The influence of social structure on the propagation of social information in artificial primate groups: A graph-based simulation approach

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Abstract

Observations of primate groups have shown that social learning can lead to the development of temporal stable traditions or even proto-culture. The social structure of primate groups is highly diverse and it has been proposed that differences in the group structure shall influence the patterns of social information transmission. While empirical studies have mainly focused on the psychological mechanisms of social learning in individuals, the phenomenon of information propagation within the group has received relatively little attention. This might be due to the fact that formal theories that allow actual testing have not been formulated, or were kept too simple, ignoring the social dynamics of multi-agent societies. We want to propose a network approach to social information transmission that (1) preserves the complexity of the social structure of primate groups and (2) allows direct application to empirical data. Results from simulation experiments with artificial group structures confirm that association patterns of group-members influence the expected speed of information transmission during the propagation process. Introducing a forgetting rate shows that under certain conditions the proportion of informed individuals will reach a stable rate in some systems while it will drop to zero in others. This suggests that the likelihood to observe temporal stable traditions shall differ between social systems with different structure.

Keywords: Information transmission; Social system; Weighted graph; Social network

1. Introduction

In the early 1950s, the Japanese primatologist Kinji Imanishi used an imaginary dialogue between an evolutionist, a layman, a monkey and a wasp to demonstrate that culture—defined as the non-genetic transmission of habits—was entirely possible, and even likely, for animals other than humans (de Waal, 1999). This proposition was of course vigorously opposed by those who wanted the term culture to be reserved for humans alone. Whether or not some animal species have a “full blown” culture was, and still is, a matter of fierce debate. However, plenty of evidence has been collected that animals are capable of transmitting information socially and that such information transmission can lead to temporally stable traditions. The most famous examples for such traditions in animals include birdsong dialects (Kroodsma and Baylis, 1982), milk bottle opening in British tits (Hinde and Fisher, 1951), potato washing in Japanese macaques (Kawai, 1965), termite fishing (Goodall, 1968; Lohnsdorf, 2006), nut cracking (Biro et al., 2003; Sugiyama and Koman, 1979) and the use of medical plants (Huffman and Seifu, 1989; Huffman and Hirata, 2004) in chimpanzees. Experimental studies with guppies demonstrated that fish are able to learn new routes and foraging tasks socially both in the laboratory and in the wild (Laland and van Bergen, 2003; Reader et al., 2003).

So far the majority of experimental studies on social information transmission have focused on the psychological mechanisms responsible for social learning (see Heyes...
and Galef, 1996; Zentall and Galef, 1988; and chapters therein) and neglected social processes as potential influences on both the likelihood of transmission and the type of information that can be acquired socially (Coussi-Korbel and Fragaszy, 1995). The traditional experimental approach to social learning where individuals are tested in isolation after they have observed a physically separated demonstrator was repeatedly criticised for two reasons. First, it was argued that the understanding of social learning from ecological and comparative perspectives would be aided by experiments on social learning in groups rather than in individuals (Lepoiyre and Pallaud, 1985). Second, it was criticised that this type of experiments says little about the diffusion processes of socially learned behaviour through populations (Laland et al., 1996) and about the influence of the social dynamics on the transmission process (Coussi-Korbel and Fragaszy, 1995).

Studies of diffusion processes in pigeons have demonstrated that information transmission can be inhibited by the individuals’ propensity to adopt certain roles as either producers or scroungers (Giraldeau and Lefebvre, 1986, 1987; Laland and Plotkin, 1990). In the laboratory transmission, chain studies (Curio et al., 1978; Horner et al., 2006; Laland and Plotkin, 1990) have tried to simulate passage of information transmission along a line of several individuals, by iterating the classical social learning paradigm and using the observer of one test as a demonstrator for the next test. This paradigm was taken a step further by Galef and Allen (1995) who adopted a method by Jacobs and Campbell (1961) for the study of the stability of arbitrary traditions in humans. In their experiment founder colonies of rats were taught an arbitrary food preference. Individual members of the founder colony were then slowly replaced with naïve subjects and even several generations after the last founder had been removed, the arbitrary food preference was still evident. The same effect could be demonstrated in guppies where preferences for routes to a food source were transmitted over several generations (Laland and Williams, 1997). While these studies have convincingly demonstrated that information can actually spread in a population by means of social learning, they have still not addressed the question how information spreads within natural populations. The lack of studies in this direction might be primarily due to missing predictions how information shall spread in such populations, or that existing theories are kept too general to allow actual testing (Laland and van Bergen, 2003; Reader, 2004).

