

ORCA - Online Research @ Cardiff

This is an Open Access document downloaded from ORCA, Cardiff University's institutional repository:https://orca.cardiff.ac.uk/id/eprint/138745/

This is the author's version of a work that was submitted to / accepted for publication.

Citation for final published version:

Figueroa, Jamie, Luna, Daniela, Salazar, Laura C., Morales, Pia, Valdivia, Catalina, Müller, Maximiliano and Dwyer, Dominic 2021. Effects of trial and error and social learning on flavour palatability in nursery pigs. Applied Animal Behaviour Science 236 , 105265. 10.1016/j.applanim.2021.105265

Publishers page: https://doi.org/10.1016/j.applanim.2021.105265

Please note:

Changes made as a result of publishing processes such as copy-editing, formatting and page numbers may not be reflected in this version. For the definitive version of this publication, please refer to the published source. You are advised to consult the publisher's version if you wish to cite this paper.

This version is being made available in accordance with publisher policies. See http://orca.cf.ac.uk/policies.html for usage policies. Copyright and moral rights for publications made available in ORCA are retained by the copyright holders.



1Effects of trial and error and social learning on flavour palatability in nursery pigs

2

3Jaime Figueroa^a*, Daniela Luna^a, Laura C. Salazar^{a,1,2}, Pia Morales^b, Catalina Valdivia^c,
4Maximiliano Müller^c, Dominic Dwyer^d

5

6^aDepartamento de Ciencias Animales, Facultad de Agronomía e Ingeniería Forestal, Pontificia 7Universidad Católica de Chile, Santiago 7820436, Chile.

8^bFloramatic S.A, Av. Marathon 1989, Ñuñoa, 7750000, Santiago, Chile.

9ºDepartamento de Fomento de la Producción Animal, Facultad de Ciencias Veterinarias y

10Pecuarias, Universidad de Chile, Santiago 8820000, Chile.

11^dSchool of Psychology, Cardiff University, Cardiff CF10 3AT, UK.

12

13*Corresponding author: Departamento de Ciencias Animales, Facultad de Agronomía e Ingeniería
14Forestal, Pontificia Universidad Católica de Chile. Avda Vicuña Mackenna 4860, Santiago, Chile.
15Tel: +56 02 23544092. E-mail address: <u>figueroa.jaime@uc.cl</u>

16

^{1&}lt;sup>1</sup> Animal Behaviour & Welfare, Animal and Veterinary Sciences Research Group, Scotland's Rural
2College (SRUC), West Mains Rd., Edinburgh, EH9 3JG, United Kingdom

^{3&}lt;sup>2</sup> The Roslin Institute and Royal (Dick) School of Veterinary Studies, University of Edinburgh, Easter

⁴Bush Campus, Midlothian, EH25 9RG, United Kingdom

18ABSTRACT

19The acquisition of behaviours that enhance the acceptability of new feeds could improve the 20performance and animal welfare in the pig industry. Pigs may learn individually by trial and error 21and/or by social learning to consume and prefer new flavoured feeds. However, there is little 22information regarding the effects of learning on the palatability of those flavours. This study aimed 23to investigate possible changes in pigs' hedonic responses, estimated by the mean consumption time 24per approach (CT/A), for flavours previously learnt through individual experiences (Experiment 1) 25and socially by a brief interaction with an experienced conspecific (Experiment 2). A total of 96 26nursery pigs were used to study their preference, acceptability and palatability for flavours 27 previously conditioned. Flavours were associated with 4% sucrose (Experiment 1) or with a 28demonstrator that recently consumed the flavour (Experiment 2). Those flavours or positive 29conditioned stimulus (CS+) were compared with control flavours that were not positively 30conditioned (CS-). In experiment 1, pigs preferred (P = 0.010) and tended to accept more (P =310.069) of the CS+ than CS- in water solutions. Nevertheless, no palatability differences were found 32(P = 0.875). In experiment 2, observer animals had a higher intake of CS+ following interaction 33 with demonstrators that consumed the same flavoured feed (P = 0.041). Snout to snout interaction 34time between those demonstrators and observers tended to present a positive correlation with CT/A 35(r = 0.497, P = 0.1). Thus both individual trial and error learning, and social learning, increased pigs 36acceptance of, and preference for, food flavours. However, only social Learning modified the 37pattern of consumption with the observation of a correlation between changes in the CT/A ratio and 38the degree of snout to snout contact time between demonstrators and observers. Thus the 39mechanisms and effects of social and individual learning appear to differ at least partially. 40Regardless of mechanism, the fact that associative learning can increase food flavour consumption 41suggests that interventions based on associative learning may be beneficial for addressing welfare 42problems in pig production linked to low consumption, in particular with respect to weaning where 43the low consumption may relate to the inexperience of the animals.

