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Social enhancement can create adaptive, arbitrary and maladaptive cultural traditions

Mathias Franz[1,2,*] **and Luke J. Matthews**[3]

[1]*Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany*
[2]*Courant Research Centre Evolution of Social Behaviour, University of Göttingen, Kellnerweg 6, 37077 Göttingen, Germany*
[3]*Department of Human Evolutionary Biology, Harvard University, Peabody Museum 11 Divinity Avenue, Cambridge, MA 02138, USA*

Many animals are known to learn socially, i.e. they are able to acquire new behaviours by using information from other individuals. Researchers distinguish between a number of different social-learning mechanisms such as imitation and social enhancement. Social enhancement is a simple form of social learning that is among the most widespread in animals. However, unlike imitation, it is debated whether social enhancement can create cultural traditions. Based on a recent study on capuchin monkeys, we developed an agent-based model to test the hypotheses that (i) social enhancement can create and maintain stable traditions and (ii) social enhancement can create cultural conformity. Our results supported both hypotheses. A key factor that led to the creation of cultural conformity and traditions was the repeated interaction of individual reinforcement and social enhancement learning. This result emphasizes that the emergence of cultural conformity does not necessarily require cognitively complex mechanisms such as 'copying the majority' or group norms. In addition, we observed that social enhancement can create learning dynamics similar to a 'copy when uncertain' learning strategy. Results from additional analyses also point to situations that should favour the evolution of learning mechanisms more sophisticated than social enhancement.

Keywords: social learning; social enhancement; imitation; conformist transmission; culture; agent-based model

1. INTRODUCTION

An expanding base of research now supports the notion that social-learning mechanisms are common throughout the animal kingdom. Captive experiments have demonstrated the social-learning capabilities of animals from a broad taxonomic sample, while studies in the wild have inferred the presence of behavioural traditions transmitted by social learning in a diversity of taxa (Galef & Giraldeau 2001; Laland & Hoppitt 2003; Perry & Manson 2003). In the context of animal research, social learning can be defined 'as any process through which one individual ('the demonstrator') influences the behaviour of another individual ('the observer') in a manner that increases the probability that the observer learns' (Hoppitt & Laland 2008). Behavioural traditions, meanwhile, are patterns of behavioural similarity across individuals which are at least partly maintained by social learning (Fragaszy & Perry 2003; Perry & Manson 2003).

Researchers have categorized alternative social-learning mechanisms by the information that is acquired socially about the learned behaviour. These mechanisms include 'rational' motor imitation of the intentions of another's action (Buttelmann *et al.* 2007), affordance or emulation learning about the use of an object (Tomasello & Call 1997; Dindo *et al.* 2008), imitation of action sequences (Whiten 1998; Byrne 2003) and teaching (Boesch 1991; Thornton & McAuliffe 2006). However, the majority of species studied to date display only stimulus and/or local enhancement learning of object manipulation tasks (Laland & Hoppitt 2003). Stimulus enhancement occurs when an animal directs its behaviours towards an object or part of an object with which it saw another individual interact, irrespective of where the object is subsequently located (Whiten & Ham 1992; Heyes 1994), while local enhancement occurs when an animal directs behaviours towards the place in which it witnessed another individual act (Galef & Giraldeau 2001; Hoppitt & Laland 2008). These mechanisms can be considered collectively to comprise simple forms of social enhancement (Hoppitt & Laland 2008). When employing social enhancement, observers do not imitate the motor actions or intentions of the demonstrators, nor do the observers gain any information about how to successfully perform the behaviour (Visalberghi 1987; Whiten & Ham 1992).

Significant debate exists regarding how these various underlying social-learning mechanisms influence the transmission and maintenance of behavioural traditions. Some researchers have emphasized that a variety of cognitively complex social-learning biases, usually to include teaching, imitation and conformity to group-typical behaviour, would be required to maintain the fidelity and adaptedness of traditions (Whiten *et al.* 2005, 2007;

* Author for correspondence (mathias.franz@zentr.uni-goettingen.de).

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Dindo *et al.* 2008, 2009; Claidiere & Sperber 2009). Other researchers have tended to see very simple mechanisms, like stimulus enhancement, as sufficient to create and maintain traditions (Kawai 1965; Warner 1988, 1990; Provenza 1995; Terkel 1996; Laland & Williams 1997, 1998; Galef 2003; Matthews 2009; Matthews *et al.* 2010).

Specifically, several researchers have proposed that social enhancement can maintain robust traditions simply through interaction with reinforcement learning (Spence 1937; Thorpe 1956; Galef 1995; Terkel 1996). In one particular example, capuchin monkeys appeared to consistently avoid the costs of early learning trials that are associated with novel behaviours, which caused reinforcement to maintain socially enhanced behavioural patterns over at least short-time scales (Matthews *et al.* 2010). One way to conceptualize such dynamics is by considering the shape of a typical learning curve (Harlow 1949) for the simple case when the curves for all alternative behavioural variants are identical (figure 1). In this situation, there is always a loss of profit for switching between alternative behaviours once an animal is highly proficient at one variation. Thus, simple social-learning mechanisms like social enhancement could conceivably produce traditional patterns of behaviour. So long as the behaviours develop through typical learning curves (figure 1), the social-learning mechanism need only cause individuals generally to start down the path of the same behavioural variant; for example, by directing their attention to the same part of an object. In this model, individuals must only be more motivated to perform a variant because of their social experience in order to produce traditions. It is unnecessary that they gain any knowledge or proficiency in the behaviour, nor need they employ any specialized psychological transmission biases.

