



## 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 (Engebretson & 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, Custance, 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, prosocial, 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 and 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

were used at least once before repetition. Call exemplars were spontaneously produced chirp vocalizations, selected and cut from >38 h of audio footage, recorded in situ from socially housed marmosets (Watson & Caldwell, 2010) within the same facility as subjects of the current study, from three matching and one different, colony rooms. The relatively frequent reorganization of marmosets, across their lifetime, within the facility meant that subjects were likely to be familiar to some degree, at least acoustically, with most if not all individuals whose chirp calls we used as stimuli; within each colony room marmosets were in acoustic contact with all other groups and in visual contact with those directly opposite. Call exemplars were produced by at least six different individuals and ranged from two to 11 syllables (0.5–2.5 s duration). We edited each call to maximize signal to noise ratio (using WavePad Sound Editor Master's Edition, NCH Software, [www.nchsoftware.com](http://www.nchsoftware.com)), and checked they remained intact by examining spectrograms of original and edited calls (with Sonic Visualiser 1.6, GNU, [www.sonicvisualiser.org](http://www.sonicvisualiser.org)). Use of multiple chirp call exemplars was necessary to minimize habituation to calls, represent the call type adequately and avoid pseudoreplication (Kroodtsma, Byers, & Goodale, 2001). Playback rate was approximately five times the average expected per colony room (47.6 calls/h), given the mean number of adult/juvenile individuals per room at the start of the study and the mean hourly chirp call rate of 1.36 per adult/juvenile, calculated from previous recordings made in the facility (Watson & Caldwell, 2010; Watson, 2011). Chirp playback tracks were created to match characteristics (chirp call rate and interchirp interval durations) of source audio recording with the highest spontaneously produced chirp call frequencies: the upper 5% of the total 463 separate 5 min-audio recording samples (Watson & Caldwell, 2010). The chosen rate of chirp call playback corresponded to the median number of chirps per 5 min sample within this upper subset of recordings: 18 calls, equivalent to 216 chirps/h per colony room. Our rationale was to ensure that playback manipulation, while intentionally well above average, was not implausible, still representing a spontaneously occurring chirp call rate, albeit an unusually high one. The control condition playback stimulus was recorded silence. Auditory stimuli were played through a stand-mounted speaker via a lap-top PC (Alesis M1 Active 520 USB monitor speaker, with flat frequency response). During experimental playback, chirp call stimuli were not audible outside the playback room. The chirp is a very quiet, within-group call. Playback volume was adjusted to match that of live calls, and the speaker volume in the control condition matched that in the experimental condition. Two example calls (of the 32 used) are available as [Supplementary material](#); play at low volume to represent experimental playback.

### Procedure

There was no additional welfare assessment or intervention involved in this study, given that the manipulation was not expected to affect the marmosets' welfare other than in a potentially positive way (Buchanan-Smith, 2010). The chirp call is associated with affiliation, a reliable behavioural indicator of positive welfare. Playback call exemplars were recorded predominantly, if not all, from familiar individuals. Chirp calls produced spontaneously by neighbouring groups are associated with simultaneous increased affiliation in marmosets (Watson & Caldwell, 2010). Neither pilot playback to nonstudy colony rooms (to determine appropriate playback volume) nor a related study investigating the immediate effect of chirp playback (with a subset of prerecorded calls used here; Watson, 2011) was associated with increases in behaviours performed in the presence of unfamiliar marmosets (e.g. anogenital present, bristle, agitated locomotion, loud shrill calls or tsik calls) or

anxiety-related negative welfare indicators (e.g. self-directed behaviours; Watson, 2009). Ethical approval for this study was given by the University of Stirling Psychology Ethics Committee. The study consisted of three phases: baseline, playback and postplayback, with 5 observation days per phase.

### Habituation

Marmosets were habituated to the presence of the observer over 5 days before baseline and for 15 days during a related study before playback, and to playback apparatus over 4 nights.

### Baseline

Observation of behaviour in this phase provided a baseline measure before any playback.