44**Keywords**: associative learning; feeding behaviour; palatability; pigs; social learning; trial and 45error learning

46

471. Introduction

48 Learning plays a significant role in food selection through the acquisition of individual 49preferences for associated sensory cues that predict oral and post-oral rewards of food (Sclafani, 502004). When animals learn to consume new foods by trial and error learning, flavours associated 51with those foods may act as conditioned stimuli. The flavour of the food is associated with the 52positive or negative consequences of consumption (unconditioned stimuli), generating a future 53attraction or rejection for the associated flavours (Ackroff and Sclafani, 2010). However, 54environment exploration requires expenditure of time and energy, exposing animals to potential 55predators or toxins (Laland, 2004). In contrast, social learning facilitates the acquisition of highly 56adaptive food information, typically from conspecifics, thereby minimizing the costs implied by 57trial and error learning (Nicol, 1995). Animals can learn to consume foods through imitation, 58monitoring of the consumption site or joining other more experienced animals during a 59consumption episode (Galef and Laland, 2005). Thus, through social learning animals can learn 60flavour preferences (Galef and Whiskin, 2008), the location of food sources (Held et al., 2000), and 61to avoid noxious foods (Laland, 2004).

Under commercial conditions, pigs are faced by nutritional challenges that may affect their G3subsequent productive performance (Main et al., 2004). At weaning, pigs are reluctant to eat new 64feeds, often resulting in a period of underfeeding or anorexia with consequent diarrhoea and poor 65growth, resulting in reduced welfare (Oostindjer et al., 2014). Learning about foods before weaning 66could be a useful strategy to reduce these detrimental effects by improving the acceptability of new 67feeds or flavours. Previous experiments have shown that pigs prefer flavours learned by both 68individual trial and error (Clouard et al., 2012; Figueroa et al., 2012a) and by social learning (Held 69et al., 2000; Figueroa et al., 2013). However, learnt flavour preferences could be explained by many 70changes, including motivation or by changes in the pleasure perception or palatability of that 71flavour at the time of consumption (Dwyer, 2008, 2009).

72 Experiments in rats have evaluated palatability through orofacial reactions at the time of 73consumption (Grill and Norgren, 1978), short-term consumption (Boughter et al., 2002), and 74analysis of lick cluster size (Davis and Smith, 1992; Dwyer, 2008). Palatability has been studied in 75pigs through the analysis of consumption patterns (Figueroa et al., 2019), analogous to lick cluster 76size analysis in rats, where the consumption time (CT) divided by the number of approaches (A) to 77the site of consumption is assessed (CT/A). However, little information exists regarding the effects 78of learning on the palatability of a flavour in pigs (Forbes, 2010; Clouard et al., 2014). Experiments 79in rats demonstrate that when a flavour is associated with carbohydrates, such as sucrose or 80maltodextrins, the palatability of the associated cues increases (Forestell and LoLordo, 2003; 81Dwyer, 2008). However, there is little information about the effect of social learning on flavour 82palatability. Recently, Figueroa et al. (2020a) did not find hedonic changes in rats' flavour 83perception after interacting with a conspecific that recently consumed a flavoured solution. The aim of this study was to investigate possible changes in pigs' responses (in terms of 84 85preference, acceptability and palatability) for flavours previously learnt during a training period by 86 individual trial and error experiences (Experiment 1) and socially by a brief interaction (30 min) 87 with a conspecific that recently consumed those flavours (Experiment 2).

