

Christine A. Caldwell · Andrew Whiten

## Testing for social learning and imitation in common marmosets, *Callithrix jacchus*, using an artificial fruit

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**Abstract** We tested for social learning and imitation in common marmosets using an artificial foraging task and trained conspecific demonstrators. We trained a demonstrator marmoset to open an artificial fruit, providing a full demonstration of the task to be learned. Another marmoset provided a partial demonstration, controlling for stimulus enhancement effects, by eating food from the outside of the apparatus. We thus compared three observer groups, each consisting of four animals: those that received the full demonstration, those that received the partial demonstration, and a control group that saw no demonstration prior to testing. Although none of the observer marmosets succeeded in opening the artificial fruit during the test periods, there were clear effects of demonstration type. Those that saw the full demonstration manipulated the apparatus more overall, whereas those from the control group manipulated it the least of the three groups. Those from the full-demonstration group also contacted the particular parts of the artificial fruit that they had seen touched (localised stimulus enhancement) to a greater extent than the other two groups. There was also an interaction between the number of hand and mouth touches made to the artificial fruit for the full- and partial-demonstration groups. Whether or not these data represent evidence for imitation is discussed. We also propose that the clear differences between the groups suggest that social learning mechanisms provide real benefits to these animals in terms of developing novel food-processing skills analogous to the one presented here.

**Keywords** Marmosets · *Callithrix jacchus* · Social learning · Imitation · Artificial fruit

### Introduction

Over recent years, there has been a considerable amount of interest in the topic of social learning, and in particular imitation, in animals (e.g. Zentall and Galef 1988; Whiten and Ham 1992; Heyes and Galef 1996; Frigaszy and Perry 2003). These subjects attract interest for a wide variety of reasons, and therefore appeal to scholars from a diverse range of disciplines. Social learning is considered by many to be intrinsically fascinating, often because of what it reveals about an animal's cognitive abilities. Imitation in particular is widely regarded as being especially interesting from this point of view (e.g. Heyes and Ray 2000; Caldwell and Whiten 2002). Researchers have also been interested in social learning because of its role in (non-genetic) behavioural inheritance (e.g. Dawkins 1976; Blackmore 1999). Others are interested in the prospect that some animal species may be regarded, alongside humans, as exhibiting "culture" (e.g. McGrew 1998; Rendell and Whitehead 2001; Whiten et al. 2003). Finally, an understanding of social learning and imitation are important within applied animal science. If animals can develop behavioural patterns through social interaction, this carries both welfare (e.g. Nash et al. 1999; Hook et al. 2002) and conservation (e.g. Brown and Laland 2001; Custance et al. 2002) implications.

There has therefore been much interest in social learning and imitation in a broad range of animals, and these phenomena have been particularly well studied within the primate order. Even within the hotly debated field of non-human imitation (e.g. Caldwell and Whiten 2002), particular doubt has been cast on whether monkeys are capable of imitation. Visalberghi and Fragaszy (1990), in their article "Do monkeys ape?", state that the social processes that lead to rapid cultural learning in humans, "may be completely absent in monkeys." (Visalberghi and Fragaszy 1990, p 269). In a more recent review, they conclude that

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C. A. Caldwell (✉) · A. Whiten  
Centre for Social Learning and Cognitive Evolution  
and Scottish Primate Research Group, University of St Andrews,  
KY16 9JU St Andrews, Fife, Scotland  
Tel.: +44-1392-264693, Fax: +44-1392-264623,  
e-mail: C.A.Caldwell@exeter.ac.uk

*Present address:*

C. A. Caldwell  
School of Psychology, Washington Singer Laboratories,  
University of Exeter, Exeter, EX4 4QG, UK

little has changed, arguing that, “despite the many efforts to find imitative learning in other monkey species, the recent data supporting it are few and ... open to alternative interpretations” (Visalberghi and Fragaszy 2002, p 493). Whiten and Ham (1992) concluded that imitation was unproven in monkeys, whilst judging that great apes, in contrast, “share with humans an imitative capacity” (p 276).

The particular species studied here, common marmosets, are a New World monkey species, from the family *Callitrichidae*, which is made up of marmosets and tamarins. Callitrichids are known for their co-operative social organisation, usually involving a dominant pair, both of whom breed, and a number of adult offspring that contribute to the care of infants (e.g. Stevenson and Rylands 1988; Rothe and Darms 1993). The particular species we have studied, *Callithrix jacchus*, show this typical social pattern. Common marmosets occur in the Atlantic coastal forests and dry thorn scrub of northeast Brazil, and are described as, “highly gummivorous”, feeding mainly from exudate gouged from tree trunks and branches, as well as fruit and insects (Rylands and de Faria 1993).