### Playback

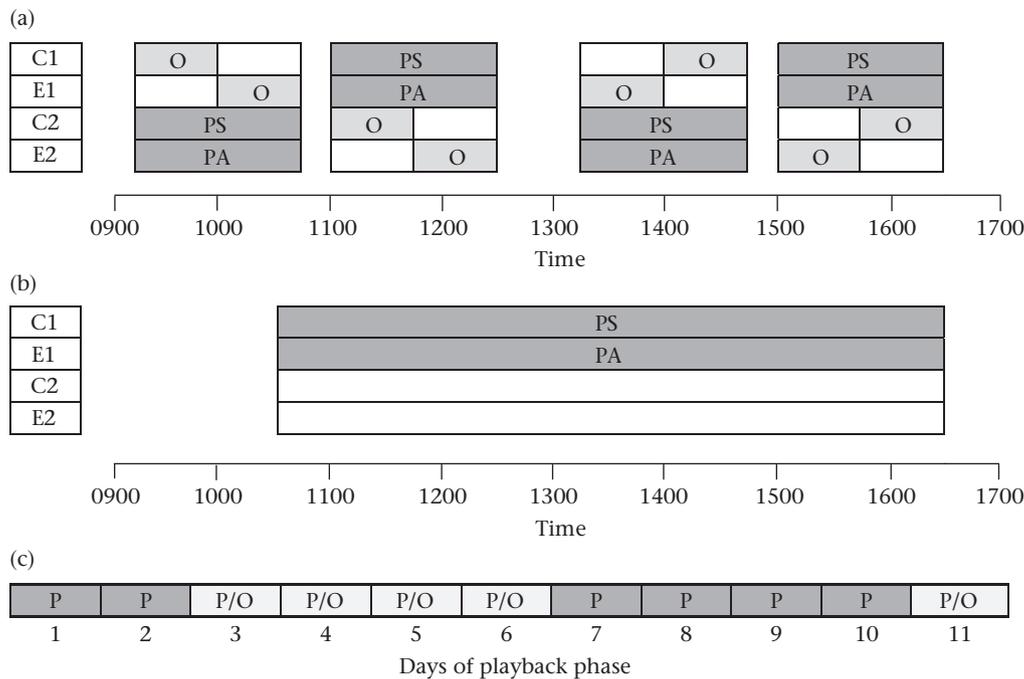
Observation during this phase allowed evaluation of continued stimuli influence on behaviour outside the hours of playback. Playback and observation were mutually exclusive. Two rooms were assigned per condition, and were exposed to playback simultaneously in matched pairs. Humans were not present during playback sessions. Mean daily playback per condition was 3 h. Each room received 33 h in total over an 11-day period: 3 playback-only days (a single 360 min playback session) and 5 playback/observation days (two 90 min playback and two observation sessions, counterbalanced across morning and afternoon; the order in which the two conditions were observed in each pair of observation sessions was also counterbalanced; see Fig. 1). Playback-only days were weekend and staff holidays with access to the facility limited to the single daily feeding session. Playback was initiated after feeding and was thus restricted to one session per matched pair of rooms daily. Continuing playback on nonweekdays allowed us to minimize the gaps between playback input. Further, nonweekdays were quieter owing to minimal husbandry, probably representing conditions maximally conducive to social behaviour (Barbosa & da Silva Mota, 2009) and thus to social contagion via the influence of affiliative call playback.

### Postplayback

Observation was carried out after all playback ended, to assess any lasting influence of the stimulus.

### Data Collection and Analysis

Continuous focal sampling (Altmann, 1974) was used to record behavioural interactions, directed either 'from' each focal individual to other group members or 'to' each focal individual from group members, during a 5 min session per subject, on each of 15 observation days. Session duration was chosen primarily to maximize sample size and was not considered to compromise behaviour sampling, given that captive common marmosets transition between behaviours relatively frequently. Data were recorded using a handheld computer (Psion Workabout) running real-time event recording software (Observer 8, Noldus Information Technology, Wageningen, The Netherlands). We recorded behavioural indicators representative of affiliation (allogroom, groom invite, affiliative contact, food share), intragroup and intergroup agonism and anxiety (chosen according to published literature). Although allogrooming can act as a tension reduction mechanism in other species of nonhuman primate indicating anxiety (e.g. Schino, Scrucchi, Maestripieri, & Turillazzi, 1988), for marmosets it is considered a reliable behavioural indicator of positive welfare (Buchanan-Smith, 2010). Administration of anxiolytic drugs in marmosets in fact results in increased duration and frequency of allogrooming while decreasing aggressive and anxious behaviour



**Figure 1.** Schedules during the playback phase of (a) a typical observation/playback day, (b) a typical playback-only day, showing observation (O) and playback (PS: playback of recorded silence; PA: playback of affiliative (chirp) calls), across matched-pair control and experimental rooms, respectively (C1 and E1; C2 and E2); time shown approximately. (c) The distribution of playback-only days (P) and observation/playback days (O/P) across all 11 days.

