowing individuals to interact spontaneously with each other and with test stimuli, with no human-imposed outcomes for the successful completion of the task (Matsuzawa 1994; Galef 2004; Huffman et al. 2008; Watson & Caldwell 2009).

Here, we took a field experimental approach to test the indirect social influence of lithic artefacts on the enduring performance of stone-handling (SH) behaviour in Japanese macaques. The SH activity is the noninstrumental and seemingly playful manipulation of stones, such as repeatedly pounding a stone on a substrate, clacking two stones together, or gathering several stones into a pile (Huffman 1984). SH is the longest studied and best-documented cultural behaviour in monkeys to date (reviewed in Huffman et al. 2008). Research on SH has already benefited from a comparative approach revealing substantial variation in SH between troops of Japanese macaques, and from long-term observational studies conducted at several points in time over a 30-year period to address the influence of environmental, sociodemographic and developmental constraints on the emergence, diffusion and maintenance of the SH tradition (Huffman 1984, 1996; Huffman & Quiatt 1986; Huffman & Hirata 2003; Leca et al. 2007a, b, 2008a, b, in press a). For example, the continuous study of mothers and infants during the first 6 months of life, in the semicontrolled conditions of an outdoor enclosure, showed that (1) the mother was the primary source of an infant's early exposure to SH, (2) the acquisition of SH behaviour by young individuals may involve direct social influences (social facilitation) through the observation by naïve infants of their mothers as SH demonstrators, and (3) some intragroup variability in the performance of SH patterns could be interpreted from the viewpoint of developmental constraints (Nahallage & Huffman 2007a, b).

However, the maintenance of the SH tradition across generations may involve not only direct social influences but also indirect social inputs through the stimulating effect of SH artefacts (Quiatt & Huffman 1993). Through the enduring practice of SH behaviour, acquired familiarity with the stones and occasional integration of SH with other daily activities, Japanese macaques often carry stones about and leave them behind when engaging in another activity. As a result of these regular transports, small piles of stones are conspicuously deposited on grassy patches, stone slabs or at the base of large trees (Huffman & Quiatt 1986). The common occurrence of such SH artefacts or 'play stations' around the feeding ground, and sometimes in the forest, may favour the frequent reuse of the same stones over time (Quiatt & Huffman 1993). However, the hypothesis that encountering physical traces of previous SH activity affects subsequent SH activity has not yet been tested.

The present work is the first to use a field experimental approach to examine the environmental and social conditions, at least partially reconstructed, under which the SH tradition may be maintained within troops of Japanese macaques. We studied the free-ranging provisioned Arashiyama E troop, in which the SH tradition has been well established for nearly three decades (Huffman 1984, 1996; Leca et al. 2008b). Therefore, it is beyond the scope of this study to address the social-learning processes involved in the initial establishment of the SH tradition. Our main goal was to investigate experimentally how the physical traces typically left in the environment by previous stone handlers might help, through a stimulus enhancement process, trigger SH behaviour in individuals on a daily basis, and thus contribute to the long-term maintenance of the SH tradition at the group level.

We tested the 'stimulus/local enhancement hypothesis' on the performance of SH, proposing that individuals should preferentially direct their SH activity towards the places where previous stone handlers left conspicuous physical traces of their SH activity, and more specifically towards piles of stones. Our specific objective was to test two predictions derived from the 'stimulus/local enhancement hypothesis'. Prediction 1 stated that the frequency and duration of SH behaviour should be significantly higher when directed to a pile of stones than when directed to randomly scattered stones for all individuals entering the experimental area, including the first one to do so, that is, when any possible direct social influence had been removed. Prediction 2 stated that if the location of the piles of stones changed during consecutive visits to the same area, a given stone handler should be more attracted to the new locations (where the piles of stones are) than the previous locations. Rejection of the 'stimulus/local enhancement hypothesis' could suggest that the persistence of the SH tradition and the motivation to engage in this activity are better explained by direct social influences such as social facilitation or social enhancement.

To explore further the environmental factors underlying the maintenance of the SH tradition, (1) we tested the possible spatial