Field observations—mainly of primate groups—revealed a long list of seemingly socially transmitted habits. However, due to the observational character of these studies it is usually not possible to exclude asocial learning processes as candidate explanations for these behaviours. To support the claim that these behaviours were in fact socially transmitted, it was suggested that the spreading pattern of the behaviour itself can reveal something about the learning process involved (Galef, 1991). Lefebvre (1995) re-analysed the data of 21 cases of presumably culturally transmitted feeding innovations in primate groups. Social learning processes are argued to result in accelerating diffusion curves, such as the logistic, the exponential, or the hyperbolic sine (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981; Laland et al., 1996) as the number of demonstrators of the behaviour increases over time. In contrast, asocial learning should result in a linear diffusion curve. According to Lefebvre, the primate data supported the assumption that the innovations were transmitted socially. However, recently (Laland and van Bergen, 2003) demonstrated that even asocial learning processes can result in accelerating diffusion curves if one incorporates variation in the individuals’ learning rates—a truly justified assumption—into the model. Reader (2004) summarises over 20 datasets where diffusion curves have been used to distinguish social from asocial learning. He reported that the shapes of the curves were quite variable and often did not fit the predictions sufficiently. As a likely reason for this discrepancy he suggested that the models were so far too simple, neglecting the effects of the population’s social structure. Recently, Kendal et al. (2007) have investigated social learning processes in small groups of callitrichid monkeys. They simulated the effects of three learning processes—stimulus enhancement, observational learning and asocial learning—and selected the model-parameters that provided the best fit to the data. Logarithmic and inverse functions provided the best fit for most diffusion curves. They found no evidence for observational learning; however that might be due to the nature of the foraging task. Socio-spatial parameters might play only a marginal role in such egalitarian species studied under spatially confined conditions and were not included in the model.

To investigate effects of the social structure on the propagation dynamics, we developed a stochastic model that allows us to make predictions about the expected patterns of information transmission in closed social units. This model shall include varying transmission rates for different individuals according to the social structure of the system and it should be formulated in a general way that does not restrict its applicability to only a small class of social systems.

2. Method

2.1. Graph-representation of social systems

Social systems can be described in many different ways. For the study of social dynamics it is, however, crucial that the complexity of the system is not lessened by an overly reductionist descriptor. A method to avoid this is to represent the group structure by a socio-matrix (Moreno, 1946). For the study of information transmission, the critical variable is the likelihood with which
information is passed from one specific individual to any other. In some cases—depending on the type of information—this likelihood might be basically determined by the proximity of the individuals (Coussi-Korbel and Fragaszy, 1995). If this is the case, some measure of proximity such as the association index (Clutton-Brock et al., 1982), might be the best descriptor of the social structure. In other cases, where more detailed information has to be obtained or where information can easily be concealed from unwanted onlookers, other measures like nearest-neighbour or grooming data might be more appropriate.