(Cilia & Piper, 1997). Behavioural definitions and data are available in Appendix Table A2.

Focal behaviour was summarized as the percentage of time spent in each affect category composite of behaviours, by each focal individual in every 5 min observation session. For each of the three phases, the mean level of behaviour for each focal marmoset was calculated from the five observation sessions within that phase. We compared the mean change in mean percentage time (per 5 min observation) spent in composite measures of each affect category, between baseline and playback, and between baseline and post-playback, for focal marmosets in the control and chirp playback conditions. Thus, each data point represented the difference between the mean percentage time per individual per phase. We chose to analyse mean change from baseline, to allow for any individual differences in behaviour. After the death of a focal individual in the control condition, the respective sample sizes analysed were 16 for the affiliative chirp playback condition and 15 for the control condition. For the analyses, we used permutation tests, approximate randomization tests, without replacement, based on unrelated samples *t* tests, performed in MATLAB (Mathworks, Natick, MA, U.S.A.) using custom-written code (data were randomly shuffled across conditions, but not across individuals, using approximate-exact tests with 200 000 iterations, the recommended minimum reliable number being 5000; Adams & Anthony, 1996). We chose a resampling method because this type of analysis does not make any assumptions regarding data distribution. Given that our data do not meet parametric assumptions, it represented the most appropriate and powerful statistical analysis available. We also carried out a post hoc analysis of the individual affiliative behaviours (allogroom, groom invite, affiliative contact and share food) between baseline and playback. All *P* values are two tailed,  $\alpha = 0.05$ . For all comparisons,  $N(\text{control}) = 15$  and  $N(\text{experimental}) = 16$ , representing the focal adult marmosets.

During the study, the number of infants increased (through births and fostering) by eight in the affiliative call playback condition and by two in the control. Affiliation, particularly affiliative

contact, licking and nuzzling, is performed most to infants (Stevenson & Rylands, 1988), especially newborns, and probably somewhat more to younger juveniles than to adults. Consequently, results for affiliation may be artificially inflated in the experimental condition. However, excluding interactions with infants would probably create the opposite bias, given that infants made up a higher proportion of focal subjects' group members for the experimental condition, especially because the presence of infants (carrying them and time attending to them) may, conversely, decrease time and opportunities for affiliative interaction with other group members. Further, other component affiliative behaviours of the composite may not be similarly affected; for example, Box (1975) observed allogrooming performed more often between breeding-pair adults than between adults and offspring. During playback and postplayback phases, both treatment groups had almost equal numbers of juveniles (control 12, experimental 11). Between baseline and the playback phase, owing to maturation, individuals of juvenile age increased by four in the control, but decreased by two in the experimental condition. If increased affiliation towards juveniles did occur, then excluding interactions with juveniles from the analysis would be expected to create a bias in favour of the experimental hypothesis. Thus, we report the results for interactions between the focal individual and all other group members, except where exclusion results in differences in significance level across categories, when we additionally report values excluding interactions involving infants, and infants and juveniles, respectively.

## RESULTS

### Composite Affiliation

The results are shown in Fig. 2 (and see the Supplementary material for the supporting data). There was fairly high interindividual variation in the level, and direction, of mean change in affiliation. As predicted, the mean change in time spent in affiliation

