Social communication with food in captive common marmosets (*Callithrix jacchus*)

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Social transfer of food is important to animals, especially to learn about novel food items and avoid noxious ones. Social transfer of food has been observed in many vertebrates and, amongst primates, extensively in the Callitrichidae family. I chose common marmosets, a cooperatively breeding primate as a model species to study food transfers. In this study, I observed the behaviour of infants after having experienced displays of food jointly with their parents. In different conditions, subjects were given both palatable and unpalatable familiar and novel food items. Following these experiences, I analysed the probabilities of eating the same food item by the infants. Furthermore, I tested the influence of the infants' age and audience composition on the probability of eating. My results revealed that infants generally followed their own experience or the one from older siblings rather than the experience of their parents when deciding to eat a food item. The audience had no effect on the infants' decisions, but older infants were more likely to eat alone and guided younger ones in their decision. In conclusion, the results of this study suggest that social transfer of food functions to learn about novel food and seem to be necessary for infants to develop individual knowledge in their early life. However, this influence decreases over time. Thus, age is the most important variable in the regulation of social communication with food.

Key words: food transfer; individual knowledge; social learning; common marmoset

Introduction

Animals gain many advantages by living in group. Social living can inform others about the presence of predators, the location of shelter or the location of food (Snowdon & Boe 2003). In some group-living animal species, social transfer of food has been observed amongst group members to be an important behaviour that is thought to give conspecifics members the opportunity to learn about novel food items and avoid noxious ones. Many species are neophobic towards novel food (Visalberghi & Fragaszy 1995) but there are some critical periods where individuals will experience novel food, i.e. during the weaning period (Voelkl et al. 2006). This process can be made more adaptive when infants observe their conspecifics and learn from them (Voelkl et al. 2006, Roush & Snowdon 2000). For example, it has been shown in captive capuchins that individuals are more likely to eat novel foods when other group members are present and even more when others are also eating (Rapaport & Brown 2008; Addessi & Visalberghi 2001). This social transmission with food has been observed in many vertebrates (Brown et al. 2005; Galef & Giraldeau, 2001; Heyes & Galef, 1996; Zentall & Galef, 1988), including mammals (Voelkl et al. 2006; Galef 1996; Visalberghi & Addessi 2003) and birds (Voelkl et al. 2006; Klopfer 1961; Mason & Reidinger 1981).

Food transfer in Callitrichidae family

In New World monkeys, different types of early social food-acquisition tactics have been described, especially in the Callitrichidae family (Rapaport & Brown 2008; Brown et al. 2004) and during the period of weaning when infants are most vulnerable (Brown et al. 2004 and 2005). In all Callitrichid genera, a provisioning period has been described by food transfers from adult to infants even from non-mothers (Rapaport & Brown 2008; Brown et al. 2004). In tamarins, food transfer is common around the weaning period and then decreases gradually (Saito et al. 2008; Price & Feistner 2001). By following older group members, infants can learn about foraging behaviour and which novel food items are palatable (Brown et al. 2005). In some species, vocalizations can be part of a complex system of food-offering and can lead to the recruitment of other individuals to a foraging site (Rapaport & Brown 2008; Caine et al. 1995). This allows other group members to learn about the quality and the location of the food (Roush & Snowdon 2001). In adult cotton-top tamarins adults vocalize more when infants are present and this allows infants to better receive food item (Rapaport & Brown 2008; Feistner & Price 1991; Joyce & Snwodon 2007). Overall, however, food transfer seems relatively rare in nonhuman primates, with common marmosets being a notable exception, a possible by-product of their cooperative breeding system (Brown et al. 2004).

Common marmosets as a promising model

Common marmosets are generalist forager. They are therefore often confronted with unknown food items (Schiel & Huber 2006, Rylands & de Faria 1993). Young individuals sometimes refuse to eat novel foods in the absence of conspecifics, suggesting that food transfer functions to overcome neophobic behaviour towards novel foods (Rapaport & Brown 2008; Voelkl et al. 2006; Yamamoto & Lopes 2004). In common marmosets, infants can receive food items from their parents, older siblings or unrelated adults (Vital & Queyras 1997; Feistner & McGrew 1989). Kings (1994), for example, reports that adults offer food to infants and mothers assist infants in locating food and in acquiring feeding skills. She also noted the same pattern in tamarins where sharing food with infants can be accompanied by vocalizations. This type of social transmission also occurs with wild common marmosets (Rapaport & Brown 2008; Schiel & Huber 2006).

As infants can eat solid food from 3-4 weeks of their life, they need to develop skills to allow them to receive information about food (Voelkl et al. 2006; Rapaport & Brown 2008). Therefore, begging for food is a good way to obtain information about an appropriate diet.

Moreover, it has been shown that adult common marmoset were more likely to give piece of food when infants were begging for novel food than familiar food (Rapaport & Brown 2008; Voelkl et al. 2006; Vitale & Queyras 1997). Furthermore, Schiel & Huber (2006) suggested that social learning in common marmosets occurs at least until the age of 3-4 months. During this period, infants showed increased interest in the foraging activities of sub-adult and adult group members (Dell'mour, Range & Huber 2009). Therefore, the fact that this pattern occurs in those families of New World monkeys must provide some benefits to infants, such as increase growth rates, reduce age of weaning and/or increase survival until independence (Brown et al. 2004; McGrew 1975; Lefebvre, 1985; Feistner & McGrew 1989; Price and Feistner 1993).

Inspirations and aim of the study

Three articles came up with interesting findings on food transfer in common marmosets that inspired me to conduct this study. I summarized them below from Price & Feistner 1993, Rapaport 1999 and Brown et al. 2005.