Based on the conceptual model of Matthews *et al.* (2010), we developed an agent-based simulation model to better investigate the long-term learning dynamics of social enhancement interactions with reinforcement. In our model, individuals employ both social enhancement and reinforcement learning in each learning trial. During social enhancement, individuals increase their probability to perform a behavioural variant (e.g. interacting more with a part of an object) but gain no information about how to perform the action successfully. The latter information is acquired only through reinforcement learning trials. Using this simulation framework, we tested two specific hypotheses:

(i) social enhancement can create and maintain adaptive traditions through interaction with reinforcement learning; and
(ii) social enhancement can create cultural conformity in the absence of any conformity bias or other learning biases.

We also incorporated an 'imitation-like' learning type in the model, in which individuals gain knowledge of how to perform an observed behaviour. Imitation-like learning can be thought of as an approximation for the gross differences between social enhancement, and mechanisms like motor imitation, rational imitation and emulation. With the latter three processes, an animal socially acquires information about how to perform a behavioural variant more effectively, rather than merely directing more of its attempts at performing the observed variant. We investigated how imitation-like learning dynamics differ from social enhancement learning. This allowed us to develop hypotheses regarding the conditions under which more sophisticated learning mechanisms such as imitation might evolve.

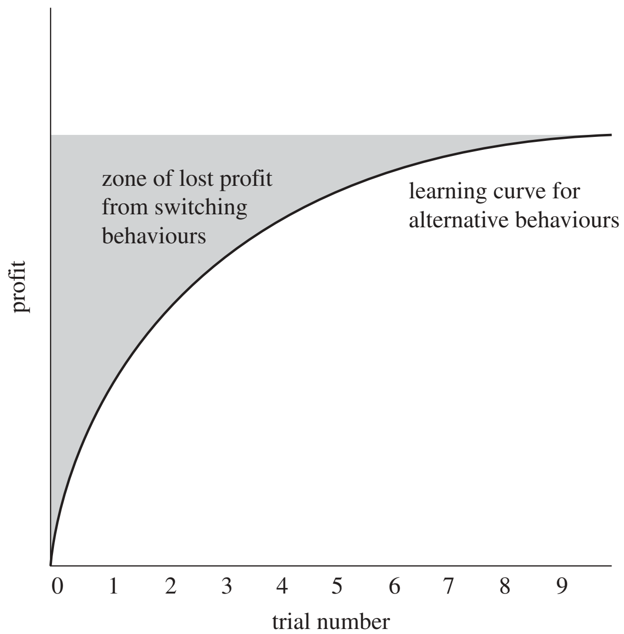

Figure 1. Hypothetical example of the profit lost by switching between alternative behavioural variations that have equivalent learning curves. By repeatedly performing a behaviour (i.e. with increasing trial number) individuals become more proficient in a behaviour and thus gain higher net pay-offs (which might involve lower cost in form of time to complete the behaviour). The increase in proficiency levels off with time which creates an upper asymptote of the learning curve. Once proficient at one behaviour, individual reinforcement learning should prevent the profit loss from switching to an alternative behaviour.

2. MATERIAL AND METHODS

(a) *Model description*

The model description is based on the Overview, Design concepts and Details (ODD) protocol for describing individual- and agent-based models (Grimm & Railsback 2005; Grimm *et al.* 2006). In the following we provide an overview. Information about model details is included in the electronic supplementary material.

(i) *Purpose*

The main aim was to implement the verbally formulated model of Matthews *et al.* (2010) in a mechanistic simulation model and explore long-term dynamics that are created by social enhancement learning. In particular, we were interested if social enhancement learning can create cultural conformity and lead to the emergence of stable traditions. Furthermore, we wanted to investigate the dynamics created by imitation-like learning to infer situations that would favour the evolution of more sophisticated social-learning mechanisms such as emulation or imitation.

(ii) *State variables and scales*

The model focuses on a group of N individuals. Each individual is characterized by its age, its probability to perform

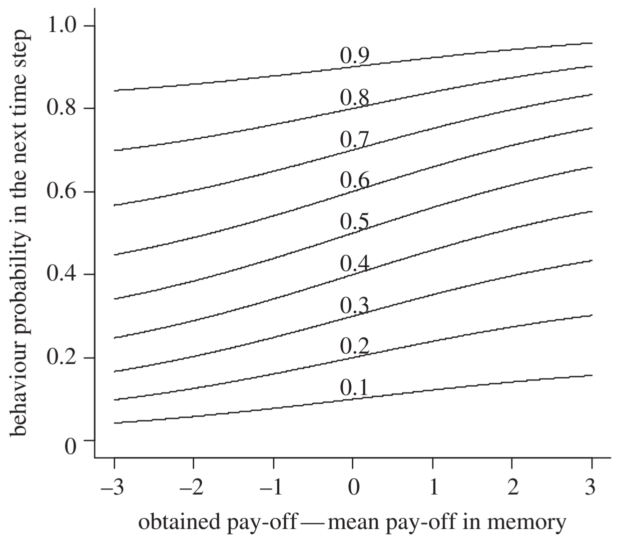

Figure 2. Illustration of reinforcement effects on the probability to continue performing a current behaviour in the next time step after reinforcement (*y*-axis). Line labels indicate the probability to perform the behaviour prior to reinforcement effects, while the *x*-axis shows the reinforcement in a single time step. For this example the parameter that determines strength of reinforcement (f_r) was set to 0.5. As indicated in this illustration, positive reinforcement (positive values on the *x*-axis) always led to an increase in the probability to perform the current behaviour and punishment (negative values on the *x*-axis) led to a decrease in this probability.