from baseline to playback was more positive in the chirp than the control playback condition. This difference was significant ( $P = 0.039$ ) and, importantly, remained so with interactions involving infants excluded from analysis ( $P = 0.046$ ). When interactions with infants and juveniles were excluded the difference fell short of significance ( $P = 0.092$ ). Since excluding interaction with juveniles from analysis was considered more liable to bias the result towards the experimental hypothesis (see above), it seems probable that removal of this relatively large proportion of the data simply meant that each focal individual's estimate was less reliable, reducing the likelihood of detecting an effect. Contrary to our prediction, although the difference was in the expected direction, the mean change between baseline and postplayback was nonsignificant ( $P = 0.769$ ). As expected, there was no significant difference, between experimental and control conditions, for change in time spent in behavioural composites of affective categories not matching stimulus affect of affiliation, either (1) from baseline to playback or (2) baseline to postplayback (intragroup aggression: (1)  $P = 0.987$ , (2)  $P = 0.289$ ; intergroup aggression: (1)  $P = 0.064$ , (2)  $P = 0.114$ ; anxiety-related: (1)  $P = 0.442$ , (2)  $P = 0.130$ ).

We analysed mean change from baseline to allow for any individual differences in behaviour. However, consideration of the mean frequencies and absolute durations of affiliation is necessary to provide context. Mean frequencies of instances of affiliation, scaled to give rate per hour, in the baseline phase were as follows: control 9.3, chirp 7.2; playback phase: control 6.1, chirp 10.5; postplayback phase: control 6.6, chirp 8.6. Mean time spent in affiliation, adjusted to give time/h, were for baseline: control 70.8 s (SE 18.0), chirp 46.4 s (SE 10.4); playback: control 39.5 s (SE 9.6), chirp 124.2 s (SE 23.4); and postplayback: control 62.2 s (SE 17.1), chirp 50.9 s (SE 12.5). Mean change in affiliation for the chirp condition from baseline to playback thus represented a relatively small increase in absolute time, but a large proportional increase. Mean time in affiliation more than doubled from the baseline to playback phase.

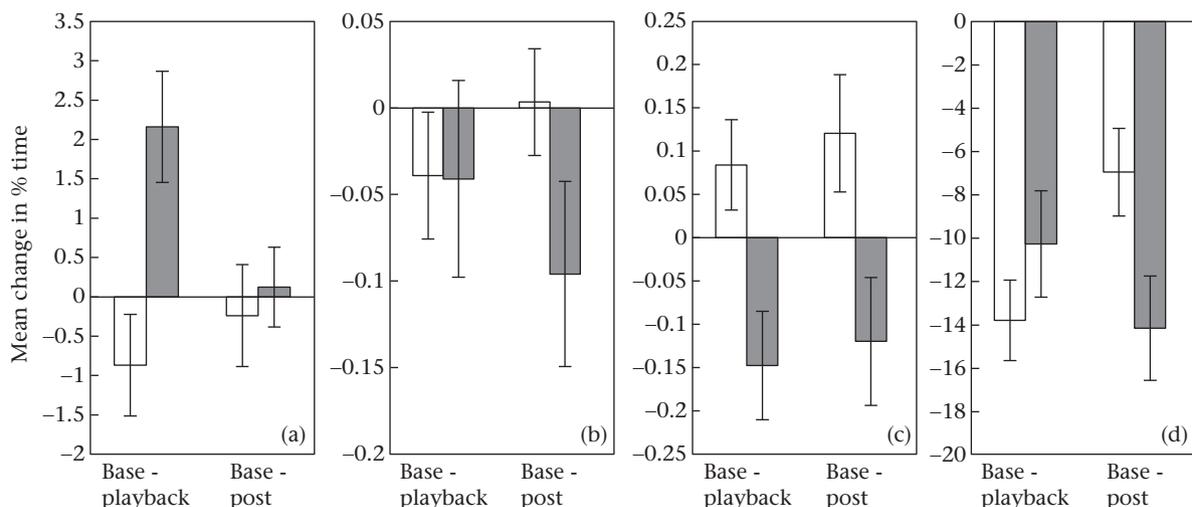
#### Individual Affiliative Behaviours

To explore the significant increase in affiliation between baseline and playback, we carried out post hoc analyses of the four individual affiliative behaviours (Fig. 3). Time spent in allogroom, groom invite and affiliative contact in the chirp playback condition