Brown et al. (2005) showed that infants were more likely to beg for novel than familiar food and that adults refused more often infant attempts to obtain novel food (Price & Feistner 1993; Rapaport 1999). Moreover, Rapaport (1999) suggested that the age of the begging individual influences the likelihood of food transfers. Thus, young infants appear to accept every kind of food from adults while older infants and juveniles prefer to accept novel food from adults. Brown et al. (2005), taking into account the palatability of food, however found that adults transferred palatable and unpalatable foods at similar frequencies. They also observed that adults refused more often to share novel compared to familiar foods with infants. These findings indicate that food transfer is a dynamic process as infants acquire skills in obtaining food items from their parents (Joyce & Snowdon 2007). This is exactly what hypothesized

Brown et al. (2004) about food transfer. This process is only effective if infants are old enough to eat solid food and if adults decrease food sharing over time to allow infant to feed independently. Despite all this progress, none of the studies mentioned so far took into account the possibility that infants have acquired individual knowledge about the food they eat, suggesting that additional factors could play a role in learning about palatable foods.

The aim of my study is to determine the relevant variables responsible for food transfers in common marmosets. To do so, I set up an experiment in which infants could freely eat familiar and novel food items after having observed their own parents interacting with the same foods. In doing so, I artificially made the different food items palatable and unpalatable. To render food items unpalatable I applied a mixture of aversive-tasting substances as done in previous studies such that unpalatability was sufficient to induce learning without causing illness (Laska & Metzker 1998). Moreover, I took into account the different age classes of the infants as it has been suggested that adults adjust their behaviours according to the age of their offspring. Therefore, I decided to take in consideration four variables that seemed to be important for food transfer: age, audience, food familiarity and food palatability.

Research questions and predictions

The main questions of my study are: Could infant common marmosets have individual knowledge with food? At what age could they have this individual knowledge? Is food transfer from parents is needed for infants to have individual knowledge?

I tried to answer these questions with the use of the four variables previously enunciated. For each variable, I made the following specific predictions.

Firstly, I predicted that there would be an age effect with young infants being more influenced by the parents than old ones. Moreover, older infants would be more independent to go and eat food items alone than younger ones, they therefore should eat more food items. Thus, older infants would have better knowledge of familiar food than younger ones. However, young infants would probably have better knowledge about novel foods as they would receive more items from their parents, according to the findings by Brown et al. 2005.

Secondly, I predicted that all infants would eat more in the presence of their parents after having had a bad experience with food. When infants have a good experience with food, older infants may eat more items than younger ones. Moreover, young infants may be more influenced by the presence of their parents and/or by the independency of older siblings. Therefore, this audience variable is dependent on the quality of food.

Thirdly, I predicted that infants would eat more familiar than novel foods, and parents would be more likely to refuse to share novel than familiar foods (Brown et al. 2005). I also predicted that this variable was age dependent to young infants receiving more food items than older ones. Moreover, all infants would eat more novel food with the presence of their parents.

Finally, regarding food palatability, I predicted that infants would eat less food items in conditions where they would have a bad experience with food. As parents would certainly also transfer unpalatable food to their infants, infants would have to learn to recognize the quality of food by trying to eat food item, even unpalatable ones (Brown et al. 2005). Moreover, young infants should be more influenced by older siblings when they would have a bad experience with food. Therefore, infants must develop their individual knowledge with food whether familiar or novel and that is what I am going to analyse.

Material and Methods

Subjects and Housing

The study was performed from October to March 2017 on common marmosets (*Callithrix jacchus*). All subjects came from the Parc Challandes, an animal refuge near Geneva (Switzerland). I used one family of eight individuals, including a breeding pair with three generations of twins (always one male and one female). The twins were born in November 2015, April 2016 and October 2016 respectively. At the beginning of the experiments, the breeding female gave birth to the twins from the third generation and gave birth again at the end of the experiment (fourth generation). Therefore, the experiment began when the twins from the third generation were big enough to eat solid food (around three weeks). During those three weeks it allowed me to learn to recognize each subject individually. Unfortunately, the male from the first generation died at the begging of the second month of the study, so I did not take his data in consideration. I finally waited until the twins from the third generation were at the age of almost four month to really perform my experiments.

The subjects were housed in the same indoor enclosure (2.8mx2.95mx2.6m) and had access to an outdoor enclosure. The access hatch to the outdoor enclosure was close during all experiments to force subjects in joining the experiments. The indoor enclosure was furnished with branches, wooden perches and two wooden nests. One wooden perches, which was 1.6m tall, was used for the experimental procedure. All animals were born in captivity and fed in the morning. They could eat whenever they wanted during all day. The diet was composed by a prepared mix with water, vitamins and baby powder, fresh fruits, vegetables and dried fruits with mealworms. Moreover, water and mealworms were available *ad libitum*. Therefore, the experiments were conducted only before the daily diet to ensure that subjects were hungry and attendant to do the task.

Foods

Four familiar (grape, apple, orange and mango) and four novel foods were used in this study. For novel foods, homemade bread was chosen as it represented an interesting novel item for all subjects, not only infants. Bread was made using 250g of flour, 8g of salt, 12g of baking powder and 2dl of water. Once the dough was ready, it was divided in eight equal pieces, stained using commercial food dyes (red, blue and violet, Vahiné, France) and baked 40min at 180°C. To render foods unpalatable, I chose to use a mixture of aversive-tasting substances. I applied a Bitrex solution (2.5%) combined with Metronidazole drops (24mg/ml). I tried various combinations with different concentration of Bitrex solution before having more and less the appropriate dose to add. I finally applied 0.25ML of Bitrex solution with 5 Metronidazole drops on each food items during the unpalatable presentation.

During the experiments, familiar and novel foods were presented separately in different bowls. For familiar food, items used for palatable conditions were organized in bowls filled of water over night and items used for unpalatable conditions were organized in another bowls filled of bitter solution over night as well. For novel food, items used for palatable conditions were organized in bowls filled of water only 15 minutes before the beginning of the experiment. Otherwise, the bread was too crumbled to be used. It was the same with items used for unpalatable conditions. Moreover, during unpalatable conditions items were sometimes readjusted with Metronidazole drops to ensure that items would really be unpalatable for subjects.

Apparatus

The apparatus consisted of a long plate (38cmx19cm), familiar to subjects as they ate on it every day. A box lid (23cmx15cm) delimited the plate allowing selection of foods by subjects.