In some respects, marmosets may represent likely candidates for showing imitative ability. It has been suggested by some researchers that social learning (and possibly also imitation) may be skills adapted for group living (e.g. Lefebvre and Giraldeau 1996; Lefebvre et al. 1997; Templeton et al. 1999). According to this adaptational perspective, there are good reasons why marmosets might have developed imitative tendencies, living as they do in extended family groups. An imitative capacity might provide valuable shortcuts to learning about current environmental conditions. Other researchers have proposed that imitative ability might be developed experientially, built up via a series of associative mechanisms (e.g. Heyes and Ray 2000; Laland and Bateson 2001). This view of imitation would also be relevant to the possibility of imitative ability in marmosets. Given that they are accustomed to foraging non-aggressively in groups, they are liable to gain much experience of synchronous behaviours. Under these associative accounts, it is precisely this type of experience that has been proposed to underlie imitative ability (Heyes and Ray 2000; Laland and Bateson 2001).

Furthermore, the tolerant nature of callitrichid social dynamics may provide the ideal conditions for an imitative capacity to be expressed. Some authors have argued that although evidence for imitation in monkeys is weak, this may be due to the social constraints of hierarchical group structures (Fragaszy and Visalberghi 1989; Visalberghi and Fragaszy 1990). Thus, in previous research on social learning in monkeys, learning may have been inhibited because more dominant individuals exploit, rather than learn from, skilled subordinates; and subordinates are inhibited from approaching, and therefore learning from, skilled dominant individuals. However, such constraints are less likely to operate within a marmoset family group (e.g. Caldwell and Whiten 2003). In addition to the co-operative breeding system, the level of food sharing observed within callitrichid family groups is noteworthy. Tardif et al. (1993) have stated that, “Callitrichids are unique amongst

primates in the degree to which group members provide solid food to youngsters” (p 231). In a review of callitrichid cognition, Snowdon (2001) has suggested that such tolerant social interactions make these species the ideal models for research of social learning and imitation.

However, other views predict that marmosets would not represent likely imitators. The idea that group living favours social learning is in fact not well supported (e.g. Reader and Lefebvre 2001). In a large-scale review of the literature on primate innovation and social learning, Reader and Laland (2002) found that social and asocial learning were positively correlated, and that both were related to measures of relative brain size. Social learning may therefore be an expression of more generalised behavioural flexibility, more likely to be correlated with opportunistic generalist lifestyles (L. Lefebvre, personal communication). According to this view, and in comparison with other primates, marmosets would be extremely unlikely to be proficient social learners. Lefebvre et al. (2003) review data for a wide range of primate species on innovation rate, tool use, learning and executive brain ratio. *Callithrix jacchus* is placed at the very bottom of the scale on every one of these measures. The question of the social learning abilities of marmosets is therefore clearly a particularly interesting one from a theoretical point of view, offering as it does the opportunity to address the broader question of the correlates and predictors of social learning across all species.

Imitation has previously been investigated in marmosets by Bugnyar and Huber (1997), Voelkl and Huber (2000) and Caldwell et al. (1999). In Bugnyar and Huber’s (1997) study, marmosets were provided with a pendulum door that could be either pushed or pulled to gain access to a food reward. These researchers allowed observer monkeys to watch a trained conspecific demonstrator monkey pulling open the door. Some observer monkeys showed a stronger tendency to use the demonstrated opening technique than control (non-observer) monkeys, whose natural response was to push the door.

However, some authors have argued that this particular study does not provide adequate evidence of imitation. Heyes and Ray (2000) describe the result as “suggestive, but not conclusive, evidence” of imitation (p 232). And Zentall (2001) makes a more specific criticism about the methodology, pointing out that only one of the two groups of subjects actually saw a demonstration. Bugnyar and Huber (1997) describe their methodology as a two-action design, but the design is only two-action in the sense that the manipulandum itself can be operated two different ways, not in terms of there being two different observer groups that each see one of these methods demonstrated (as has been done in other “two-action” studies, such as those carried out by Akins and Zentall 1996; Whiten et al. 1996; and Zentall et al. 1996). Therefore, there were important differences between the two groups that might potentially account for the difference in subjects’ subsequent behaviour. The “push” group had seen no demonstrator. In fact they were not provided with any kind of pre-test observation period, so not only had they not seen a conspe-

cific operate the apparatus, they had never seen it before. Subjects from this group therefore came to the task entirely ‘cold’. Their behaviour was clearly affected by this, as evidenced by the finding that subjects in this group were more exploratory than those that had seen the demonstration. The difference in their operation of the door may have arisen for a similar reason.