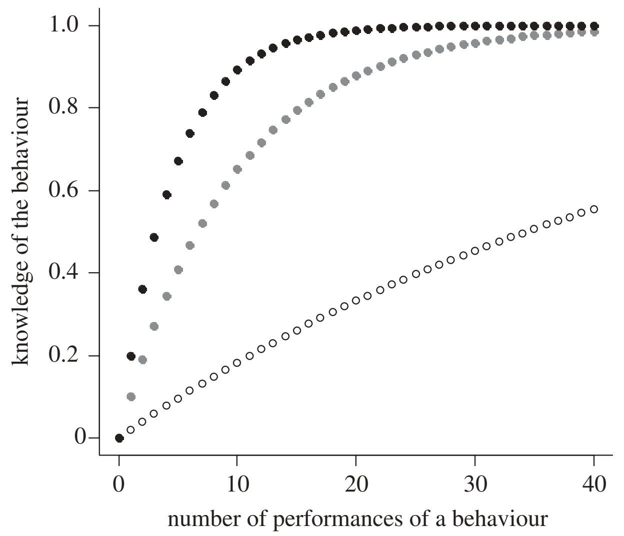

Figure 3. Illustration of knowledge increase for different values of parameter *g*, which determines the difficulty of learning a behaviour. Open circles correspond to $g = 0.02$, grey circles to $g = 0.1$ and black circles to $g = 0.2$.

one out of two alternative behaviours (X and Y), its knowledge of how to perform each behaviour and its memory, which stores all pay-offs that it has received from performing a behaviour.

(iii) *Process overview and scheduling*

The model proceeds in discrete time steps. To simulate population dynamics in a simple way, at every τ time steps the oldest individual is removed from the group and a new, naive individual is introduced. For each individual in each time step, learning dynamics involve (i) deciding which behaviour to perform (based on probabilities for both behaviours), (ii) receiving a pay-off from performing this behaviour (based on the knowledge for this behaviour), (iii) updating its probabilities to perform each behaviour in the next time step (based on the received pay-off, see figure 2), and (iv) updating its knowledge for the performed behaviour (figure 3). Individuals who only perform these four processes are individual learners. Social enhancement learners additionally observe, in each time step, one other individual at random. The observations occur concurrently with individual learning. Afterwards, social enhancement learners increase their probability to perform the behaviour they observed. Individuals who use imitation-like learning in addition to individual and social enhancement learning also increase their knowledge of the observed behaviour.

Individual learning dynamics depend on parameters g_X, g_Y, max_X and max_Y, which determine the steepness and the upper asymptote of the learning curves of the alternative behaviours X and Y (figure 1), and a parameter f_r, which determines the strength of the reinforcement effect on probabilities to perform each behaviour. In addition, a parameter f_{se} determines the strength of social enhancement effects on probabilities to perform each behaviour and a parameter f_{im} determines the strength of knowledge increase owing to imitation-like learning.

(b) *Model analysis*

Model analysis was designed to provide a proof of concept that social enhancement can create cultural conformity and stable traditions. To keep results as simple and clear as possible, we focused in the main set of analyses on a specific parameterization in which values of many parameters were held constant. In additional analyses, we explored the effects of varying parameter values that were kept constant in the main analyses.

In the main set of analyses, we investigated how different combinations of learning parameters for the two behaviours affect learning dynamics in groups composed entirely of individual learners, social enhancement learners or individuals who used imitation-like learning. We performed simulations with groups that consisted of 20 individuals and in which every 20 time steps the oldest individual was replaced by a naive individual. At the beginning of each simulation, all individuals were naive, i.e. they had an empty memory, no knowledge of how to perform any behaviour and the probability to perform each behaviour was set to 0.5. Furthermore, each individual was randomly assigned a different age at the start of each simulation.

We kept the learning parameters for behaviour X constant (knowledge increase $g_X = 0.1$ and maximum pay-off $max_X = 1$) while systematically varying parameters for behaviour Y (g_Y from 0.02 to 0.2 in steps of 0.02 and max_Y from 0.2 to 2.8 in steps of 0.2). The factor that regulates the strength of individual reinforcement learning f_r was set to 0.5, the factor that determines the strength of increase in the probability to perform behaviours owing to social enhancement learning f_{se} was set to 0.05. The factor that determines the effect of imitation-like learning on knowledge acquisition f_{im} was set to 0.1.