To investigate information flow in small-scale societies we mapped the social networks as graphs where the vertices represent individuals and edges between the vertices represent the “connections” between the individuals (see Scott, 1991; Wasserman and Faust, 1994 for extensive treatment of this method). Such an approach has been used to study network dynamics in human (e.g. Moreno, 1946; Nyblom et al., 2003; Watts, 1999; Watts and Strogatz, 1998) and animal (e.g. Croft et al., 2004; Fewell, 2003; Flack et al., 2006; Lusseau and Newman, 2004) social systems. For a recent review on the network approach in the behavioural sciences see (Krause et al., 2007). In our case, the edges represent spatiotemporal associations of a kind that enable the transmission of a specific information unit. The weight of an edge represents the likelihood that such an association is formed between the two individuals of a specific dyad. Henceforth we will refer to the formation of such an association as an interaction. In our examples, data were either derived from proximity matrices where entries in the matrix represent the numbers of instances where two individuals were observed close to each other or from grooming matrices where entries represent the numbers of grooming interactions between two individuals. As we define a group as a set of individuals that interact with each other on a regular basis, the group is represented as a complete graph with \( \binom{2}{1} \) edges. Social groups can differ in the total amount of interactions during a certain time period and the distribution of these interactions between the individuals. As it is trivial that information will be transmitted faster when individuals interact more frequently (all other parameters being constant), we investigated only the question how the group structure, i.e. the distribution of interaction likelihoods might affect information transmission. For this reason interaction likelihoods for dyads were always standardised by dividing through the sum of all matrix elements. For groups of equal size, a higher sum of all matrix elements would mean that individuals were interacting at a higher rate or spent more time in close proximity. However, this conclusion is only valid if data were collected with the same sampling protocol. As this is often not the case when comparing data from different field studies, standardisation will not only eliminate effects due to group size but also due to different sampling procedures.

\[ \omega(v) = \begin{cases} 0, & \text{if } \omega(u) = \omega(v) = 0, \\ 1, & \text{if } \omega(u) = 1 \lor \omega(v) = 1 \end{cases} \forall [u, v] \in V(G, w). \]  

(1.2)

(4) The simulation is terminated as soon as all individuals have acquired the information.

This scenario is basically equivalent to the SI-model in epidemic modelling, where there are only two classes of individuals, susceptibles and infected, and once an individual got infected it will not change its status thereafter. The simulation was implemented as a routine for the Mathematica 6.0 software package from Wolfram Research Inc.

3. Experiment 1

The first simulation experiment was carried out in order to determine whether the group structure can influence transmission speed and spreading pattern of socially...
propagated information. For this purpose we constructed five artificial group structures (Fig. 1), termed equal, chain, star, linearA and linearB. By using artificial structures we can apply the same construction algorithm to any required group size. Furthermore, this approach allows us to investigate a broader range of networks than when we were just relying on existing data of real social groups. However, to demonstrate how real world data from observational studies fit into this modelling approach we included a socio-matrix of a group of 16 rhesus monkeys (Macaca mulatta) studied by (Sade, 1972), termed rhesus16. The simulation was run 1000 times for each of the five systems for the group sizes of 6–60 in increments of 6 and 10,000 times for the rhesus16 system.

3.1. Results: transmission times

To compare average transmission times for the five systems, we plotted the mean time (measured in rounds) for the first to the $n$th transmission in each group of group size $n$ (Table 1). We found clear differences between the investigated systems in both the mean time until the individuals acquired the information and the shape of the transmission curve (Fig. 2). Out of the five investigated systems, the system equal seems to be the most efficient system (i.e. fastest in terms of transmission speed). The system star shows lower transmission times in the intermediate phase of the transmission process, but only for group sizes larger than 12 and it has still higher transmission times in the early and late phases. Not surprisingly (except, perhaps, for some military officers), the system chain where information can only be passed down along one line performed worst. The systems linearA and linearB were designed to be more similar to natural societies where some individuals are more in the centre in the sense that they enjoy more interactions with others or

![Fig. 1. Representation of the five artificial systems used in this study. In the graph representations vertices are individuals and edges are interactions between individuals. The thickness of the edges is proportional to the interaction rates between the individuals. Vertices are arranged in a circle and the distance between vertices has no specific meaning. Examples are given for group size $n = 6$. The systems are (a) “equal” with equal interaction rates between all individuals; (b) “chain” which can be thought of as a row of individuals where each one interacts just with its two neighbours, except for the outmost individuals which have only one neighbour; (c) “star” where all individuals interact only with one individual in the centre of the group; (d) “linearA” and (e) “linearB” where interaction rates vary systematically with some individuals having overall high interaction rates and others having overall low interaction rates. The equations describe the construction algorithms for group size $n$.](image-url)