More recently, however, Voelkl and Huber (2000) addressed such criticisms. Their task involved opening photographic film canisters, and two trained conspecific demonstrators were used, one of which removed the lid with their hand, and another, which used their mouth. Voelkl and Huber (2000) found a significant difference between the two observer groups in the method used to open the canisters: subjects that saw the hand method all used their hands every time, and of the subjects that saw the mouth method, most used their mouth for at least some of the test trials. Voelkl and Huber (2000) therefore presented their results as evidence of “true imitation”, as the difference could be attributed to neither stimulus enhancement nor emulation.

Caldwell et al. (1999) investigated imitation in marmosets using the “artificial fruit” methodology. The artificial fruit (as used by Whiten et al. 1996) is a box locked by several defences, each of which can be operated in two alternative ways. It is designed to represent an ecologically valid test for imitation, in that a certain amount of manipulation is required before the edible “core” (a food reward inside) can be reached. The artificial fruit is therefore a slightly more complex task than that employed by Voelkl and Huber (2000), as a combination of actions are involved. Success on this task is therefore less likely to be dismissed by critics such as Byrne (Byrne and Russon 1998; Byrne 2002) as a case of “response facilitation”. Furthermore, Huber et al. (2001) have also suggested that the artificial fruit is the ideal methodology for showing how the investigative behaviours of explorative species may be influenced by observation of a demonstrator. The combinations of complex manipulations allow for the analysis of exploratory responses in a way that tasks involving minimal manipulations of simple objects cannot.

Caldwell et al. (1999) trained two conspecific demonstrators to manipulate a marmoset-sized version of the artificial fruit in order to investigate whether observers produced demonstrator-consistent responses, indicative of imitative ability. The artificial fruit methodology proved difficult to replicate in this manner, in comparison with studies with other primates that have employed human demonstrators (Whiten et al. 1996; Custance et al. 1999, 2001; Stoinski et al. 2001; Stoinski and Whiten 2003). However, Caldwell et al. (1999) identified two potentially interesting phenomena: localised stimulus enhancement, and possible evidence of imitation.

Here we present further data from this study, which has been analysed in greater depth, to investigate these phenomena further. We also investigated whether success levels in these observer groups were greater than those for a third, non-exposed control group, which would suggest that social learning played a functional role in terms of enhancing performance on this particular task.

## Methods

### Subjects

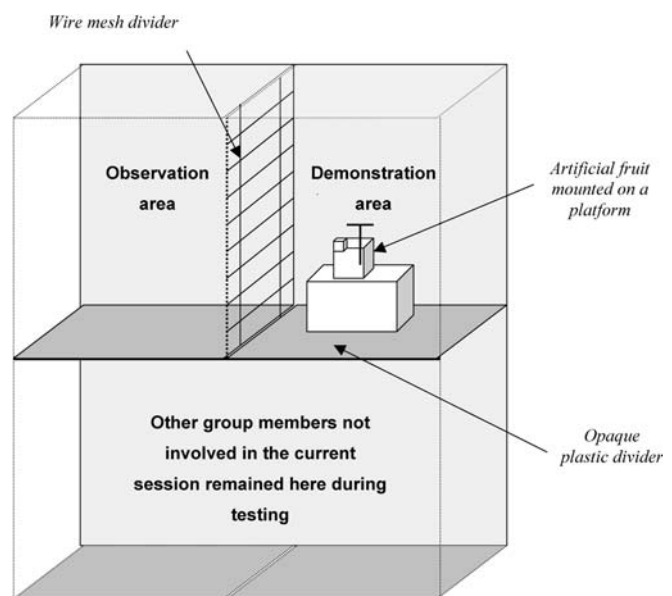
Fourteen marmoset (*C. jacchus*) subjects were involved in this study: eight females, and six males. These included juvenile, sub-adult and adult animals, ranging in age from 6 months to 7 years old. Of these animals, 12 were subjects in the study, and two were trained as demonstrators. The animals were drawn from the breeding colony of a population of animals housed in a Medical Research Council facility. None had been subjected to any invasive research. They were housed in family groups of between three and eight individuals with similar group structure to wild common marmosets (see Introduction). All animals came from a total of three of these family groups and all testing was done within the family group, so that subject and demonstrator came from the same home cage. Figure 1 depicts the layout of the home cages. All cages were 230 cm(h)×110 cm(d)×120 cm(w) and were equipped with branches, ropes and platforms. All animals were fed a diet of fruit, commercial marmoset food, and protein and vitamin supplements, with water supplied ad libitum.