For the experiment, I used a transparent box lid with holes to allow visual and olfactory contact with the food. Both sides of the plate were full of food items to provide subjects to have at least two or three pieces each. The box lid could be moved from both sides of the plate to reveal the food (**Figs. 1 & 2**).

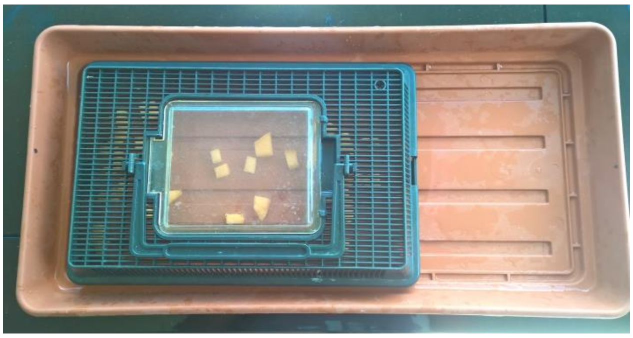

Figure 1: The plate (brown) with the box lid (black)
The box lid allows subjects to visualize and smell food items before performing the task.

Figure 2: The two positions of the box lid
The box lid can move from both sides. On the left picture, the lid was moved from the right to reveal food items on the left. On the right picture, the lid was moved from the left to reveal food items on the right. Therefore, one side would contain palatable items while the other side unpalatable ones.

This system of plate/lid allowed me to control the items parents and infants could select during each condition (see next section). Moreover, I changed the side of palatable and unpalatable items after each trial to ensure that subjects did not develop a side bias to avoid the unpalatable side. I also washed plate and lid after each trial to remove the smell for next food items.

Experimental procedure

The study was divided in four experimental condition each consisting of two phases, the Learning phase and the Test phase. In the Learning phase, which lasted around 5 minutes, parents and infants both had access to food items under the box lid. Then, the plate was removed during approximately one minute after which the Test phase started. The Test phase lasted around 3 minutes where only infants had access to the palatable items. Overall, the presentation of food items lasted around 10 minutes. I carried out multiple trials per day with different food items (**Table 1**), while the weekly schedules differed to prevent subjects from getting used to the procedure. For example, on Day 1, I performed one time Condition B with orange item and two times Condition D with Mango and Grape items. Day 2 does not mean that I came the next day of the week but that it is the second day of observation. During this day, I performed two times Condition A with apple and blue bread, one time Conditions B and C with mango.

Table 1: Example of experimental procedure for a period of three days

	Day 1	**Day 2**	**Day 3**
Condition A	-	Apple, Blue bread	Grape
Condition B	Orange	Mango	Red bread
Condition C	-	Mango	Mango
Condition D	Mango, Grape	-	Grape, Mango

The four experimental conditions examined the positive (palatable) or negative (unpalatable) experience of parents and infants during the Learning phase.

In Condition A, only infants obtained palatable familiar or novel food items while their parents got unpalatable ones. To do so, one side of the plate had palatable items under the box lid and unpalatable items on the other side of the lid (see Apparatus section). Condition B was the opposite, i.e. infants obtained access to unpalatable items on one side of the plate while their parents had palatable items on the other side. For Condition C, subjects got access to familiar or novel foods that were both unpalatable. It was the opposite for condition D where all subjects got access to palatable familiar or novel foods.

Then, as described above the Test phase follows the Learning phase. In this phase, only palatable items were offered only to infants to observe their behaviour. The procedure is summarized below (**Fig. 3**):