<table>
<thead>
<tr>
<th>Average transmission times</th>
<th>Mean number of rounds in which the $n$th ($i = 1, \ldots, n-1$) transmission took place, averaged over all simulations for each system and group size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Characteristic path length</td>
<td>Mean of the means of the shortest path lengths connecting each vertex $v \in V(G)$ of the graph $G$ derived from the socio-matrix to all other vertices of $G$</td>
</tr>
<tr>
<td>Average path length*</td>
<td>Mean of the means of the shortest path lengths connecting each vertex $v \in V(T)$ of the transmission tree $T$ derived from the simulation to all other vertices of $T$</td>
</tr>
<tr>
<td>No. of informed individuals</td>
<td>At a given round of a simulation the number of vertices with a vertex weight of 1, $</td>
</tr>
</tbody>
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*While some authors use the terms characteristic path length and average path length interchangeably, we use average path length for the transmission tree that resulted from a simulation and characteristic path length for the graph representing the group structure.
have higher association indices, while other individuals are more in the periphery in the sense that they have fewer interaction with others or lower association indices. These systems, too, transmit information slower than the equal system, even though linearB is in its performance still quite close to system equal.

3.2. Results: path length

We calculated the average path length for the transmission tree of each simulation as \( \text{apl} = \frac{1}{(n-1)} \sum d(v_i) \), where \( n = |V(T)| \) and \( d(v_i) \) is the distance of vertex \( v_i \) from the root \( r \) of tree \( T \) (Fig. 3). The average path length is a measure for the closeness of the vertices of the graph. Median values for the average path length over all simulations for each structure are plotted against group size in (Fig. 4). The two systems chain and star are exceptional with respect that they are not complete graphs. While these systems do not conform with our original definitions of a group, we still included them in our study because they represent two extreme cases. The system star is the system with the shortest characteristic path length which is given by \((2n-2)/n\), and the system chain is the system with the longest characteristic path length given by \((n+1)/3\). These systems deliver the lower and upper benchmark (Lovejoy and Loch, 2003) for the expected average path length. All other systems are expected to have average path lengths between these two extremes. The systems linearA and linearB did not differ from system equal in their average path length and even the average path length of the rhesus16 system with several zero weights did not deviate substantially from these systems. As the path length might have considerable consequences for the expected variation of a trait in a population (see Section 6), we set up a second simulation experiment to investigate this phenomenon more closely.

4. Experiment 2

While in experiment 1 the average path length of the constructed systems equal, linearA and linearB was nearly identical and also the average path length of the system rhesus16 did not deviate much from the former, it is...
possible to construct systems that will yield much higher (or lower) average path lengths. For example, one can take the chain system and fill up the missing connections by connections with weights very close to zero. This system would then fulfill all requirements of a regular group but would still yield an average path length close to the one of the chain system. The same procedure can, of course, be used for the star system. By gradually increasing the weights of these groups, one can generate systems for any expected average path length between the lower and upper benchmark. However, systems with extreme average path lengths might be both highly arbitrary and highly unlikely. While the question of arbitrariness awaits empirical surveys, we tried to answer the question of likelihood by sampling systems with randomly allocated interaction rates. To estimate the expected variance in the average path length we constructed 1000 systems by randomly allocating edge weights (representing interaction likelihoods) between 0 and 1 to each edge of a complete graph for group size 16. Additionally, we constructed 200 systems where random interaction rates \( s \) were assigned to the individual agents and edge weights were given by the product of the interaction rates of the two agents \( s_{ij} \). For each of these 1200 systems, we ran the simulation as described above with 1000 repetitions.