### Apparatus

The task employed was an “artificial fruit”, of the kind used by Whiten et al. (1996) to test for imitation in chimpanzees. The version used in this study was a much smaller one, designed for manipulation by small monkeys (6×6×8 cm). Only one of the original defences was used, due to the limited manipulative abilities of marmosets (see next section for details of how a demonstrator was trained on this defense). Figure 2 shows the artificial fruit used in this study, which was a box locked by a handle which must be removed to release a lid and gain access to the enclosed food reward.

### Training of demonstrators

Each of the demonstrators was the breeding female of her group. Training of the demonstrators was done in the home cage, with the animal isolated from the rest of the group members. Only one demonstrator was successfully trained to open the artificial fruit. This individual turned the handle from the bottom and lifted the lid



**Fig. 1** The marmoset home cages, where testing was carried out



**Fig. 2** The trained marmoset demonstrator opens the artificial fruit (full demonstration)

by pulling it up (see Fig. 2) from the bolt-holes (Note: although no bolts were used in this study, the artificial fruit still had bolt-holes, being based on the design used in Whiten et al. 1996). However, in order that there were still two comparable conditions each involving a conspecific interacting with (and gaining a food reward from) the artificial fruit, another was shaped to eat food from the outside of the box.

Shaping of the “full-demonstration” model, who opened the artificial fruit, took place over several weeks. She was initially allowed to remove food from inside the artificial fruit with the lid open. Over subsequent sessions, the lid was closed further until the demonstrator could access the food reward from the artificial fruit with the lid fully closed. Following this, the handle was added, initially only slightly overlapping the lid, such that it did not need to be moved far to free the lid. Over several more sessions the demonstrator became able to access the food reward with the handle in the fully locked position. Despite a variety of approaches towards training this individual to remove the bolts (including placing them only part-way in, and replacing the metal bolts with bolts constructed from carrot and hard fruits), she never succeeded in removing this defense. Food rewards were varied in accordance with the demonstrator’s apparent motivation for them. Chopped banana was used, as was chopped grape, and occasionally raisins. These were items, which were included in the animals’ daily diet, but they were known to be preferred food items within the diet. Training was generally carried out before lunchtime, when the animals received their daily feed.

Shaping of the other (“partial-demonstration”) model was more straightforward as she was only required to eat food from the lid of the apparatus. However, she was introduced to the artificial fruit and allowed to eat from it on several occasions, until she was regularly approaching and eating from the apparatus whenever she was isolated with it. The food reward used in this case was mashed banana.

#### Procedure

Each subject received three trials, each consisting of an observation phase followed by a test phase. Due to the way in which the home cage could be divided (into four equally sized sections), trials commenced when the required combination of individuals from the group had entered the top two sections (see Fig. 1). The artificial fruit was then introduced and the observation phase began. During the observation phase the demonstrator performed (opening the artificial fruit at least three times and removing chopped banana from the inside for the full-demonstration group; eating mashed banana from the lid of the artificial fruit for the partial-demonstration group), and the subject could observe this from the

other side of a wire mesh divider (see Fig. 1).<sup>1</sup> The experimenter reached into the cage several times during each observation phase in order to reload the artificial fruit when the demonstrator had removed all of the food. For the full-demonstration condition this also involved re-locking the artificial fruit. The control group were also allowed to view the apparatus through the wire mesh, although no demonstration was performed. Each observation phase took 5 min (including reloading time), after which the demonstrator was released into another section of the cage to rejoin the rest of the group (see Fig. 1). In between each observation and test phase, the outside of the artificial fruit was wiped clean of any residual food. During the test phase the subject was isolated with the artificial fruit for 5 min. All trials were videotaped for later analysis, including observation and test phases.

#### Data coding

Independent coders were instructed to record the behaviour of the subjects during the test phases, using the following categories: touches made to lid (bolt-holes and top of lid), and handle (top, shaft, bottom, turn from top, and turn from bottom). For each of the categories, they recorded the number of touches to the artificial fruit that the subject made, and whether these were made with the hand or the mouth. Since these were divided into specific parts of the artificial fruit, and also the body part used (hand or mouth), it was expected that these data could be used to identify whether the subjects were showing demonstration-consistent behaviours.