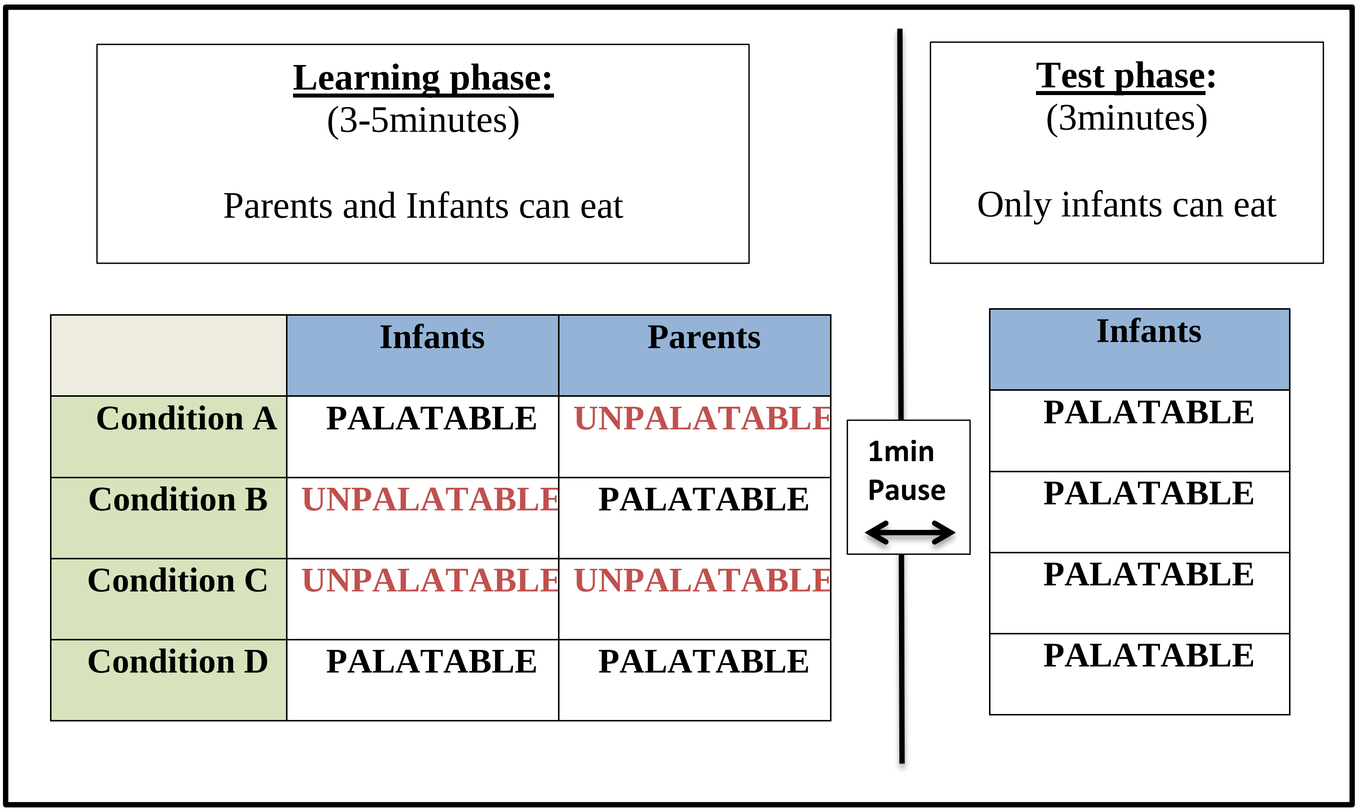

Figure 3: **Overview of the experimental procedure**

Each condition was divided into a Learning phase and a Test phase where food was used at different level of palatability. In Condition A, the parents had bad experience with food while infants had good experience. It was the opposite for Condition B. In Condition C, both subjects had bad experience while in Condition D both had good experience. There was a 1 minute pause between phases.

Data collection and Analysis

To collect my data, I recorded all behaviours of subjects using two cameras. A Sony camera recorded an overview of subjects and a GoPro camera recorded subjects from the above of the plate. For each trial, I scored each individual if they had eaten one food item or not during the Learning phase and only the infants during the Test phase. Moreover, I recorded the presence or absence of parents during the Test phase to observe their impact on the infants' behaviour. Despite the fact that I really tried to have almost the same amount of trial per types of food and conditions I faced some difficulties to perform Condition A. I sometimes did not have enough trials to take this condition in consideration for my results. For example, I had to remove it from the analysis of the audience because I had not one trial where parents were not present.

As the data were binomial (eat or not), the whole analysis was performed using a GLMM model. I firstly tested for an interaction between the parents' experience, if they had eaten palatable or unpalatable food with the experience from infants. I also take in consideration the fact that the age, the type of food and the audience may have an impact on the experience during all experimental conditions. Moreover, I put aside the sex of subjects as it had no real effect for my experiment. Then, I had to test the same model by removing the interaction as the interaction was not significant (see Appendix section).

Results

I conducted N=42 trials, N=19 for familiar and N=23 for novel food. Infants and parents had experienced N=23 trials of unpalatable and N=29 trials of palatable food. For Condition A, I collected a total of N=5 valid trials, for Condition B N=11 trials, for Condition C N=12 trials and for Condition D N=14 trials respectively. Thus, subjects experienced familiar and novel food at the same level and had the same experience per condition with familiar and novel food. I divided my results per variables to have a better visualization of all findings.

The importance of food familiarity

When I considered the results of all infants combined, they had a tendency to follow their own experience after a palatable experience (Condition A and D). When they had an unpalatable experience (Condition B), they tended to follow their parents to eat novel food. However, they seem to have individual knowledge about familiar food as they did not eat many familiar food items compared to novel food items. Finally, when both parents and infants had had an unpalatable experience (Condition C) infants tended to prefer novel rather than familiar foods (**Fig. 4**).

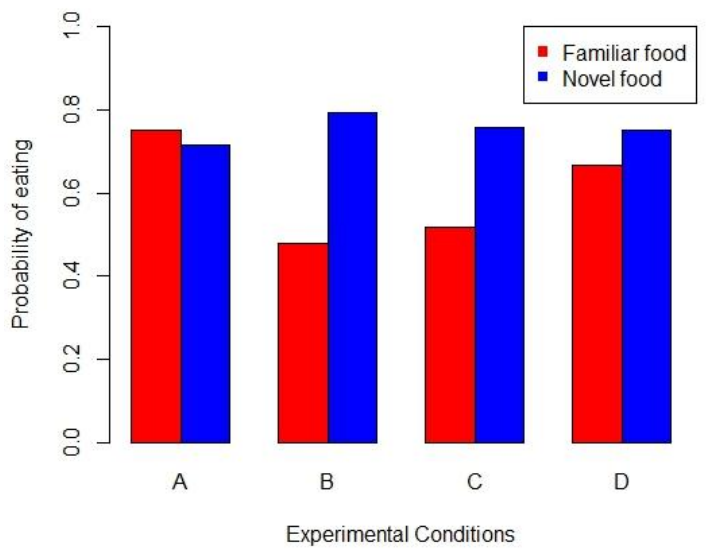

Figure 4: Interaction between food familiarity and the four experimental conditions

The four conditions represent the probability of all infants eating during the Test phase. The bars in red represent the probability of eating familiar food and the blue ones the probability of eating novel food.

The importance of age

When analysing the data from the three age groups separately, some patterns emerged (**Fig. 5**). Concerning first generation only the data from the female were analysed as her brother died at the beginning of the experiment. The female from this first generation seem to follow her own knowledge with food instead of following her parents. She ate more familiar food during the Treatment conditions (A and B) while she ate more novel food during the Control conditions (C and D). Concerning second generation they seem to eat more novel foods following an unpalatable experience (Condition B and C) and more familiar foods after a palatable experience (Condition A and D). And finally, the twins from the third generation ate much more novel food no matter what they had experienced. However, they seem to always eat less than older infants and follow older ones' decision most of the time.