For each parameter combination we performed 100 simulations, each lasting 2000 time steps. For each simulation, we calculated the average frequency of behaviour Y and the average of all received pay-offs of all individuals during the last 1000 steps. These measurements were used to calculate the mean frequency of behaviour Y and mean received pay-offs over the 100 simulations. To measure behavioural diversity in the group, we calculated the frequency of the most frequent behaviour during the last 1000 time steps. Based on these values, we then calculated the average frequency of the most frequent behaviour over the 100 simulations. As an indicator for the performance of pure individual learning, we also calculated the mean pay-off divided by the maximum possible pay-off, max_b, of the behaviour that had the largest value of max_b. For simulations with social enhancement and imitation-like learners we calculated the per cent difference of mean pay-off relative to corresponding mean pay-offs across all individual learners.

3. RESULTS

(a) *Test of hypothesis 1*

To test hypothesis 1 we compared mean behaviour frequencies among groups in which individuals had different learning mechanisms. In what follows, we show that both social enhancement and imitation-like learning can cause almost all group members to perform the more profitable behaviour in situations when individual learning alone causes a substantial minority to perform the less profitable behaviour.

Individual learning led to high frequencies of behaviour Y when this behaviour yielded higher maximum pay-offs and was easier to learn. A behaviour was 'easier to learn' when knowledge increase parameter (g) of the behaviour was greater than the knowledge increase parameter for the alternative (upper right part of figure 4*a*). Low frequencies of behaviour Y were observed when this behaviour had lower maximum pay-offs and was harder to learn (lower left part of the plot). Intermediate frequencies could be observed when both behaviours were identical in learning parameters (where dashed lines intersect in plots of figure 4) and when one behaviour was easier to learn but the other one yielded higher maximum pay-offs (upper left and lower right parts of the figure 4*a*).

Consistent with our first hypothesis that social enhancement can create adaptive traditions, social enhancement led to increased frequencies of behaviour Y compared with individual learning when this behaviour yielded higher maximum pay-offs and was easier to learn, i.e. g_Y was greater than g_X (upper right part of figure 4*d*). Figure 5*d* shows how this effect occurred during a single example simulation, while figure 4*d* shows the effect across the two parameter dimensions that we varied systematically, relative pay-off and ease of knowledge increase. Also consistent with the first hypothesis, behaviour frequencies for Y decreased when behaviour Y was harder to learn and yielded lower maximum pay-offs (lower left part of figure 4*d*).

Imitation-like learning had a similar effect as social enhancement. However, in contrast to social enhancement learners, we also observed high frequencies of behaviour Y when this behaviour yielded higher maximum pay-offs but was harder to learn (upper left part of figure 4*g*).

(b) *Test of hypothesis 2*

To test hypothesis 2 we focused on simulations in which both behaviours were identical ($g_X = g_Y = 0.1$, $max_X = max_Y = 1$). As expected, the mean frequency of behaviour Y was about 0.5 for all learning mechanisms (figure 4*a*,*d*,*g*). However, the mean frequencies of the more frequent behaviour strongly differed between groups of individual learners (0.54) and social enhancement learners (0.98; Mann–Whitney U-test: $U = 0$, $N_{individual} = 100$, $N_{social\ enhancement} = 100$, $p < 0.001$). Thus, in groups of individual learners behavioural conformity was low, and each behaviour was performed about half of the time in each simulation. By contrast, in groups of social enhancement learners (and also imitation-like learners) behavioural conformity was very high. In each simulation that included social-learning mechanisms, all individuals in a group performed only one behaviour almost exclusively. This result is consistent with our second hypothesis that social enhancement can create an emergent pattern of conformity to arbitrary traditions without the operation of any conformity bias or other learning biases in the psychology of the agents.

(c) *Performance of different learning mechanisms*

Mean pay-offs gained by individual learning were generally close to the maximum possible pay-off, except for conditions in which behaviour Y yielded much higher pay-offs and was much harder to learn compared with behaviour X (upper left part of figure 4*c*). For some parameter sets, social enhancement learning resulted in higher mean pay-offs compared with the mean pay-offs gained by individual learners, which confirms the possibility that adaptive traditions can emerge from this learning mechanism. These parameter sets mainly included conditions in which behaviour Y yielded higher maximum pay-offs but was harder to learn than behaviour X (figure 4*f*). In these cases social enhancement led to the emergence of traditions to perform behaviour Y. However, for more extreme conditions in which behaviour Y was even harder to learn, social enhancement resulted in mean pay-offs that were lower than mean pay-offs of individual learners (figure 4*f*). This drop in mean pay-offs emerged because behaviour X consistently became a tradition in groups of social enhancement learners (figure 4*d*), which indicates the emergence of maladaptive traditions.

In general, imitation-like learning led to higher mean pay-offs compared with social enhancement learning (compare figure 4*f*,*i*). In addition, for the investigated parameter values we did not observe the emergence of maladaptive traditions for this learning mechanism. The strongest difference in mean pay-offs between social enhancement and imitation-like learners existed for parameter sets in which social enhancement resulted in the emergence of maladaptive traditions, i.e. when social enhancement yielded lower mean pay-offs than individual learning (compare figure 4*f*,*i*).

(d) *Additional analyses*

The electronic supplementary materials provide additional analyses about the robustness of our results to (i) changes in learning parameters f_r, f_{se} and f_{im}, (ii) population dynamics, i.e. interval at which individuals are replaced, and (iii) group size. The supplementary materials show that the results reported above remain qualitatively unchanged.