## Results

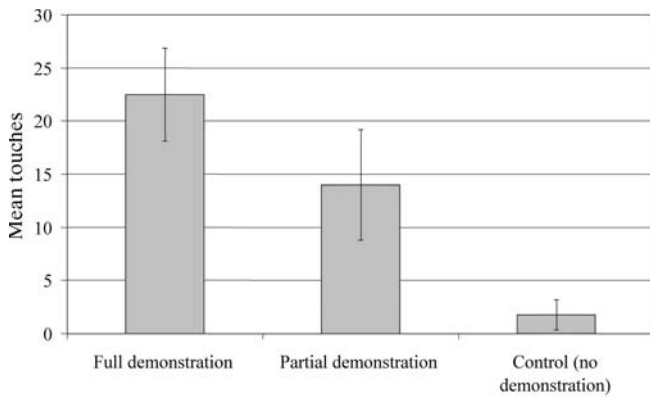
### Overall performance and success

The average trial performance of each subject was always calculated by taking the median value of their scores for trials one, two and three.

None of the subjects from any of the groups succeeded in opening the artificial fruit and gaining the food reward, a result which contrasts strongly with those found with other primates that have been tested using this methodology. This issue will be returned to in the discussion. It was still possible however to investigate whether social learning had an effect on the subsequent performance of the subjects. The totals reported for each of the coding categories were lumped for each subject, in order to determine whether there were any differences between the three groups in terms of the amount of exploration and manipulation that occurred during trials.

It was found that there was a difference between the three groups in the amount of overall touches they made to the artificial fruit. Each of the coding categories detailed in the methods section was collapsed for each subject to give the total number of touches they made. As shown in Fig. 3, the mean number of touches was 22.5 (SD=8.70) for the full-demonstration group, 14.0 (SD=

<sup>1</sup> Demonstrator and observer were kept separated in this manner despite our previous results (Caldwell and Whiten 2003), which indicated that social learning effects might be enhanced by close social interaction. It was considered that, in terms of investigating the effects of two different demonstrations, it was crucial that the potentially different individual learning experiences between the two demonstration groups did not produce a confound.

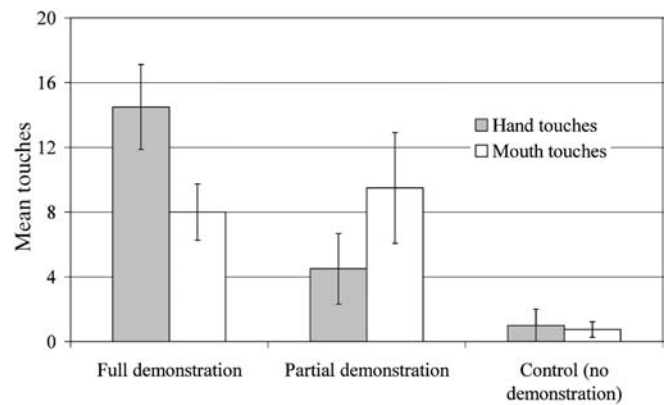


**Fig. 3** Mean ( $\pm$ SD) touches to the artificial fruit, for full- and partial-demonstration groups, and the no-demonstration control group

10.39) for the partial-demonstration group, and 1.75 (SD=2.87) for the no-demonstration control group. A one-way analysis of variance showed there was a difference between the three demonstration groups in the total number of touches made (ANOVA:  $F_{2,9}=8.353$ ,  $P < 0.01$ ). Post-hoc tests showed that there were significant differences between the full-demonstration and control group (LSD:  $P < 0.005$ ) but not between the partial-demonstration and control group (LSD:  $P = 0.059$ ), or between the full- and partial-demonstration groups (LSD:  $P = 0.087$ ).

#### Body part copying

Since the individuals from the full-demonstration group saw predominantly manual exploration of the apparatus, and those from the partial-demonstration group saw primarily mouthing behaviours, we expected that the observer groups would show significant differences in the amount of hand and mouth touches that they made during the trials. The data from the coding categories was therefore collapsed into hand and mouth touches. As illustrated in Fig. 4, the mean number of hand touches was 14.5 (SD=5.25) for the full-demonstration group, 4.5 (SD=4.36) for the partial-demonstration group, and 1.0 (SD=2.0) for the no-demonstration control group. The mean number of mouth touches was 8.0 (SD=3.46) for the full-demonstration group, 9.5 (SD=6.86) for the partial-demonstration group, and 0.75 (SD=0.96) for the no-demonstration control group. A mixed two-way analysis of variance showed a significant interaction between the number of touches made with hand versus mouth and the type of demonstration seen (ANOVA:  $F_{1,6}=19.120$ ,  $P < 0.005$ ). Thus, those individuals that saw the full demonstration, did make proportionally more hand touches, and those that saw the partial demonstration, made proportionally more mouth touches. There was no main effect of group (ANOVA:  $F_{1,6}=1.574$ ,  $P = 0.256$ ), consistent with the post-hoc comparison between full- and partial-demonstration group reported above. There was also no main effect of body part preferred (ANOVA:  $F_{1,6}=0.325$ ,  $P = 0.589$ ).

