



# Call playback artificially generates a temporary cultural style of high affiliation in marmosets



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Cultural variation can be conceptualized in two main ways: as culture-specific qualitative differences in behavioural form, and also as quantitative variation in performance of constellations of universal behaviours (cultural style). Despite observation of both types in wild nonhuman primates, diffusion of qualitative culture has been scrutinized extensively experimentally while within-species transmission of cultural style has remained entirely unexplored. Here we investigated whether a cultural style of high affiliation could be artificially generated in a nonhuman primate (*Callithrix jacchus*), by daily playback of conspecific affiliative calls simulating nearby amicable individuals. We found that vocalization playback influenced monkeys to spend more time in affiliative behaviours outside playback hours, relative to silent playback. The effect was specific to affiliation, with no impact on other categories of affect. This change did not persist into the final phase of observation after all playbacks were complete. Findings are consistent with a temporary shift in cultural style effected through vocalization playback, supporting existence of this conception of culture in wild primates and indicating auditory social contagion as a potential diffusion mechanism. The method presented here will allow researchers to test hypotheses concerning cultural transmission of cultural style, and the underlying processes, across a range of contexts and species.

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Culture influences both the way and the extent to which we express affection. Human culture encompasses not only culture-specific qualitative differences in behavioural form (e.g. customary nonverbal greetings: Firth, 1972), but also atypical quantitative variation in performance of constellations of universal behaviours (Leach, 1972, p. 345). For example, dyadic social interactions occur in all cultures, yet the level of social contact involved lies along a continuum. 'High-contact' cultures (e.g. Latin American) show short interpersonal distances (Engelbreton & Fullmer, 1970; Sussman & Rosenfeld, 1982), high frequencies of touching (Diabise & Gunhoe, 2004; Remland, Jones, & Brinkman, 1995) and a more direct degree of orientation (Sussman & Rosenfeld, 1982) relative to 'low-contact' cultures (e.g. Japanese) at the opposite extreme (Hall, 1966; Remland et al., 1995).

Furthermore, cultural variation exists in the magnitude to which universal emotions are expressed publicly; for example, Costa Ricans appear less willing to express negative emotions than do Americans (Stephan, Stephan, & Cabezas de Vargas, 1996). Quantitative culture is therefore demonstrably present in humans, and determining the extent to which it exists in other primates will help elucidate the evolutionary origins of this type of culture.

Definitions of culture in nonhuman primates share prerequisites that behaviour patterns are group-specific and transmitted socially (Caldwell & Whiten, 2006), applicable to both qualitative and quantitative conceptions of culture. Yet, the predominant process for recognizing potential traditions in wild primates, the 'method of exclusion' (Whiten et al., 1999) or 'ethnographic approach' (Wrangham, McGrew, & de Waal, 1994), disregards species-universal behaviours assessing only qualitative intergroup differences, and thus excludes quantitative culture a priori. Although species-atypical behaviours are more easily identified as having been socially learned, behaviours within species repertoires can also be influenced socially. Differing rates in performance of variants of single universal behaviours have been identified as possible traditions in wild spider monkeys, *Ateles geoffroyi*, (Santorelli, Schaffner, & Aureli, 2011). Further, a distinctive quantitative multidimensional 'pacific' culture has been reported in a wild troop of baboons, *Papio anubis* (Sapolsky, 2006; Sapolsky & Share, 2004).

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Uncharacteristically low rates of male displacement aggression and abnormally high proportions of time spent in male–female affiliation resulted after aggressive males died from illness (Sapolsky & Share, 2004). This sociality persisted transgenerationally, even after immigrants replaced all progenitor males (Sapolsky, 2006). Newcomers behaved atypically only after integration, indicating social assimilation of group style. Although extreme levels of a single behaviour were observed in another troop, critically, this pattern of unusual levels of performance, together representing an affective style, was unprecedented (Sapolsky, 2006). Referred to variously as social milieu/atmosphere/style (Sapolsky & Share, 2004)/culture (Sapolsky, 2006), with no inherent restriction to the social domain, we hereafter use the term ‘cultural style’ for atypical degrees of performance across an array of species-typical behaviours, specific to particular group(s) and transmitted socially.