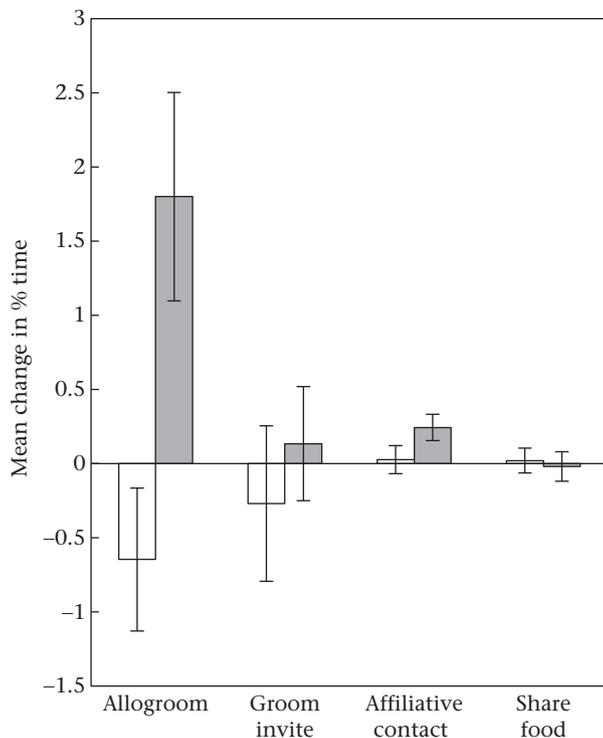
increased by a larger amount than in the control condition, but these differences were nonsignificant. Only allogroom approached significance (allogroom:  $P = 0.060$ ; groom invite:  $P = 0.104$ ; affiliative contact:  $P = 0.284$ ). For sharing food, the difference was in the opposite direction to the prediction but was also nonsignificant ( $P = 0.842$ ).

#### DISCUSSION

Our results are consistent with a temporary shift to a cultural style of high affiliation. They provide empirical support for playback of affiliative vocalizations being sufficient for increases in amicable behaviours outside playback hours. The possibility that raised affiliation was due instead to general heightened arousal can be discounted because we found no effect on behaviours indicative of affective states not matching the stimulus: anxiety, intergroup or intragroup aggression. Lack of a concomitant increase in anxiety-related behaviours, those associated with elevated levels of stress, precludes the small chance that increased affiliation represented a coping mechanism, should subjects have responded to the few playback chirp exemplars recorded from potentially unfamiliar marmosets, as to the presence of unfamiliar conspecifics. However, the change in style did not persist into postplayback days, i.e. beyond daily input from simulated progenitors. None the less, the relatively long-term influence between specific playback hours (therefore not simultaneous with playback) is itself noteworthy. In terms of underlying cognitive processes it represents lasting changes in behaviour, not mere 'momentary' alterations (Coussi-Korbel & Fragaszy, 1995). In general, researchers predominantly limit investigation in playback studies to immediate effects (Kitzmann & Caine, 2009). In an experiment assessing both immediate and delayed influence, an increase in feeding behaviour detectable 20 min after call playback was considered remarkable (Kitzmann & Caine, 2009). Our manipulation could only approximately simulate an influx of highly affiliative individuals which could exert social influence daily over years. The relatively short duration of exposure to playback may simply have been insufficient to effect a more permanent adjustment. Future research can examine whether extending playback period facilitates more enduring effects.



**Figure 2.** Effect of playback of conspecific affiliative (chirp) calls (grey bars) and recorded silence (control; white bars) on composite measures of affect categories (a) affiliation, (b) intragroup agonism, (c) intergroup agonism and (d) anxiety-related. Results are shown as mean change in percentage time  $\pm$  1 SE per 5 min observation spent performing or receiving behaviour, from baseline to playback (base–playback) and from baseline to postplayback (base–post).



**Figure 3.** Effect of playback on mean change between baseline and playback, in mean percentage time  $\pm$  1 SE per 5 min observation, spent performing affiliative behaviours: allogroom, groom invite, affiliative contact and share food in silent (control, white bars) playback and affiliative (chirp) call (grey bars) playback.

The magnitude of the changes represented by our results were small in terms of absolute time, but were large proportionally, more than doubled compared to baseline, and likely to be functionally meaningful. Marmosets in captivity typically perform affiliative behaviours relatively infrequently and for very short durations. Affiliation, even of very brief duration or infrequent occurrence, is likely to have significance for strengthening and maintaining social relations (e.g. affiliative contact is related to the pair bond between breeding pairs, Evans, 1983; allogrooming is related to association between breeding and nonbreeding females, Lazaro-Perea, De Fatima Arruda, & Snowdon, 2004). Thus, even small changes in time spent in affiliation are likely to be behaviourally and biologically relevant.