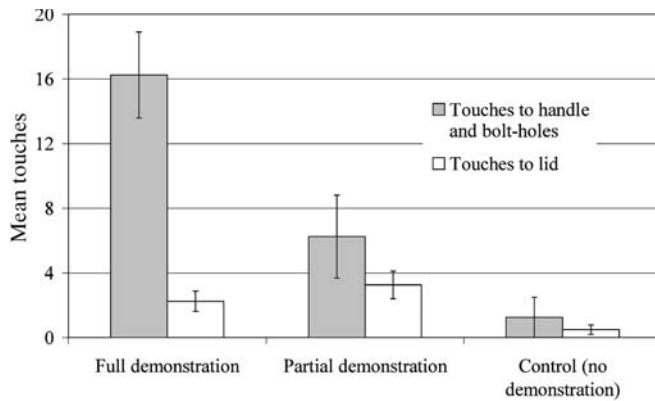


**Fig. 4** Mean ( $\pm$ SD) hand and mouth touches to the artificial fruit for the three trials, for full- and partial-demonstration groups, and the no-demonstration control group

One-way analyses of variance were also carried out to find out how the three groups differed in terms of the absolute number of touches by hand and mouth. There was a significant difference between the three groups in terms of the number of hand touches made (ANOVA:  $F_{2,9}=11.625$ ,  $P < 0.005$ ). Post-hoc tests showed significant differences between the full-demonstration and partial-demonstration group (LSD:  $P < 0.01$ ) and between the full-demonstration and control group (LSD:  $P < 0.001$ ) but not between the partial-demonstration and control group (LSD:  $P = 0.259$ ). Mouth touches also showed significant variation between the groups (ANOVA:  $F_{2,9}=4.385$ ,  $P < 0.05$ ). Post-hoc tests showed no significant difference between the full and partial-demonstration groups (LSD:  $P = 0.646$ ), but there was a significant difference between the full-demonstration and control group (LSD:  $P < 0.05$ ), and between the partial-demonstration and control group (LSD:  $P < 0.05$ ). These comparisons with the baseline control group are important in terms of determining whether or not imitation was a likely mechanism. This will be addressed in the discussion.

#### Place copying

Demonstrator-consistent effects of the specific areas of the artificial fruit explored by subjects were also investigated. The full-demonstration model had turned the handle and lifted the lid using the bolt-holes. We therefore predicted that the observers from this group would concentrate on these areas more, compared with the partial-demonstration group. The partial-demonstration group, in contrast, had seen their demonstrator lick the lid of the artificial fruit, so we expected them to show a greater focus on this particular area. Again, the data provided by the independent coders was collapsed in such a way that each subject was given a total number of touches for the lid, and for the handle and bolt-holes. As illustrated in Fig. 5, the mean number of touches to the handle and bolt-holes was 16.3 (SD=5.32) for the full demonstration group, 6.25 (SD=5.12) for the partial-demonstration group, and 1.25



**Fig. 5** Mean ( $\pm$ SD) touches to handle and bolt-holes, and to lid, of the artificial fruit, for full- and partial-demonstration groups, and the no-demonstration control group

(SD=2.5) for the no-demonstration control group. The mean number of touches to the lid was 2.25 (SD=1.26) for the full-demonstration group, 3.25 (SD=1.71) for the partial-demonstration group, and 0.50 (SD=0.57) for the no-demonstration control group. A two-way analysis of variance was again carried out to investigate the effects of the two different demonstrations. A significant interaction was found between these measures and the demonstration seen (ANOVA:  $F_{1,6}=11.344$ ,  $P < 0.05$ ). There was also a main effect of place, with the handle and bolt-holes being touched more overall than the lid (ANOVA:  $F_{1,6}=27.094$ ,  $P < 0.005$ ). Again the main effect of group was non-significant (ANOVA:  $F_{1,6}=4.301$ ,  $P = 0.083$ ). This was consistent with a prediction of demonstration-consistent responding as the full-demonstration group were contacting handle and bolt-holes proportionally more, and the partial-demonstration group were contacting the lid proportionally more.

