

Trade-offs between social learning and individual innovativeness in common marmosets, *Callithrix jacchus*

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Social learning and innovation are two different ways to acquire novel behaviours, and the form of the relationship between these two processes strongly affects cultural evolution. Whereas modelling results suggest a negative correlation between the two processes within a species, comparative data show, and the cultural intelligence hypothesis predicts, positive covariation across species. Thus, there is considerable uncertainty about the form of the relationship between social learning and innovation. We explored this problem experimentally in common marmosets. Social learning of 18 subjects was assessed by presenting a video clip of a conspecific demonstrator solving a complex foraging task and comparing their success to a control group. For the same subjects, the propensity to innovate was assessed with two tasks that operationalize different types of innovation: (1) a multistage problem-solving task to estimate goal-directed Type I innovation, that is, the ability to find a solution to a novel problem or a novel solution to an old problem, and (2) a flexibility task testing for more incidental Type II innovation, that is, the propensity to realize and switch to a novel, but easier solution after the establishment of a well-learned solution. Social learning was negatively correlated with Type II innovation, but not with Type I innovation. We discuss these results with regard to competition within an individual of the various attentional processes aimed at conspecifics' behaviour or aspects of the environment, and whether they might be the result of the cooperative breeding system shared by humans and callitrichids.

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Primates, and many other large-brained gregarious species, have two nonexclusive strategies of coping with novel environmental challenges. They can either confront novel problems individually and devise innovative solutions or, alternatively, they can rely on social learning. Species that systematically rely on social learning eventually build up distinct behavioural repertoires that vary from one population to another, resulting in simple animal cultures (e.g. chimpanzees, *Pan troglodytes*: Whiten et al. 1999; orang-utans, *Pongo* spp. van Schaik et al. 2003; capuchin monkeys, *cebus capucinus*: Panger et al. 2002; Perry et al. 2003; whales and dolphins, *Tursiops* sp., *Megaptera novaengliae*, *Physeter macrocephalus*, *Orcina orca*: Rendell & Whitehead 2001; Krutzen et al. 2005). In its simplest form, culture can be described as a set of socially transmitted innovations (e.g. Ramsey et al. 2007), and much research effort has been devoted to investigating social transmission, often asking whether the social-learning mechanism is limiting the evolution of more complex animal cultures (reviewed in Henrich & McElreath 2003; Caldwell & Whiten 2007). However, growing evidence suggests that additional factors are also important, for example, because observational forms of social

learning and some tendency towards conformity can also be found in nonhuman primates (Whiten et al. 2005; Caldwell & Whiten 2007; Dindo et al. 2008; Fredman & Whiten 2008).

Cultural systems can only develop and be maintained if social learning is ubiquitous but nevertheless supplemented by individual evaluation, problem solving and innovation. Otherwise, such systems are susceptible to the spread and infinite maintenance of non- or even maladaptive behavioural variants (Henrich & McElreath 2003; Kendal et al. 2005). As a consequence, the necessity also to investigate the second fundamental component of culture, innovation, has become evident (e.g. Reader 2003; Reader & Laland 2003; Ramsey et al. 2007; Burkart & van Schaik 2008). Besides the processes involved in the emergence of new innovations (e.g. Greenberg 2003; Lefebvre & Bolhuis 2003; Reader 2003; Burkart & van Schaik 2008), it is the interplay between innovation and social learning that is of particular relevance, because it has consequences not only for the emergence of cultural systems, but also for the evolution of cognition more generally (van Schaik 2006; Whiten & van Schaik 2007; van Schaik & Burkart, in press).

The relationship between social learning and innovation can be considered both across and within species and populations. Across primate species, social learning and innovation are positively related, as indicated by a large set of comparative data; in addition, both components covary positively with brain size (Reader & Laland 2002).

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Incidents of social learning and innovation were defined very broadly for this study; innovations, for example, were counted as such if the behaviour in question was judged by the original authors as ‘novel’ or ‘never seen before’ (Reader & Laland 2001). Even though the processes leading to innovations are only partially understood (Greenberg 2003; Reader 2003; Burkart & van Schaik 2008), many definitions of innovation and intelligence show considerable overlap by stressing the aspect of flexible, novel problem solving (e.g. for intelligence: Byrne 1994, 1995; e.g. for innovation: Kummer & Goodall 1985; Reader & Laland 2003; Ramsey et al. 2007). The above findings are therefore consistent with a broad version of the cultural intelligence hypothesis, according to which species that rely strongly on social learning are more likely to evolve larger and thus more powerful brains (Deaner et al. 2006; van Schaik 2006; Whiten & van Schaik 2007; van Schaik & Burkart, in press; cf Herrmann et al. 2007). The rationale for this hypothesis is that social learning increases the effectiveness of brain tissue, leading to increased cognitive performance, and thus lowering the threshold for organisms to respond to selection pressures to add cognitive abilities.