We acknowledge that data points in this study were not incontrovertibly independent; however, this would have been impossible at a practical level without drastic reduction in sample size and thus statistical power and there is good reason to believe that nonindependence of these data is not a concern. Although the absolute ideal, it is particularly difficult to sample totally independent data points in behavioural research. Data independence can be viewed as a continuum from completely independent to extremely dependent (Wehnelt, Buchanan-Smith, Ruxton, & Colegrave, 2005). We had, initially, a sample size of 16 focal marmosets per treatment condition (eight focal individuals in each of four colony rooms, two rooms per condition). Thus, ensuring absolute independence (i.e. one focal individual only sampled per playback room) would have entailed playback to 32 different rooms, or, with only four comparable rooms, reducing sample size to  $N = 2$  per condition. Although multiple focal animals within each room experienced the same playback with focal individuals in auditory (and olfactory) contact with other focal individuals in the same colony room, they were in visual contact only with those individuals housed in cages directly opposite to them. Further,

although some individuals were housed in the same room, and some focal individuals in the same group (never more than two and always of opposite sex), individuals were observed one at a time, never concurrently. We did not consider that sampling multiple focal individuals within the same social group would affect results of the analyses substantially. There is no evidence to suggest nonindependence: results of Spearman correlations on the baseline-to-playback data for the affiliation composite, using both the pairs of focal individuals housed within the same social group from the control and another from the experimental group, are nonsignificant, supporting our assertion that our data points are independent (control:  $P > 0.5$ ; experimental [negative relationship]:  $P > 0.4$ ).

Because our analysis involved combining percentage time per focal individual per 5 min observation across the 5 observation days in each phase, it is important to evaluate whether longitudinal changes were missed in doing so. In the playback phase, mean percentage absolute time spent in affiliation was consistently higher, across all 5 days of observation, for marmosets in the chirp than in the control condition. This consistent difference was not evident across baseline and postplayback phases. (These results are shown in Appendix Fig. A1.) This suggests that playback exerted an influence after only one or a few exposures (the first being 6 h) and then continued to exert a fairly consistent influence throughout playback.

Sapolsky (2006, p. 642) warned that for cultural style: ‘discerning the mechanism of transmission will be particularly difficult ...; it will be far easier to observe the circumstances under which an individual adopts a type of tool use than to identify the performance of a pre-existing behaviour but to a unique extent’. This study represents the first empirical attempt to address this challenge. Diffusion of cultural style, entailing changes in levels of performance of behaviours already in the repertoire, not adoption of novel behaviours, is likely to be supported by different, cognitively simpler, processes than qualitative culture. Previous proposals include facilitation (Sapolsky & Share, 2004; de Waal & Johanowicz, 1993), observational learning perpetuated by repeated behavioural exchanges (Sapolsky, 2006) and social contagion (Watson & Caldwell, 2010). We suggest playback initiated a self-reinforcing positive-feedback loop, sustaining influence beyond playback exposure through cycles of social interaction and social contagion between individuals, leading to a shared community pattern. Social influence between groups may also have contributed. Our findings indicate auditory social contagion represents a potential transmission mechanism for cultural style, and our method will allow researchers to test further hypotheses about underlying processes.

Our evidence supporting social diffusion of cultural style in marmosets suggests either that the phenomenon is phylogenetically ancient, preceding the split between Old World and New World primates, or that it appeared in marmosets as a result of convergent evolution, perhaps associated with characteristics as cooperative carers of infants (Burkart et al., 2009). Comparative study should clarify phylogenetic distribution. The method presented here offers scope for experimental application across diverse species (MacLean et al., 2012) because it examines alteration in levels of pre-existing, and thus spontaneously occurring, behaviours, rather than depending on rare behaviours, innovations or introduction of novel behavioural variants. For the same reasons, our method opens a new, promising avenue for empirical exploration of social culture, a relatively underinvestigated and more challenging subject of inquiry than instrumental, food-related traditions. Although cultural style is demonstrably present in human societies (e.g. Remland et al., 1995), underlying transmission processes have yet to be studied experimentally. Simultaneous

influence via positive social contagion on the productivity of a group has been demonstrated, with actor confederates (Barsade, 2002) initiating a 'group affect' (Barsade & Gibson, 2012). Could a longer-lasting change, an alteration in cultural style, be generated in humans? Transgenerational persistence could potentially be investigated using a microculture serial replacement paradigm (Caldwell & Millen, 2008; Jacobs & Campbell, 1961).