As with the results for body part copying, we also carried out one-way analyses of variance to determine differences between the three groups in terms of the absolute number of touches to the handle and bolt-holes, and to the lid. There was a significant difference between the groups in terms of the number of touches to the handle and bolt-holes (ANOVA:  $F_{2,9}=11.523$ ,  $P < 0.005$ ). Post-hoc tests showed significant differences between the full- and partial-demonstration groups (LSD:  $P < 0.05$ ), and between the full-demonstration and control group (LSD:  $P < 0.001$ ). There was no significant difference between the partial-demonstration and control group however (LSD:  $P = 0.151$ ). The number of touches to the lid also showed significant variation between the groups (ANOVA:  $F_{2,9}=4.810$ ,  $P < 0.05$ ). There was no significant difference between the full-demonstration and partial-demonstration groups (LSD:  $P = 0.294$ ), nor between the full-demonstration and control groups (LSD:  $P = 0.083$ ). However there was a difference between partial-demonstration and control groups (LSD:  $P < 0.05$ ).

## Discussion

Demonstration-consistent responding was observed in marmosets, both in terms of body part used to investigate the artificial fruit, and the parts of the apparatus which were touched most. Additionally, the group that saw the full demonstration manipulated the apparatus more overall, followed by those subjects from the partial-demonstration group. Those in the control group that saw no demonstration manipulated the artificial fruit the least of all of the groups. The implications of these results will be discussed below. As noted in the methods section, demonstrator and observer always came from the same family group. It is therefore an inherent limitation of our study that family groups were being compared with each other when conditions are compared. However, we feel that in terms of the particular effects being looked for (e.g. number of hand/mouth touches) it is unlikely that the relatedness of the animals could produce a confound.

### Imitative effects

In contrast with results found with chimpanzees (Whiten 1998; Whiten et al. 1996), capuchin monkeys (Custance et al. 1999), gorillas (Stoinski et al. 2001), and orangutans (Custance et al. 2001; Stoinski and Whiten 2003), none of the marmoset subjects succeeded in opening the artificial fruit during any of their trials. It should also be emphasised once more that the design of our current experiment was crucially different to those of the studies mentioned previously. Whereas the previous artificial fruit experiments with primates have used human demonstrators, we trained conspecific models. Furthermore, in the previous studies, two alternative methods of opening the artificial fruit were demonstrated, whereas only one of our trained marmoset demonstrators actually opened the artificial fruit. The other ate food from the outside of the apparatus. These differences meant that unfortunately it was not possible to directly compare the performance of the marmosets with these other primates.

However, there was definite evidence of demonstration-consistent responding in the subjects, both in terms of the body part they preferred for exploration of the artificial fruit, and the areas on which they concentrated. Particularly noteworthy with regard to the issue of imitation is the reproduction of the part of the body used. Animals that watched predominantly mouthing behaviours used their mouths more, and those that watched predominantly manipulation used their hands more. This effect is logically similar to results reported by Zentall with pigeons and quail (Akins and Zentall 1996; Zentall et al. 1996) and those reported by Voelkl and Huber (2000), also studying marmosets, each of which has been labelled “true imitation”.

This result should be interpreted with caution, however. As Kaiser, Zentall and Galef (1997) and Zentall (2001) have pointed out, conclusive evidence of imitation (as opposed to a combination of a number of other social learning effects; in particular stimulus enhancement, con-

tagion and emulation) on a two-action test is only shown clearly when the frequency of both of the demonstrated behaviours is increased in the respective observer groups, compared with a non-exposed control group. If, for example, mouthing responses in particular did not appear to be facilitated in the partial-demonstration group, this then leaves open the possibility that the increased use of the hand to manipulate the artificial fruit in the full-demonstration group was not an imitative effect, but dependent on any one (or a combination) of several other social learning effects. For instance, it may be the case that reaching or grasping behaviours are in some way contagious in marmosets, an interpretation Byrne (Byrne and Russon 1998; Byrne 2002) would label “response facilitation”.

In the data presented here, analysis of the absolute number of hand and mouth responses showed that the full-demonstration group produced more hand touches than both the partial-demonstration group and the control group. Also in line with an interpretation of imitation, the partial-demonstration group showed no such increase in hand touches compared with the control group, but did show an increase in mouth touches compared with the control group. Interestingly, so did the full-demonstration group, although this may be due to their overall higher level of exploration of the artificial fruit.

However, there are still obstacles to interpreting the marmosets’ behaviour as imitation. In a number of two-action studies of imitation, the movement of an object has varied between two demonstration groups (e.g. Whiten et al. 1996; Campbell et al. 1998; Custance et al. 1999). Such data can potentially be interpreted as “emulation” (e.g. Tomasello 1996) or more specifically, “object movement re-enactment” (Custance et al. 1999). Since the movement of the apparatus was clearly different for both groups (i.e. no movement for the partial-demonstration group, vs. the handle turning and the lid rising for the full-demonstration group) it is possible that this could have accounted for the effect. Those from the full-demonstration group may have been motivated to recreate the observed effect, and those from the partial-demonstration group subject to a much more generalised enhancement of interest in the apparatus.