4.1. Results

For a group size of \( n = 16 \) the mean average path length for the random systems was \( 2.41 \pm 0.46 \) (mean ± S.D.; based on 1000 random systems with 1000 simulations, each). These values were very close to the estimates for the mean average path length of system equal, \( 2.39 \pm 0.46 \) (Fig. 5). For the 200 systems with randomly allocated interaction rates for the individuals, the mean average path length was slightly higher with \( 2.46 \pm 0.51 \), but still very close to the mean for the system equal. In total 95% of the estimates for the mean average path length of the random systems were between 2.38 and 2.44, thus covering only 1.5% of the bandwidth of possible mean values given by the expected means for the system star (1.87) and chain (5.67).

5. Experiment 3

So far we have assumed that once an individual acquired the information it will keep it until the end of the simulation. Now we want to ask, how a propensity to forget the information again would influence the performance of the systems. To do this we ran another set of simulations with an additional rule: After each round a randomly chosen individual will forget the information with a certain probability (forgetting rate \( P(eo_{ij} \rightarrow 0) \)) and become a naïve individual again. This scenario is equivalent to the SIS-model in epidemic modelling. Furthermore, we had to introduce a new stopping rule: instead of terminating the simulation as soon as all individuals are informed (a criterion that might not be reached when the forgetting rate is reasonably high), the simulation was terminated after 2000 rounds. This simulation series was carried out with all five systems for a group size of 16 and the rhesus16 system. We simulated transmission with forgetting rates of 0.1%, 0.5%, 1%, 2%, 3% and 5%.

5.1. Results

Transmission curves for single simulations of this experiment differed from the previous ones in that they are not necessarily monotonically increasing. If in one round no naïve individual adopts the information, but one individual forgets it, then the transmission curve is actually decreasing (Fig. 6a). If the number of informed individuals
becomes at one point of the simulation zero, the information cannot be transmitted any further and we say that the information “died out” (Fig. 6b). For low forgetting rates, the information died out in a small proportion of the simulations within the first hundred rounds but this proportion reached a stable phase thereafter for all six systems. Though, the time until this equilibrium state was reached differed between the systems (Fig. 7a and b). Almost trivial, for high forgetting rates the information died out in all systems (Fig. 7f). However, for intermediate forgetting rates we found that the information died out only in some systems, while it remained stable over the 2000 rounds period in others (Fig. 7c–e).

6. Discussion

As information propagation in social groups cannot be understood without considering the underlying social network structure (Croft et al., 2005), any formal or stochastic model that is put up to produce testable hypotheses has to incorporate the specifics of the social system. Here we presented a network approach to study the propagation of information in small-scale social groups. Simulating information-flow in artificial as well as natural group structures we found that the speed of information transmission increased as a function of the proportion of informed individuals in a group. Such a “bush-fire effect”...
is a general characteristic of social trait propagation and well documented in the literature (Cavalli-Sforza and Feldman, 1981; Girardeau and Caraco, 2000). However, we could also show that the strength of this effect varied markedly between the investigated systems. This is in accordance with the suggestions made by Coussi-Korbel and Fragaszy (1995), that the structure of an animal group shall influence the efficiency of social learning. Empirical studies on primates (Bonnie and de Waal, 2006; Nahallage and Huffman, 2007) and fish (Reader and Laland, 2000) delivered evidence that information spreads faster within classes of closely related animals or individuals of the same sex. As members of such classes often spend more time with each other than with members of other classes, these findings are in accordance with our model. By introducing a forgetting rate (Section 5) we could show, that such differences in propagation speed can have considerable impact on the longevity of cultural traditions. Interestingly, the systems’ sensitivity to forgetting is not equivalent with their efficiency to transmit information: the most efficient system in terms of propagation speed (system equal) was not the most robust against forgetting. This forgetting rate can either be understood as the forgetting of the information by single individuals or that informed individuals die or leave the group and are replaced by naïve individuals. While the former case will be of interest primarily when modelling horizontal propagation within individuals of one generation, the latter interpretation enables us to model vertical transmission over many generations.