Affiliative call playback additionally represents a novel potential application for refining captive welfare. While the enrichment potential of conspecific territorial call playback has been investigated (Shepherdson, Bemment, Carman, & Reynolds, 1989) that of positive vocalizations remains untested. Playback in the current study prompted increased time in affiliative behaviours indicative of positive welfare and no significant increases in negative welfare indicators (Watson, 2011; Watson, 2009). Prerecorded affiliative calls thus represent ecologically valid stimuli for auditory non-contact social and sensory enrichment (Buchanan-Smith, 2010).

Our study successfully trialled an innovative method for examining cultural transmission experimentally, generating findings that clearly warrant further investigation. We hope to stimulate further research on cultural style in humans and nonhuman animals.

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### Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2014.04.027>.

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## Appendix

**Table A1**

Details of focal subjects

Condition	Identity	Sex	Source (at birth)	Date of birth	Age at start of study (in years and days)
Control	158g	M	MRC	4 Jun 2006	3 years 48 days
Control	279y	F	MRC	26 Oct 2004	4 years 269 days
Control	198g	M	MRC	10 Feb 2008	1 year 163 days
Control	355y	F	MRC	7 Oct 2007	1 year 288 days
Control	189g	M	MRC	19 Dec 2007	1 year 215 days
Control	357y	F	MRC	19 Nov 2007	1 year 245 days
Control	190g	M	MRC	19 Dec 2007	1 year 215 days
Control	1116	F	HL	25 Sep 2006	2 years 300 days
Control	792b	M	MRC	1 Jan 1998	11 years 202 days
Control	331y	F	MRC	12 Jan 2006	3 years 191 days
Control	157g	M	MRC	4 Jun 2006	3 years 48 days
Control	311y*	F	MRC	12 Feb 2006	3 years 191 days
Control	749b	M	MRC	26 Aug 1996	12 years 331 days
Control	276y	F	MRC	3 Oct 2004	4 years 292 days
Control	155g	M	MRC	1 May 2006	3 years 82 days
Control	234y	F	MRC	18 Mar 2007	2 years 126 days
Experimental	088g	M	MRC	20 Aug 2003	5 years 336 days
Experimental	345y	F	MRC	17 Jul 2007	2 years 5 days
Experimental	961b	M	MRC	22 Jun 2001	8 years 30 days
Experimental	319y	F	MRC	28 Jun 2006	3 years 24 days
Experimental	862b	M	MRC	9 Apr 1999	10 years 104 days
Experimental	055y	F	MRC	2 Jan 2001	8 years 201 days
Experimental	120g	M	MRC	28 Sep 2004	4 years 297 days
Experimental	291y	F	MRC	30 May 2005	4 years 80 days
Experimental	176g	M	MRC	3 May 2007	2 years 80 days
Experimental	007v	F	HL	15 Jan 2007	2 years 188 days
Experimental	177g	M	MRC	3 May 2007	2 years 80 days
Experimental	335y	F	MRC	2 Apr 2007	2 years 111 days
Experimental	036g	M	MRC	30 Sep 2002	6 years 296 days
Experimental	347y	F	MRC	20 Aug 2007	1 year 336 days
Experimental	173g	M	MRC	4 Dec 2006	2 years 229 days
Experimental	145y	F	MRC	17 Jul 2002	7 years 5 days