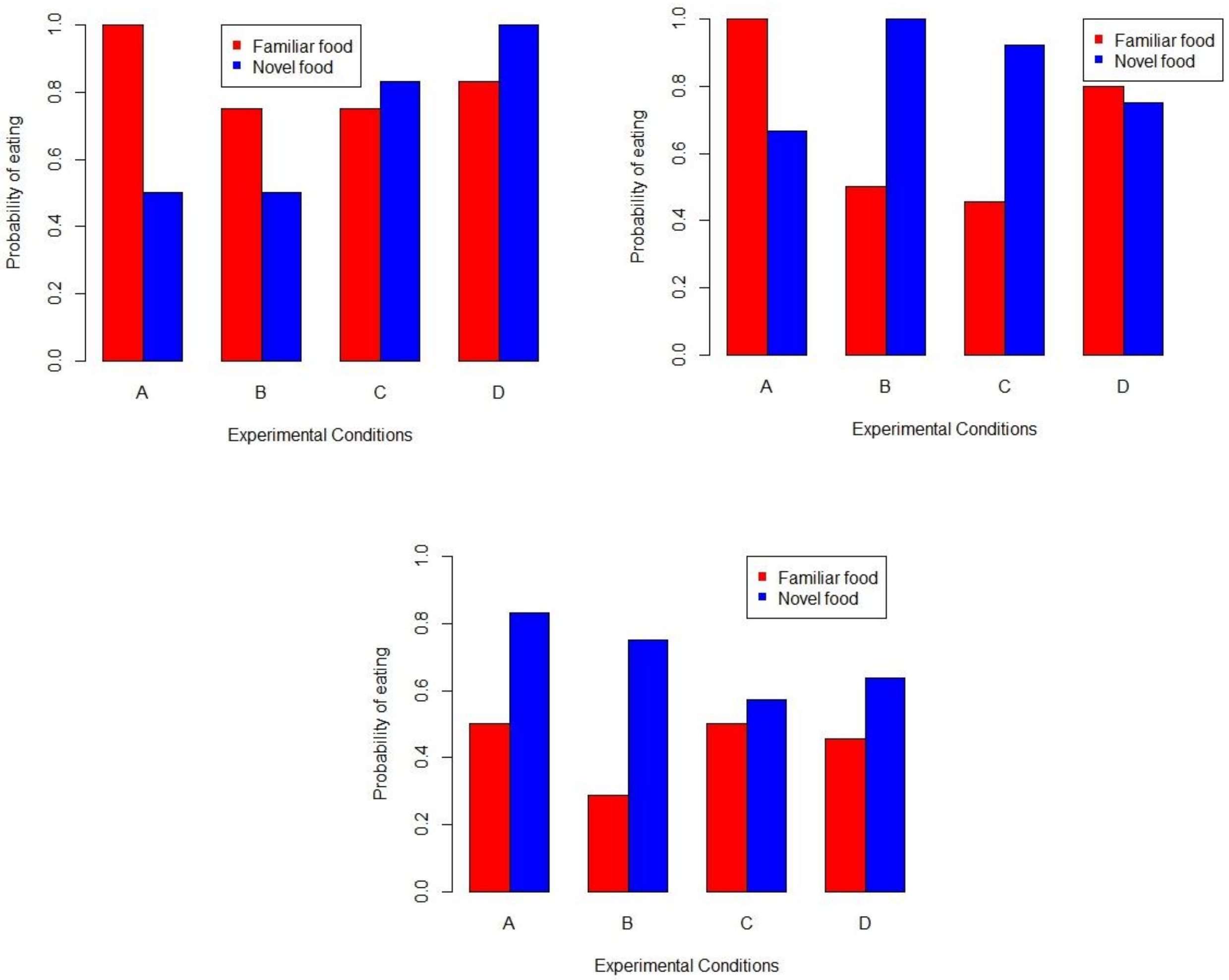

Figure 5: Interaction between food familiarity and the four experimental conditions
The four conditions represent the probability of infants eating during the Test phase. The bars in red represent the probability of eating familiar food and the blue ones the probability of eating novel food.
The left graph represents the probability of eating by the female from the first generation. The right graph represents the probability of eating by the twins from the second generation. The middle graph represents the probability of eating by the twins from the third generation.

The importance of the audience

The presence of parents during the Test phase appeared to change the probability of infants eating (**Fig. 6**). Infants ate more food items when their parents were present following an unpalatable experience (Condition B). However, the presence does not seem to be an important factor for infants as they ate much more food items without audience in the condition where both had an unpalatable experience (Condition C). Therefore, in general, infants seemed to eat more food items when their parents were not present, regardless of whether it was familiar or novel food items (**Fig. 7**).

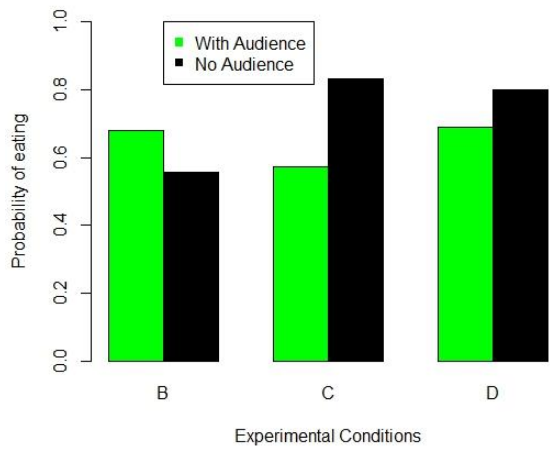

Figure 6: Interaction between the audience and three experimental conditions
The three conditions represent the probability of infants eating during the Test phase. The bars in green represent the probability of eating with audience and the black ones the probability of eating without audience.

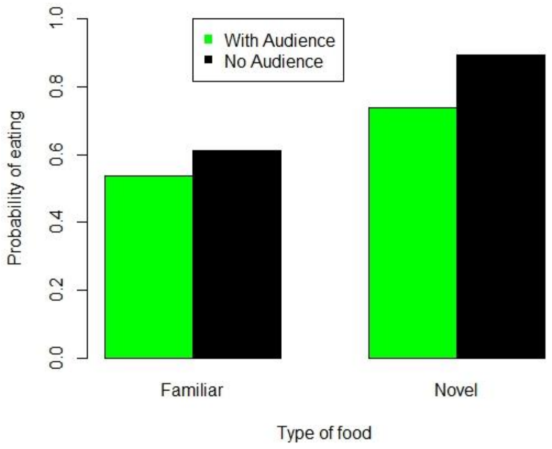

Figure 7: Interaction between audience and food familiarity

The type of food represents the probability of infants eating during the Test phase. The bars in green represent the probability of eating with audience and the black ones the probability of eating without audience.