It is also possible that the subjects may have acquired what Mitchell (2002) has labelled an “attitude” to the apparatus. Mitchell (2002) suggests that in Voelkl and Huber’s (2000) study, the demonstrations constituted attacking (the mouth-opening demonstration) versus exploratory (the hand-opening demonstration) responses. Presumably the criticism therefore lies in the possibility that the learning of the subjects was more akin to observational conditioning (e.g. Mineka and Cook 1988) than imitation. Similarly, it is possible that the marmosets in our study were learning that the apparatus should either be explored (full demonstration), or eaten (partial demonstration).

#### Non-imitative aspects of social learning

Perhaps the most striking result of the study is the finding that observers specifically focussed on the areas of the ap-

paratus that the demonstrator had contacted. There was a clear difference between the full-demonstration group and the other two groups in terms of where they directed their touches. This effect could be interpreted as a case of very “localised” stimulus enhancement (compared with a general stimulus enhancement effect that would account for the difference in total touches between the full- and partial-demonstration groups compared with the control group). The only other study to date which has described such an effect is Huber et al.’s (2001) artificial fruit experiment with keas (*Nestor notabilis*). There was a significant interaction between place of touch (to handle and bolt-holes compared with lid) between the full-demonstration group and the partial-demonstration group. Furthermore, analyses of the absolute number of touches again showed that the full-demonstration group appeared to be selectively facilitated towards the handle and bolt-holes (as compared with the other two groups). The partial-demonstration group performed more touches to the lid compared with the control group (an effect not reproduced in the full-demonstration group). Therefore, it appears that the demonstration groups learned which specific parts of the artificial fruit should be manipulated. Such effects could potentially form a very powerful drive in social learning, without actually requiring imitation. If individuals are drawn to the functionally relevant parts of an object following observation of a demonstration, then this will certainly move them more quickly towards finding solutions. Indeed, it may be only under relatively rare or specific circumstances that imitation confers greater benefit to the individual than would be provided by a combination of enhancement effects and individual learning.

Although we did not find conclusive evidence of imitation, social learning in a more general sense clearly influenced the behaviour of the subjects. The non-observer control group showed much lower levels of general exploration of the artificial fruit. This is an important result from a practical perspective. Custance et al. (2002), in their review of the relevance of social learning to primate reintroduction, note that it is important to compare demonstration groups with non-exposed controls in order to determine whether social learning confers any real benefit to the animal. The results of this study suggest that demonstrations may benefit observers in many different ways. In addition to the difference between control and observer groups, there were also important behavioural differences between subjects from the full-demonstration group (that saw the complete demonstration) and those from the partial-demonstration group. Individuals from the full-demonstration group had the highest success rate in that not only were they making the most touches of all of the groups, but they were also using their hands relatively more and directing their touches to the relevant locations.

It is interesting that, despite the obvious difficulty (near impossibility) of this task for the marmosets, these clear differences between the groups were found. This supports the point made by Huber et al. (2001) that difficult tasks such as the artificial fruit may be very useful for identify-

ing a variety of (not necessarily imitative) social learning effects on exploratory actions.

Difficult tasks such as the one presented here may also be preferable for identifying the practical benefits of social learning. Despite finding evidence for imitation, Voelkl and Huber (2000) initially found no actual benefit to observer animals in terms of success rate, as control animals opened just as many canisters. However, when the task was made more difficult by closing the lid of the canisters much more firmly, they found a large difference in success rate between one of their demonstration groups and the non-observers. Social learning may in fact provide particular practical benefits to individuals when it induces an individual to persist with unrewarded manipulations of an object (or specific parts of that object), as individual learning alone is unlikely to be successful under such circumstances.

### Social learning in evolutionary perspective

With regard to the broader issue of the correlates and predictors of social learning across species, it appeared that marmosets were probably less proficient social learners than many of those species previously tested. Although, as mentioned above, there are difficulties associated with comparing our results with those of the previous artificial fruit studies with other primates, our study was clearly unusual in that none of the observer individuals succeeded in accessing the food reward from within the artificial fruit. Combined with the relative difficulty of training marmoset demonstrators in the first place, this may provide tentative support for the proposals made by Reader and Lefebvre (2001) and Lefebvre et al. (2003), that social learning emerges as part of a more general package of cognitive flexibility, predicted by factors such as diet. According to this view, the predominantly gummivorous marmoset would be expected to be, in comparison with other primates, poor in terms of both individual learning, and social learning. The limited success of our subjects appears to substantiate this prediction.

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