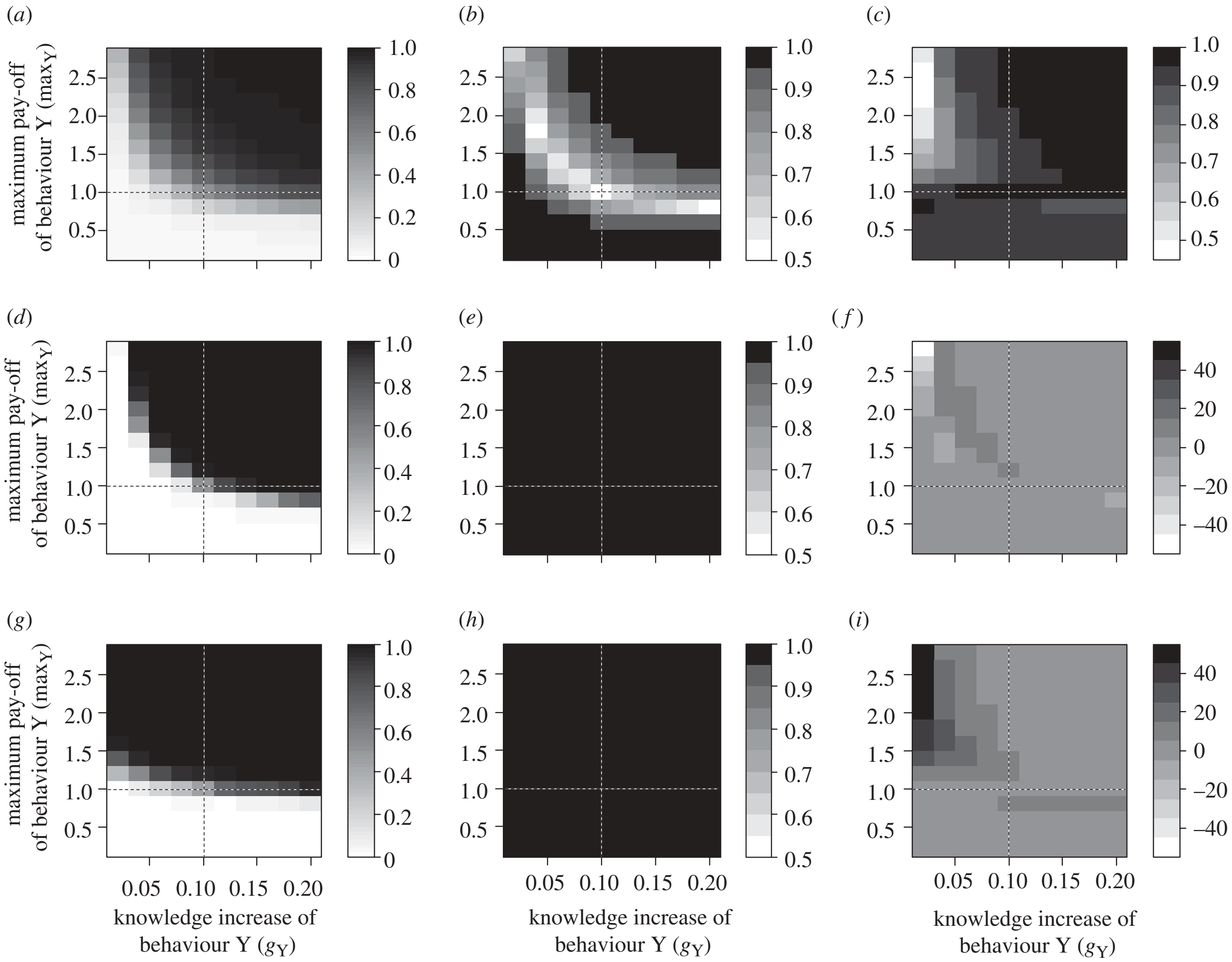

Figure 4. Outcomes of learning dynamics in groups of (*a*,*b*,*c*) individual, (*d*,*e*,*f*) social enhancement and (*g*,*h*,*i*) imitation-like learners, which were calculated from simulations that were repeated 100 times for each parameter set. The calculated values include the mean frequency of behaviour Y (*a*,*d*,*g*) and the mean frequency of the more frequent behaviour (*b*,*e*,*h*). For individual learners we also calculated mean pay-offs as proportions of the maximum possible pay-offs (*c*) and for social enhancement and imitation-like learners we calculated the per cent difference in mean pay-offs relative to mean pay-offs received by individual learners (*f*,*i*).

4. DISCUSSION

Our results showed that social enhancement can create adaptive, arbitrary and maladaptive traditions. Thus, our findings support both hypotheses we set out to test: (i) social enhancement can create and maintain adaptive traditions through interaction with reinforcement learning and (ii) social enhancement can create cultural conformity in the absence of conformity bias or any other learning biases. Furthermore, our results indicate that the strongest selection pressures to favour the evolution of more sophisticated learning mechanisms, such as imitation, may occur when more profitable behaviours are harder to learn than less profitable alternatives.

(a) *Model assumptions*

To avoid misleading interpretations of our results, we want to emphasize the limitations of our model, as its various simplifications may limit the generality of our results. One influential assumption is that social enhancement will always lead to an increased probability that an individual will perform the behaviour of the observed individual. This is certainly not always the case, for instance, when an object or part of an object can be manipulated in different ways.