The same correlation between social learning and innovation is not necessarily present within a species or population, even though a corresponding relationship has been found for birds (reviewed in Reader 2003; Bouchard et al. 2007). Indeed, modelling results rather suggest trade-offs between social learning and innovation which depend on various environmental conditions as well as the distribution of social versus asocial learners within a population (Boyd & Richerson 1985, 1996; Rogers 1988; Giraldeau et al. 2002; reviewed in Henrich & McElreath 2003; Kendal et al. 2005). For example, social learning should be favoured over individual learning when most potential demonstrators are individual learners who have acquired accurate information about the environment, or when individual learning is particularly costly. Empirical evidence for this kind of information quality trade-off is available for various species of fish, birds and mammals (reviewed in Kendal et al. 2005) including callitrichid monkeys (Day 2003; Day et al. 2003; cited in Kendal et al. 2005) and humans (Efferson et al. 2008). Additionally, however, at least for humans, the propensity to rely on social learning or innovation also partially seems to reflect an individual characteristic (e.g. Asch 1955; Riding & Read 1996; Efferson et al. 2008); in particular, the readiness to adopt social information varies widely (Rogers 1995). Such a differentiation of roles, with some individuals specializing on innovation, is particularly suitable for building and maintaining stable, nonmaladaptive cultural systems and might even be a precondition for cumulative cultural processes to emerge. If individual preferences for either social learning or innovation are present, we would expect to see a negative correlation among individuals between the propensities to innovate and learn socially.

Thus, once information quality is held constant, the nature of this correlation between social learning and innovativeness in a set of conspecific individuals should reveal underlying processes. We tested for this relationship in common marmosets by exposing the same subjects to three different tasks, a social-learning task and two innovation tasks. The cultural intelligence hypothesis predicts a positive relationship, resulting from the coevolution between social-learning and more general cognitive abilities: some individuals will simply be more intelligent and thus score higher on both components. If, however, subjects possess individual preferences or propensities for relying on social learning or innovation, one would expect a trade-off, that is, a negative correlation between the two processes.

EXPERIMENT 1: SOCIAL LEARNING

To assess individual differences in social learning, we set up a standardized social-learning situation in which we tested the subjects

individually using video clips of trained conspecifics as models. This set-up allowed us to standardize a variety of factors that could influence individual performance, such as the identity of the model, its relationship to the subject and, most importantly, its behaviour during the test. Virtual demonstrators have successfully induced social learning previously in budgerigars, *Melbopsittacus undulatus*, macaques, *Macaca mulatta*, and colobus monkeys, *Colobus guereza kikuyuensis* (Dawson & Foss 1965; Galef et al. 1986; Cook & Mineka 1989; Heyes & Suggerson 2002; Mottley & Heyes 2003; Price & Caldwell 2007).

The social-learning task had a high level of difficulty for the animals, as determined in pilot experiments, because we did not use a two-action procedure, making the experiment vulnerable to the probability that control animals could come up with the solution of the task individually. The rationale for not using a two-action procedure was that we aimed at capturing the whole array of social-learning mechanisms that might arise, that is, social facilitation, stimulus and local enhancement, and observational forms of social learning (Whiten et al. 2004).

The design of the task (a Perspex box baited with a cricket, Fig. 1) allowed us to discriminate between social facilitation and stimulus/local enhancement, because the position of the box where individuals would most likely look for a solution through individual learning was locally dissociated from where the actual, demonstrated solution to the problem was. Hence, as summarized in Table 1, the exploration pattern of the animals could reveal whether the presence of the demonstrator simply resulted in the subjects searching for the solution more actively in the ‘presence’ of a conspecific than when alone (i.e. social facilitation, a general increase in activity, Zajonc 1965), or whether the demonstrator had a more specific influence on the learner. This could be guiding where (enhancement) or how (imitation) the subject explored and interacted with the box. We predicted that the animals from the test group would be more likely and quicker to find the solution than the control group. Based on earlier experiments with common marmosets (reviewed in Burkart 2009), we also predicted we would find both social facilitation and more specific social-learning effects.

Methods

Subjects

Thirty-eight adult common marmosets from the Primate Station of the Anthropological Institute and Museum, University of Zurich, participated in the experiment. Two animals were trained as models, 18 were assigned to the experimental group (Table 2) and 18 to the control group. The control group consisted of 10 males and eight females kept as pairs (three pairs) or in family groups (three

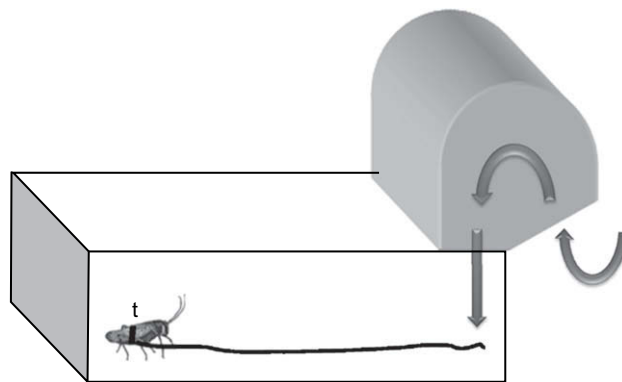


Figure 1. Social-learning task. The cricket attached to the yarn can only be retrieved from the box along the arrow. Therefore, the place where the cricket is visible to the animal is different from where it has to act upon the apparatus to obtain the reward.

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