As a summary, the infants ate more food items when they had had a good experience (Condition A and D) but they did not take in consideration the knowledge of their parents (**Fig. 8**). In fact, infants had the highest probability of eating during Condition A where they had had a good experience with food. In other words, they followed their own knowledge about food most of the time and sometimes followed decisions from other more experienced siblings.

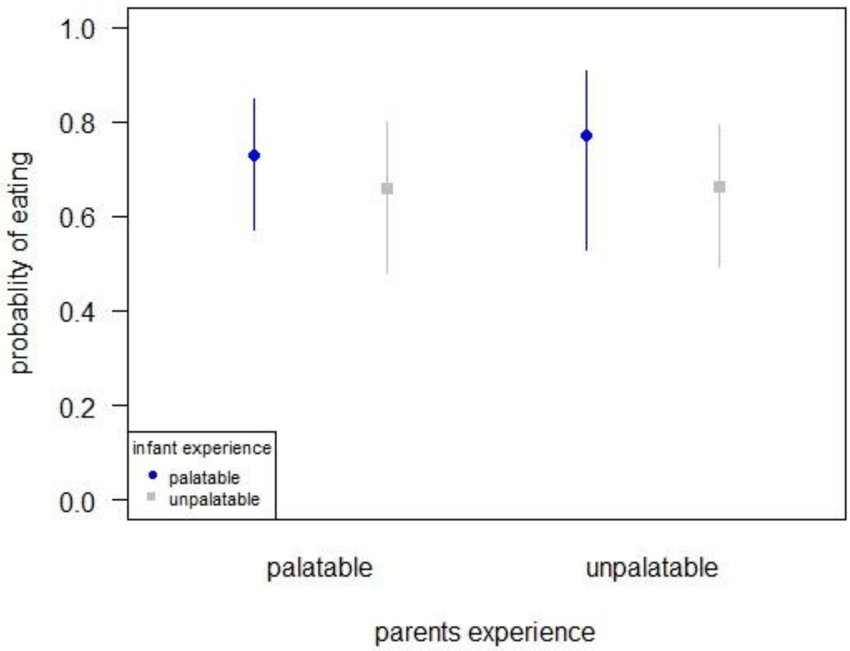

Figure 8: The parents experience compared with the infants experience
The experience represents the probability of all infants eating during the Test phase. The blue bars represent the probability of infants eating during palatable food items conditions (Condition A and D). The grey bars represent the probability of infants eating during unpalatable food items conditions (Condition B and C).

Discussion

The results of this study revealed that infant common marmosets appear to rely mostly on individual knowledge about food when making foraging decisions, rather than following the experience of their parents (Fig. 8). Moreover, a hierarchy occurs through the different experiences they had as younger infants that seem to follow the decision from other older siblings most of the time (Fig. 5). The only possible influence visible from parents was when only the infants had a bad experience about food (Condition B; Fig. 4). Considering the hypothesis that infants acquire knowledge about food choices through social learning, the data suggest that infants may learn socially about novel food types (Fig. 4). However, social learning seems to occur more often on young infant (i.e. third generation) than on older ones (Fig. 5; in the middle), a conclusion in agreement with findings by Schiel & Huber (2006) and Dell'mour, Range & Huber (2009) which noticed that social learning was especially important around the age of 3-4 months in common marmosets.

The influence of food familiarity

In general, infants ate at the same level familiar and novel food in conditions where they had good experience (Condition A and D; Fig. 4). However, when they had a bad experience with food (Condition B and C) they preferred to eat novel food items at a high rate compared to familiar ones (Fig. 4). These findings indicate that their experiences about food influenced the eating rate and the probability of eating one type of food. Young infants and juveniles were only influenced by parents in Condition B and that indicates that they still need some information from adult members (Fig. 4). On the opposite, the female from the first generation exhibits a reverse pattern. She does not seem influenced by her parents at all as she ate at a low level novel food. This pattern can be explained by the fact that the female is already old enough to be totally independent and act as a sub-adult. This could also explain why the younger siblings follow her decisions.

The fact that these results only occur for novel food indicate that parents transfer more novel food than familiar food. It also indicates that they transfer more food items to young infants rather than older ones as old infants do not have the same patterns. Thus, these findings are consistent with the ones from Brown et al. (2015). However, as I did not test for food transfer I cannot conclude that it would always be the case. The rate of interest, begging, transfer and refusal could have given some interesting cues to analyse my results. If the level of interest and begging were high for novel food it could explain the fact that young infant ate more novel food in Condition B. As social learning occurs at early life it gives an advantage for young infants to receive food item from their parents more often than old infants. Thus, food familiarity is an important variable in the regulation of social learning.

The influence of age

When comparing the results separately for the three generations (i.e. old infants, juveniles and young infants) I noticed that the three generations responded differently to some of the experimental conditions.

The pattern from the female of the first generation showed that she was affected if she or her parents had had a bad experience (Condition A and B). Therefore, she preferred eating familiar rather than novel foods (Fig. 5; on the left). This could indicate that she prefers to be cautious about food and eats only food that she knew. However, she exhibits opposite patterns when both infants and parents had the same experience (Condition B and C) as she ate a bit more novel food. This particular finding cannot be explained, except maybe because she has to show young siblings how to proceed.

Now, regarding juvenile marmoset they seem to be very influenced by the different experimental conditions as they exhibit opposite patterns when they had bad or good experiences. They ate more familiar food when they had good experience (Condition A and D) and ate more novel food for the two other conditions (Fig. 4; on the right). These patterns indicate that juveniles are influence by parents and other siblings. Therefore, they seem to follow the old infant when their parents had bad experience about food (Conditions A and C). In Condition B, they ate much more novel food indicating that they were intensively influenced by parents and not by old infants. This finding allows the author to deduce that food transfer must occur and works preferably for novel food.