In the current model, individuals do not use information about the pay-off received by the observed individual in either of the learning mechanisms as implemented in our model. One can easily imagine that such a learning bias could be very beneficial and thus many animals might be equipped with a ‘copy if better’ learning strategy (Laland 2004). On the other hand, many animals might not be able to infer the pay-offs gained by others with sufficient reliability (Laland 2004). The limited number of studies on pay-off biases during social learning have not revealed consistent results. While humans and nine-spined sticklebacks have exhibited pay-off biases (McElreath *et al.* 2008; Kendal *et al.* 2009), other studies on capuchin monkeys and chimpanzees found no support for such biases (Bonnie & de Waal 2007; Marshall-Pescini & Whiten 2008). While we do not expect that including pay-off biases in social learning would affect most of our results, it can be expected that it would prevent the emergence of maladaptive traditions.

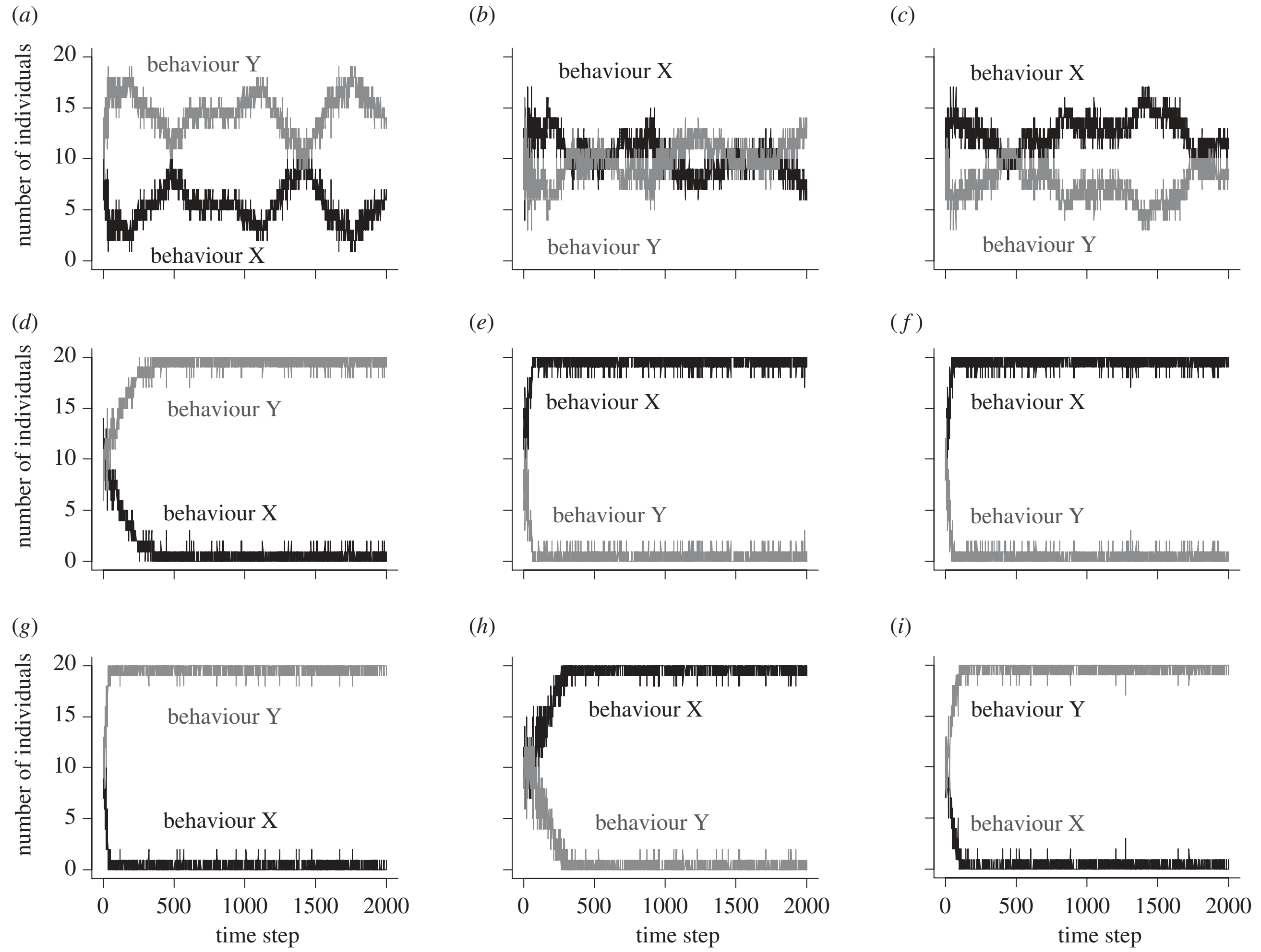

Figure 5. Examples of temporal dynamics of behaviour frequencies in groups of (*a*,*b*,*c*) individual, (*d*,*e*,*f*) social enhancement and (*g*,*h*,*i*) imitation-like learners. (*a*,*d*,*g*) Behaviour Y yielded higher maximum pay-offs ($max_Y = 1.2$) compared with behaviour X ($max_X = 1$) with learning difficulty being identical for both behaviours ($g_b = 0.1$). (*b*,*e*,*h*) Both behaviours had identical learning parameters $g_b = 0.1$ and $max_b = 1$. (*c*,*f*,*i*) Behaviour Y yielded higher maximum pay-offs ($max_Y = 1.2$) compared with behaviour X ($max_X = 1$) and was harder to learn ($g_Y = 0.06$) compared with behaviour X ($g_X = 0.1$).