If we assume that the transmission process from one individual to the other is a source for “transcription errors”, then the length of a transmission chain shall influence the extent to which the behaviour is modified. Therefore, the average path length of the information chain can provide us with an estimate which variability of a trait we might expect in a population with a given structure. Except for the highly arbitrary systems chain and star, we could not find clear differences in the expected path lengths of the investigated systems. This was also the case for 1200 systems with randomly allocated interaction rates. Thus, it seems that contrary to our expectations for a broad range of systems group structure does not influence the expected average path length, and hence the expected variability of a trait. In this respect, the systems resemble “small worlds” (Watts and Strogatz, 1998) where the mean path length is proportional to the logarithm of the group size.

The dynamics of information transmission within populations equal those of disease transmission which have been studied extensively in the past (see Daley and Gani, 1999; Hethcote, 2000). If populations are fully mixed, that is, any individual has the same fixed probability per unit of time of contracting the disease from any infected individual in the population, the number of infected individuals can be modelled by a system of ordinary differential equations. While the basic SI model allows only for two classes of individuals, susceptibles and infected, the SIR model assumes that infected become removed probabilistically or after a certain time period and the SIS model considers infected that become susceptible again (Hethcote, 2000). However, modelling the number of infected and susceptible individuals as continuous variables gives only poor approximations in small populations. In such cases, the system can be modelled as a Markov process with discrete population and time, where the probabilities of transmission from \((s, i)\) to \((s - 1, i + 1)\) and \((s, i - 1)\) are given by \(b si \Delta T\) and \(g i \Delta T\), respectively (Witten and Poulter, 2007). Recently, network approaches to disease (Eubank et al., 2004; Liljeros et al., 2001; May and Lloyd, 2001; Newman, 2003; Nowak and Bangham, 1996; Verdasca et al., 2004; Witten and Poulter, 2007) and information (Kincaid, 2000; Kossinets and Watts, 2006; Valente, 2005; Watts and Strogatz, 1998) transmission have proven to allow more detailed predictions as they release the assumption of fully-mixed populations.

Primate groups are small—they usually consist of less than hundred animals—and despite the fact that every animal interacts with any other they are not fully-mixed as interaction rates differ significantly between dyads. To account for these characteristics we represented the groups as complete weighted graphs. As several frequently used measures like characteristic path length, connectivity or betweenness are only of limited or no use to analyse such graphs (Barrat et al., 2004; Lovejoy and Loeh, 2003), we opted for a simulation approach, where information flow was modelled as a stochastic process. The outcome of each simulation was a propagation tree that allowed us to measure transmission speed and average path length. Because we hypothesised that relative interaction frequencies are basically determined by spatial proximity we used a measure of proximity as predictor for information transfer. As proximity matrices are by their very nature symmetric (whenever A is close to B, B is also close to A), the systems could be represented as simple graphs. However, if there is reason to believe, that the likelihood of information-flow between two individuals is not symmetric (e.g. subordinates are more likely to learn from dominants), then our approach can be easily extended using directed multigraphs where each pair of vertices is connected by two edges, one in each direction.

We did not attempt to develop a framework that requires to classify social systems or to rank them along a single dimension. While a simple classification scheme would facilitate generalisations about system behaviour, we believe that the representation of social systems by socio-matrices has several advantages. (1) It is less reductionist than any classification system, as it preserves the complexity of the system. (2) It is more flexible and allows the investigation of any possible system. There is no uncertainty about class-membership and there are no exceptional structures that do not fit into the framework. (3) Is directly applicable to empirical data, as socio-matrices are well-established tools in the social and behavioural sciences and as these socio-matrices can be mapped directly onto the adjacency matrix of the graph.
With this study we could demonstrate the potential influence of group structure on the propagation of information. The next steps will be to extend the bandwidth by investigating properties of a broad range of existing social systems, and to test predictions stemming from these models experimentally in captive and wild primate groups. Such tests will consist of four components: establishing the social structure of the study group, making predictions for the most likely spreading patterns based on the social data, introducing a novel behaviour and recording its spreading pattern within the group. The suggestion that mechanisms of cultural learning in non-human primates might be homologous to those in humans, stimulated research on cultural traditions especially in primates. However, this modelling approach shall not be restricted to primates, but it can be applied to any species living in social groups.

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