Finally, young infants exhibited eating novel food no matter what they had experienced (Fig. 4; in the middle). In my study, young infants ate at a high level novel food rather than familiar food when they had bad experience (Condition B). This means that they were influenced by the good experience of the parents during the Learning phase. Therefore, strong social learning occurs on this generation of twins. As they are the youngest they are not familiar enough with familiar food and strongly influenced by the parent’s food-transfer. They received more food than older siblings and received even more novel food. In fact, they received more information from novel than familiar food which explained why they always ate more novel food items in each condition. However, they ate less food items than their older siblings because a hierarchical pattern occurs between categories of infants where older ones impose themselves first to eat food items. Nevertheless, young infants are still learning and acquiring skills at this age of life. In fact, they also learn to acquire those skills by watching the foraging activities from older siblings, as described by Dell'mour, Range & Huber (2009). Therefore, the age is also an important variable in the regulation of social learning.

The influence of food palatability

Concerning food palatability it does not seem to have an influence on the level of eating by the infant during the Test phase (Fig. 4). Infants ate food items at a high rate in conditions where they had bad experience. Brown et al. (2005) found that adults transferred palatable and unpalatable food at the same level. It could be one explanation of the high probability of eating of each generation of twins in Condition B & C (Fig. 5). As adults refuse more sharing food when infants beg for novel food and refuse even more sharing food when older infant beg, this could also explain the low level of novel food eating by the female from the first generation in Condition B. Another explanation is that the unpalatable foods were not unpalatable enough to disgust the infants from avoiding the food. As it did not provoke strong aversive reactions, subjects still continued to come and try to eat unpalatable food. Therefore, I cannot conclude anything concerning the influence of food palatability on social learning. My results need some adjustments (See Limitations section).

The influence of audience

The presence of adults helps infants develop new cues for the quality of the food as they learn by watching others. For my study I wanted to know if the presence of their parents could influence their behaviour during the Test phase. I only observed some small influence of the audience in Condition B where infants had bad experience (Fig. 6). They ate a bit more food items during the Test phase when their parents were present. That could indicate that infants were a bit influenced by the good experiences of their parents. However, they ate even more food items when their parents were not present in Condition C where both parents and infants had bad experience (Fig. 6). This could inform on the individual knowledge of the infants as they preferred to eat in the absence of their parents. Moreover, as they did not eat food item during the Learning phase they were certainly hungry and simply wanted to eat food. On the opposite, in Condition D where both parents and infants had good experience they ate more food items when their parents were not present (Fig. 6). This indicates that parents prevent infants to eat first, so it explains the fact that infants ate more without audience. By looking at the type of food infants ate more novel food items than familiar ones but they always ate more food in the absence of their parents in both cases (Fig. 7). Therefore, the audience is not an important variable in the regulation of individual knowledge. The infants are strong enough to experience foraging alone without adults. In my study there are three age classes which allow young individual to certainly follow the older ones' experience.

Limitations of the study

When I designed my experiment I really thought it would be quite simple to conduct it. As soon as I performed the first trials I was already lost and realized that my experiment would be delicate. Therefore, I faced four considerable problems which were the small sample size, non-representative study group, the appropriate dose of bitter solution and separation of subjects. I would need to modify and solve these problems before conducting my experiment again.

The biggest problem was in finding the appropriate dose of bitter solution to add to the food. Despite the fact that the foods were unpalatable, infants and parents still continue to eat food items. They maybe get used to it and finally accept the food as it was. Thus, Bitrex solution does not seem to be enough unpalatable for them to avoid the food. When I used the combination with another bitter agents it was more unpalatable but did not provoke aversive reactions like alarm calls. The use of other bitter agent could be a solution to be more efficient to render palatable food unpalatable. Laska & Metzker (1998) used quinine hydrochloride combined with ascorbic acid as a bitter solution and could observe some aversive reaction. They added the bitter taste in the dough of their cookies directly instead of adding it as I did. The fact that the bitter agent is already inside the cookie must be more powerful to render the food unpalatable.

Furthermore, the fact that I use only one type of novel food (colour bread) instead of two or three biased my results. It is certain that subjects could have developed some knowledge about bread and do not care about the different colours. I did not find some difference on the subjects' behaviour between the 4 colour breads. They had eaten the different coloured bread presented to them during each condition at the same amount.

Another problem was on the small sample size. I had only one family with 5 infants. I would need more infants with different age classes to ensure that those results would be consistent with mine. The fact that I did not have subordinate adults also biased my results. Therefore, I did not have a representative study group.

Finally, I had problems to separate my subjects. I could not physically separate them so I used the box/lib technique. This technique does not seem to be appropriate as sometimes parents or infants got food even if it was not their time to eat.

Perspectives and conclusions

Previous studies have revealed that food transfer occurred in early life-time and decreased over time. I could observe the same pattern in my study and measured that infants could have individual knowledge about food even at early stage of life. However, the mechanism that promotes infants to proceed to acquire skills in foraging activities needs further experimenting. Therefore, to really verify my results I would need to conduct all my experiments differently.

First, I would need to physically separate infants from their parents in distinct enclosures. Secondly, I would also need to try other bitter solution and directly add it to the dough as I mentioned above. Finally, I would need to select various novel foods to be sure that subjects do not assimilate the food presented to them. These three adjustments have to be tested on various families of common marmosets with different sample size to test all combination of infant class ages. Moreover, as the other species in the Callitrichidae family have the same behaviour with food it could be interesting to perform my experiments on various species. Cotton-top tamarins seem to be another appropriate species to test as they have a panel of vocalization for food. It has been shown that adult members vocalize when approaching food, suggesting communication about the quality and the location of the food (Roush & Snowdon 2001). It would also be interesting to test first the level of food transfer (Interest, Begging, Refusal and Transfer rate) as Brown et al. (2005) did. Therefore, my study is a first step in the understanding of individual knowledge versus social learning behind the phenomenon of food transfer.