In the current model, individual learning frequently results in nearly optimal pay-offs (figure 4*c*). Important reasons for this result include that gained pay-offs were deterministically linked to the knowledge of a behaviour, and that these pay-offs could be perceived accurately by individuals. Including variability in perceived pay-offs would certainly increase the realism of our model. However, we do not expect that this would qualitatively change the results.

Some parts of our model, especially assumptions about dynamics of social enhancement, are similar to assumption in the models of Van der Post & Hogeweg (2009) and Van der Post *et al.* (2009), which focus on learning about food preferences. In Van der Post's models, stable traditions emerged from a form of social learning that strongly resembles our assumptions about social enhancement learning. Therefore, our results are likely to be valid in context of learning what to eat.

(b) *The emergence of adaptive and maladaptive traditions*

The mechanism that led to the emergence of traditions in groups of social enhancement learners appears to be the interaction between individual reinforcement learning and social enhancement as proposed by Matthews *et al.* (2010). By observing another individual, the observer becomes more likely to engage in the same behaviour as the observed individual. The increased practice of this behaviour then causes the observer to become more proficient in the behaviour, which increases the probability to perform the same behaviour in future. Such behaviours might be appropriately termed 'habitual' (Matthews *et al.* 2010). These dynamics can lead to feedback effects between group members, because the frequency with which an individual performs a particular behaviour naturally affects the probability of observing an individual with this behaviour for other group members. As a consequence, in our simulations the more common behaviour in the group was amplified over time by feedback effects that are created by social enhancement learning (compare figure 4*a*,*d*). If the behaviour performed more frequently in groups of individual learners was the more profitable behaviour, then social enhancement led to the emergence of adaptive traditions (figures 4*f* and 5*d*). However, if the more frequent behaviour in groups of individual learners was the less profitable behaviour, then social enhancement led to the emergence of maladaptive traditions (figures 4*f* and 5*f*). Individual learners tended to perform the more profitable behaviour when it was only slightly harder to learn than the less profitable alternative, but if the more profitable behaviour was much harder to learn then individual learners usually performed the less profitable, but easier, behaviour. Thus, the interaction of social enhancement with reinforcement-induced habit explains the emergence of adaptive and also maladaptive traditions in our simulations.

Our finding that social enhancement learning in combination with individual reinforcement learning can lead to the emergence of maladaptive traditions adds to a recent debate on this topic. The term 'maladaptive' in this case means that individuals acquire a behaviour that is less adaptive than an alternative. Social-learning theory predicts that social learning can lead to the emergence of such maladaptations (Laland 1996; Giraldeau *et al.* 2002; Richerson & Boyd 2005). However, these predictions have been criticized because they overlook the fact that social and individual learning are not independent processes. Instead, both learning mechanisms interact with each other and thus individual reinforcement generally prevents animals from adopting maladaptive behaviours (Galef 1995, 1996). Previous research has focused on maladaptive behavioural traditions resulting from individuals relying on social information in the absence of available reinforcement trials, or from informational cascades in which the influence of social learning increases with an increase in demonstrations of a given behaviour (Bikhchandani *et al.* 1992; Giraldeau *et al.* 2002). By contrast, in our model maladaptive traditions emerge despite the integration of information that is acquired socially and individually. The key mechanism that allows the emergence of maladaptive traditions is that individual learning results in a learning curve (figure 1). If a behaviour is hard to learn then several individual learning trails are required to obtain information about the maximum pay-off that can be obtained from performing this behaviour. If another behaviour is less profitable but much easier to learn, then individual learning can lead to individuals getting stuck on the less profitable behaviour. As a consequence, individual learners in our model only rarely performed the more profitable behaviour under these conditions (upper left part of figures 4*a* and 5*c*). As explained above, under such conditions, stimulus enhancement dynamics are likely to create a tradition of performing the less profitable behaviour (upper left part of figures 4*d* and 5*f*), and thus effectively amplify the maladaptive decisions that result from reinforcement effects.

(c) *Conformity without copying the majority*

Conformist transmission has been thought of being an important psychological social-learning bias that creates cultural conformity in groups of individuals (Boyd & Richerson 1985; Henrich & Boyd 1998). It is usually also referred to as 'copying the majority'—an individual-level learning strategy (Laland 2004). Based on simple models it is argued that conformist transmission will be favoured by evolution under many conditions (Boyd & Richerson 1985; Henrich & Boyd 1998), (but see also Eriksson *et al.* 2007; Nunn *et al.* 2009) and results of many empirical studies are interpreted as evidence for the existence of conformist transmission in humans (Coultas 2004; McElreath *et al.* 2005, 2008) (but see Eriksson *et al.* 2007) and in animals (Day *et al.* 2001; Kendal *et al.* 2004; Whiten *et al.* 2007; Dindo *et al.* 2008; Galef & Whiskin 2008). Additionally, conformist transmission sometimes has been interpreted as synonymous with the existence of group norms (Whiten *et al.* 2005).