Following observation of potential cultural variation between wild populations, controlled experimental manipulation of captive groups allows unambiguous demonstration that behaviour patterns can be socially transmitted within a species. Empirical approaches are thus fundamental to substantiating existence of cultures in the wild, elucidating cognitive processes underlying transmission, and thus delineating phylogenetic origins of human culture. Accordingly there exists a vast body of experimental work on qualitative cultural diffusion. Although overwhelmingly biased towards food-related over social behaviours (Watson & Caldwell, 2009; Whiten & Mesoudi, 2008), such research covers diverse species and methodologies (Whiten & Mesoudi, 2008). Apparent traditions in wild chimpanzees, *Pan* (Whiten et al., 1999), orangutans, *Pongo* (van Schaik et al., 2003) and capuchin monkeys, *Cebus* (Panger et al., 2002; Perry et al., 2003) prompted empirical investigation (e.g. Dindo, Stoinski, & Whiten, 2010; Dindo, Thierry, & Whiten, 2008; Whiten, Cusance, Gomez, Teixidor, & Bard, 1996; Whiten et al., 2007; Whiten, Horner, & de Waal, 2005). Additional species studied include other primates, from marmosets, squirrel monkeys, colobus and vervet monkeys to prosimian lemurs (*Callithrix jacchus*, Voelkl & Huber, 2000; *Saimiri boliviensis*, Hopper, Holmes, Williams, & Brosnan, 2013; *Colobus guereza kikuyuensis*, Price & Caldwell, 2007; *Chlorocebus aethiops*, van der Waal, Cladière, & Whiten, 2013; *Eulemur rufifrons*, Schnoell & Fichtel, 2012), and nonprimates, from guppies and tortoises to mongooses, meerkats and mountain parrots (Laland, Atton, & Webster, 2011; *Geochelone carbonaria*, Wilkinson, Kuenstner, Mueller, & Huber, 2010; *Mungos mungo*, Mueller & Cant, 2010; *Suricata suricatta*, Thornton & Malapert, 2009; *Nestor notabilis*, Gajdon, Fijn, & Huber, 2004). With social transmission itself demonstrated, research has extended to transmission biases (Rendell et al., 2011), including the frequency-based bias, conformity (Haun, Rekers, & Tomasello, 2012) and the model-based bias, prestige (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010).

In stark contrast, one experimental study only, to our knowledge, has examined transmission of cultural style, and only between species. Cross-species housing of rhesus with stumptailed macaques led to the adoption of a species-atypical cultural style of high reconciliation (de Waal & Johanowicz, 1993). Crucially, rather than assuming the host species’ manner of reconciliation, rhesus monkeys increased only the frequency of existing reconciliative behaviour, with three times more conflicts followed by reconciliation relative to proportions in matched-control juveniles cohoused with rhesus adults and in the original group. Atypically high rates were maintained on reintegration (de Waal & Johanowicz, 1993). Thus, despite field observation of both culture types, within-species diffusion of cultural style remains entirely unexplored whereas transmission of qualitative culture has been scrutinized extensively experimentally. This discrepancy highlights a huge gap in our knowledge. Empirical analysis of this wider conception of culture is

of great interest and importance, given the parallels with human culture, and the need to verify assumed social diffusion in the wild and elucidate underlying cognitive mechanisms.

Here we present a novel approach, directly investigating transmission of social cultural style using a playback paradigm. We asked whether a cultural style of high affiliation could be artificially generated in captive primates through playback of conspecific affiliative vocalizations. Specifically, we predicted that daily playback of affiliative calls at a high rate (simulating extremely amicable individuals located nearby) would induce groups of monkeys to spend longer in affiliative behaviours outside playback hours and beyond cessation of all playback, demonstrating a shift in cultural style. Marmosets, *Callithrix jacchus*, are cooperative rearers, pro-social, and very socially tolerant (Burkart, Fehr, Efferson, & van Schaik, 2007; Burkart, Hrdy, & van Schaik, 2009), and are therefore likely to be especially susceptible to social influence. Furthermore, in an observational study, spontaneous neighbour affiliative (chirp) calls were associated with simultaneous increased affiliation in nearby marmosets (Watson & Caldwell, 2010), indicating call playback would be similarly effective, and may exert a longer-term influence.

## METHODS

### Subjects

Focal subjects were initially 32 adult breeding-pair marmosets (16 females; 16 males: age range 1 year 163 days–12 years 331 days) housed within 19 family groups and breeding pairs in four colony rooms at the MRC Human Reproductive Sciences Unit, Edinburgh, U.K. Further information on each focal subject is available in Appendix Table A1. One focal individual died during the study (leaving  $N = 31$ ). All marmosets remained in the colony after the study. Each room was 4.5 × 6.5 m containing eight cages; two rows of four along the longest facing walls. Each cage measured 1.1 × 1.5 m and 2.3 m high (vertically bisected if used for pair housing) and contained enrichment items. The mean total number of individuals per room was 35 in a mean of nine groups, with all cages per room occupied, with one exception. Each home cage contained a log to facilitate gouging and locomotion, at least one rubber matting platform to facilitate allogrooming and a nestbox positioned at the top. Cages had a thick layer of sawdust on the floor to encourage foraging; a scatter feed of bran flakes, dry spaghetti, mixed whole nuts, chopped malt loaf and plain popcorn was added once weekly when sawdust was replaced. Marmosets were fed fresh fruit and vegetables twice daily (once on weekends and holidays); water and pellet diet were available ad libitum. Every other day the diet was supplemented with pellet diet soaked in sugar-free Ribena, dried fruit and peanuts in their shells or ‘porridge’ (plain yoghurt and baby rice with supplements: Casilan 90 protein powder, vitamin D and Complian). Housing was maintained at ca. 21–25 °C and humidity at ca. 53–55%, with a light:dark cycle of 12 h (0700–1900 hours).

### Stimuli for Playback

For the experimental condition, stimuli were affiliative (chirp) calls played at above-average rate (mean 18 calls/5 min). This vocalization type was selected because it is associated with affiliative behaviour in the literature (see Watson & Caldwell, 2010). For our definition of the call and a spectrogram example, see Watson & Caldwell (2010). Auditory tracks were created by alternating 32 different call exemplars with intercall intervals of 18 different durations. The order of exemplars (generated at <http://www.random.org>) was random within the constraint that all exemplars

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