To conclude I could answer my three research questions with the fact that infants can have individual knowledge with food and already at early life. The first generation, which had one year of age, had a strong individual knowledge with familiar food and were independent enough to make their own decision. On the opposite, the third generation which had almost 4 month of age had a better knowledge with novel food as they were strongly influenced by their parents and older siblings. Therefore, food transfer from parents is a necessary phenomenon to acquire individual knowledge with food at early life. However, this influence decreases over time. Old infants are big enough to influence younger siblings in following their foraging skills instead of their parents. Thus, I found that age is the most important variable in the regulation of social learning with food.

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Appendix

Model with interaction:

```
xdata <- marmosets

null=glmer(EatorNot~ Sex + (1|ID) + (1|Item) + (1|TrialID),data=xdata,
family=binomial, control=glmerControl(optimizer = "bobyqa"))

res=glmer(EatorNot~ infpal*parpal +Food+Age+Audience+Sex+(1|ID) +
(1|Item)+(1|TrialID),data=xdata, family=binomial, control=glmerControl
(optimizer = "bobyqa"))


anova(null, res, test="Chisq")
Data: xdata
Models:
null: EatorNot ~ Sex + (1 | ID) + (1 | Item) + (1 | TrialID)
res: EatorNot ~ infpal * parpal + Food + Age + Audience + Sex + (1 |
res:     ID) + (1 | Item) + (1 | TrialID)
     Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
null  5 232.01 248.08 -111.00   222.01
res  12 233.75 272.32 -104.87   209.75 12.264      7     0.0922 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


summary(res)
Generalized linear mixed model fit by maximum likelihood (Laplace Approxima
tion) [glmerMod]
 Family: binomial  ( logit )
Formula: EatorNot ~ infpal * parpal + Food + Age + Audience + Sex + (1 |
    ID) + (1 | Item) + (1 | TrialID)
   Data: xdata
```

```
Control: glmerControl(optimizer = "bobyqa")


AIC      BIC   logLik deviance df.resid
   233.7    272.3   -104.9    209.7      172

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.0408 -0.9103  0.4648  0.6352  1.4727

Random effects:
 Groups  Name        Variance Std.Dev.
 TrialID (Intercept) 0.0000   0.0000
 Item    (Intercept) 0.0000   0.0000
 ID      (Intercept) 0.1549   0.3936
Number of obs: 184, groups:  TrialID, 42; Item, 8; ID, 5

Fixed effects:
               Estimate Std. Error z value Pr(>|z|)
(Intercept)    0.599272   0.663210   0.904  0.36621
infpal         0.547825   0.602577   0.909  0.36328
parpal        -0.003472   0.440446  -0.008  0.99371
FoodNovel      0.925070   0.343764   2.691  0.00712 **
AgeG2         -0.473841   0.762764  -0.621  0.53446
AgeG3         -1.394487   0.753268  -1.851  0.06413 .
AudienceNo     0.712976   0.458172   1.556  0.11968
SexM           0.470709   0.541373   0.870  0.38459
infpal:parpal -0.208902   0.755155  -0.277  0.78206
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) infpal parpal FodNvl AgeG2  AgeG3  AudncN SexM
infpal      -0.214
parpal      -0.319  0.339
FoodNovel   -0.216 -0.028  0.019
AgeG2       -0.689 -0.022  0.004 -0.032
AgeG3       -0.688 -0.041  0.014 -0.066  0.745
AudienceNo  -0.135  0.184  0.079  0.048 -0.037 -0.064
SexM        -0.004  0.018 -0.014  0.034 -0.362 -0.361  0.030
infpal:prpl  0.166 -0.799 -0.589  0.025  0.031  0.037 -0.157 -0.022
```

<u>Model without the interaction</u>:

```
red <- update(res, .~. -infpal:parpal)

anova(red, res)
Data: xdata
Models:
red: EatorNot ~ infpal + parpal + Food + Age + Audience + Sex + (1 |
red:     ID) + (1 | Item) + (1 | TrialID)
res: EatorNot ~ infpal * parpal + Food + Age + Audience + Sex + (1 |
res:     ID) + (1 | Item) + (1 | TrialID)
    Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
red 11 231.82 267.19 -104.91   209.82
res 12 233.75 272.32 -104.87   209.75 0.0767      1     0.7818
```

```
summary(red)
Generalized linear mixed model fit by maximum likelihood (Laplace Approxima
tion) [glmerMod]
 Family: binomial  ( logit )
Formula: EatorNot ~ infpal + parpal + Food + Age + Audience + Sex + (1 |
    ID) + (1 | Item) + (1 | TrialID)
   Data: xdata
Control: glmerControl(optimizer = "bobyqa")

     AIC      BIC   logLik deviance df.resid
   231.8    267.2   -104.9    209.8      173

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.9533 -0.8958  0.4555  0.6460  1.4425

Random effects:
 Groups  Name        Variance Std.Dev.
 TrialID (Intercept) 0.0000   0.0000
 Item    (Intercept) 0.0000   0.0000
 ID      (Intercept) 0.1553   0.3941
Number of obs: 184, groups:  TrialID, 42; Item, 8; ID, 5

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  0.63012    0.65445   0.963  0.33563
infpal       0.41521    0.36077   1.151  0.24978
parpal      -0.07566    0.35440  -0.214  0.83094
FoodNovel    0.92789    0.34360   2.700  0.00692 **
AgeG2       -0.46735    0.76288  -0.613  0.54014
AgeG3       -1.38736    0.75322  -1.842  0.06549 .
AudienceNo   0.69314    0.45270   1.531  0.12574
SexM         0.46762    0.54157   0.864  0.38789
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
           (Intr) infpal parpal FodNvl AgeG2  AgeG3  AudncN
infpal     -0.141
parpal     -0.279 -0.259
FoodNovel  -0.224 -0.014  0.043
AgeG2      -0.705  0.005  0.028 -0.032
AgeG3      -0.705 -0.019  0.045 -0.066  0.745
AudienceNo -0.111  0.102 -0.021  0.052 -0.032 -0.059
SexM        0.000  0.000 -0.033  0.034 -0.362 -0.360  0.027
```