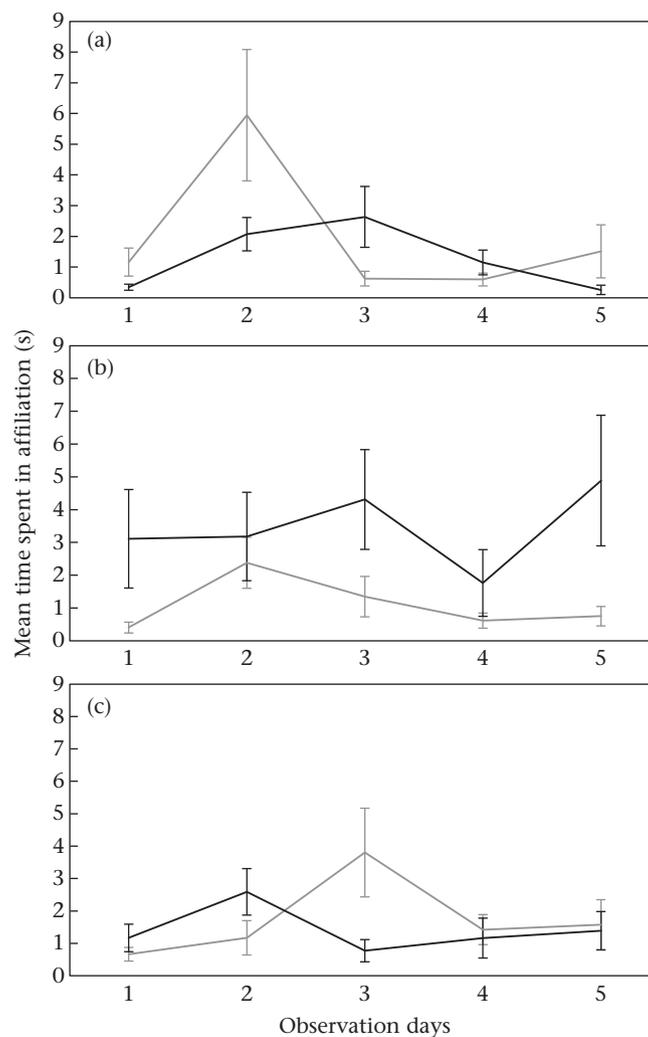
M = male; F = female; MRC = Medical Research Council, Human Reproductive Sciences Unit, Edinburgh, U.K.; HL = Harlan Laboratories, Shardlow, U.K.

\* Individual died after baseline and was therefore excluded from analysis.

**Table A2**  
Definitions of behavioural terms used during focal sampling

Behaviour	Definition
<b>Affiliative behaviours</b>	
Allogroom	Individual is cleaning the fur or skin of another individual using hand or mouth
Groom invite	Individual stretches out on back or side next to another individual: frequently elicits allogrooming
Affiliative contact	Individual performs active affiliative contact (excluding allogrooming) towards another individual: nuzzling (rubbing muzzle) or licking (including the anogenital area)
Share food	Individual shares food or allows food to be taken when another reaches towards them with hand or mouth (tolerated scrounging). No aggressive or threatening behaviour is seen
<b>Behavioural composites</b>	
Affiliation	Individual performs allogroom, groom invite, affiliative contact or share food (see above)
Intergroup agonism	Individual performs anogenital present (present genitals while raising tail)
Intragroup agonism	Individual chases (pursues another aggressively), attacks (lunges at, and/or either attempts to or does bite, cuff or scratch another individual or steals food (takes food directly and rapidly from another, often chased by the individual they have stolen from)
Anxiety-related	Individual performs inactive alert (stationary, awake and attentive to their surroundings), agitated locomotion (rapid movement between locations (walking running, climbing or jumping) with an exaggerated gait, excluding play), self-scratch (repeated movement of hand or foot with claws rapidly drawn across fur), scent-mark (rubs sternal or anogenital area over substrate), self-groom (cleans own fur or skin with hands or mouth), gouge (gnawing wood with teeth)

Definitions modified from [Stevenson and Poole, 1976](#); [Stevenson and Rylands, 1988](#); [Bassett, Buchanan-Smitih, and McKinley, 2003](#), [Watson & Caldwell, 2010](#); [Watson 2011](#); and [Buchanan-Smith and Badihi, 2012](#).



**Figure A1.** Longitudinal change in mean absolute time (s) spent in affiliation per observation session  $\pm 1$  SE by marmosets in the control condition (grey line) and the chirp condition (black line) across observation days in the (a) baseline, (b) playback and (c) postplayback phases.