Our results reveal that cultural conformity can arise in the absence of any individual level rule to copy the majority, group norms or any other learning biases. The mechanism that caused the emergence of conformity in our model is the same as described above for the emergence of cross-generational, durable traditions; namely, that social enhancement leads to the amplification of the more frequent behaviour in the group. Although, for identical behaviours reinforcement learning should not result in any preference for one behaviour, performance of behaviours are probabilistic processes that can result in temporal variations of behaviour frequencies. This is especially the case in small groups (figure 5*b*). These temporal variations can then be used as 'signal' by social enhancement and result in the arbitrary fixation of one behaviour by the interaction of social enhancement and reinforcement learning (figure 5*e*).

Similarly to a 'copy the majority' learning rule, social enhancement can integrate information about many group members in the learning process, which finally causes the convergences of the whole group to a single behaviour. However, unlike 'copy the majority', social enhancement does not require individuals to assess the frequencies of a particular behaviour in the group. This finding emphasizes that the emergence of cultural conformity does not necessarily imply the existence of individual level strategies to copy the majority or group norms. Thus, our results suggest that studies to date claiming to demonstrate conformist bias have not provided clear evidence of conformist biases as individual-level learning strategies in animals (Whiten *et al.* 2005; Bonnie *et al.* 2007; Dindo *et al.* 2009; Perry 2009). Developing suitable experiments and tools to infer when patterns of conformity are caused specifically by 'copying the majority' remains a challenge for future research. A productive research direction may be found in longitudinal studies of development that also control for individual histories of reinforcement (Perry (2009) did the former but not the latter).

(d) *Social enhancement can create similar learning dynamics as 'copy when uncertain'*

We observed that the repeated interaction of individual reinforcement and social enhancement learning in our model can lead to emergent learning dynamics similar to those associated with a 'copy when uncertain' learning strategy. 'Copy when uncertain' has been proposed as an individual-level social-learning strategy that combines individual and social learning in an adaptive way (Boyd & Richerson 1988; Laland 2004). In this strategy individuals are assumed to first learn through an individual learning process that estimates the pay-offs of alternative behaviours. If pay-off estimates allow individuals to clearly identify the more profitable behaviour, then they adopt this behaviour. If this is not possible, i.e. when individuals are *uncertain* about which behaviour is more profitable, then they copy the behaviour of another individual.

In our model, individuals always learn socially and they do not explicitly estimate the uncertainty that is related to individual learning results. Therefore, it is not possible that they employ a 'copy when uncertain' strategy considered as a property of their individual psychology. Nevertheless, similar to a 'copy when uncertain' strategy, in our model social enhancement has a greater impact on behaviour choice when individual learning reveals uncertain results. This is possible because information from individual and social enhancement learning is integrated in the probabilities to perform alternative behaviours. Importantly, the effect of individual learning, but not that of social enhancement, depends on gained pay-offs. As a consequence, if perceived pay-off differences between alternative behaviours are large (i.e. individual learning reveals certain results), then individual learning has a strong effect on the probabilities to perform alternative behaviours. By contrast, if perceived pay-off differences between alternative behaviours are small or inconsistent (i.e. individual learning reveals uncertain results), then individual learning has a much weaker effect on the probabilities to perform alternative behaviours. Because social enhancement is not influenced by pay-offs of observed behaviours, its influence on behaviour choice increases with increasing uncertainty of individual learning.

Several theoretical and empirical studies suggest that humans and other animals have evolved mechanisms to adaptively integrate social and individual learning (Boyd & Richerson 1988, 1995; Kameda & Nakanishi 2002, 2003; Laland 2004; McElreath *et al*. 2008; Kendal *et al*. 2009). Commonly such mechanisms have been thought of being individual-level strategies such as 'copy when uncertain' that involve explicit decision making of when to rely either on social or individual learning (Laland 2004). By focusing on the interaction of individual and social learning on small time scales, our model shows that an adaptive integration of social and individual learning can also emerge from cognitively simpler mechanisms. While this does not rule out the possibility that animals have evolved complex cognitions and individual-level social-learning strategies, it calls for more theoretical and empirical work to identify the animals that use such strategies as well as the conditions that favour the evolution of cognitively complex strategies.

(e) *Evolution of imitation*

We did not include evolutionary dynamics in our model. Nevertheless, our results provide a new hypothesis for the evolution of more sophisticated learning mechanisms such as imitation. Based on gained pay-offs of alternative strategies, we can infer selection pressures that would drive the evolution of different learning mechanisms. In our model, at least for the investigated values of learning parameters, imitation-like learners created dynamics that were similar to dynamics created by social enhancement learners. The strongest differences in obtained mean pay-offs emerged when social enhancement led to the emergence of maladaptive traditions, which occurred when the behaviour that yielded higher pay-offs was much harder to learn (upper left part of figure 4*f*,*i*). Such learning conditions would most strongly favour the evolution of imitation-like learning. These conditions might also create a bridge over the adaptive valley that has been suggested to restrict the evolution of imitation (Boyd & Richerson 1996). However, this bridge might be rather narrow since it seems that specific conditions must be fulfilled to favour the evolution of imitation-like learning in our model. Specifically, the behaviour that yields higher pay-offs has to be sufficiently difficult to learn so that social enhancement creates maladaptive traditions. If the behaviour's learning difficulty increases too much, however, then our model produces conditions with an adaptive valley as proposed by Boyd & Richerson (1996).

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