88

892. Materials and methods

90 Experiments were conducted at the nursery unit of Pontificia Universidad Católica de Chile pig
91 facilities. The experimental procedures were approved by the Ethical Committee on Animal
92 Experimentation of the Facultad de Ciencias Veterinarias y Pecuarias at the Universidad de Chile,
93 certificate Nº 252014.

94

952.1 Experiment 1: Flavour conditioned palatability after individual trial and error learning

972.1.1 Animals and housing

A total of 32 castrated male and female nursery pigs were used (PIC® genetics, Hendersonville, 98 99Tennessee, USA). Animals (weaned at 21 days; 6.094 ± 0.148 kg) were transported from a 100commercial pig farm (Metropolitan de Santiago region, Chile) to the swine experimental facilities 101experimental nursery facilities belonging to the university. They had been offered an unflavoured 102creep-feed diet during the suckling period from day 10 using a commercial pan feeder at the 103commercial farm. On arrival at the experimental facility, animals were individually identified using 104numbered plastic ear tags and were randomly allocated into 16 fully slatted pens (2 pigs/pen; 1.28 105m x 1.8 m x 0.7 m). The pens had full walls, therefore the animals in each pen had no visual or 106tactile contact with the animals from other pens during the whole experimental procedure. The 107nursery room was equipped with automatic forced ventilation and controlled environment 108 temperature ($27.3 \pm 2.70^{\circ}$ C). The animals had ad libitum access to a commercial powder feed 109offered with a hopper feeder with 3 feeding spaces according to their nutritional requirements 110(NRC, 2012) and water provided by stainless steel nipples. Hanging steel chains were used as 111environmental enrichment during the nursery period but there were removed during the 112experimental period. Before experimental procedures started, pigs were acclimated for one week to 113the new environment and management conditions.

114

1152.1.2. Experimental procedure

After the acclimation period, animals were trained to drink during 8 days (alternate sessions) a 117flavoured solution (CS+Suc) that was mixed with 4% sucrose and a different flavoured solution 118(CS-) mixed in water. Flavour products used as CSs (garlic or aniseed, 0.075%; Floramatic ®, 119Santiago, Chile) were selected because of their similar preferences in naive animals and were 120balanced across pens to act as CS+ or CS- flavours. Thus half of the pens (Group 1, 8 pens) were 121trained to drink garlic flavoured solutions mixed with 4% sucrose during sessions 1, 3, 6 and 8,

122while the remaining pens (Group 2, 8 pens) were exposed to the garlic flavour solution without 123sucrose at those sessions. During the other 4 sessions (days 2, 4, 5 and 7), half of the pens (Group 2, 124n8) were trained to drink an aniseed flavoured solution mixed with 4% sucrose, while the remaining 125pens (Group 1, n8) were exposed to aniseed flavoured solution without sucrose. Training sessions 126involved giving one experimental pan with 800mL of the respective CS solution at 10:00 am at the 127front of each pen for 30 min/day. Animals were feed and water restricted for 1 hour before sessions 128and no feed or water was available during the training. Consumption was measured by calculating 129the difference between the initial and final weight of the pans.

Flavour preference, acceptability and palatability for CS+ and CS- flavours were estimated in 131each pen on days 10 and 11. Flavour preferences were assessed using a two-choice test. Pig pairs 132were exposed for 30 min to two equidistant pan-feeders simultaneously placed in the front of each 133pen containing the CS+ and CS- flavoured solutions without sucrose. The right-left position of the 134CS+ and CS- flavours was balanced across subjects and days: half of the pens of each group 135received the garlic solutions at the right position the first day and aniseed solutions at the left 136position. In the other half of pens of each group, aniseed solutions were at the right position and 137garlic solutions at the left position. The flavour positions were swapped on the second test day. 138Subsequently, the acceptability of that flavours (CS+ and CS-) was estimated on two consecutive 139days (experimental days 12 and 13), where the animals received a single pan placed in the front of 140each pen containing one of the flavoured solutions (without sucrose) for 30 min, balancing the 141flavours (CS+ and CS-) between animals and days. One hour of feed and water restriction was 142applied before each test and no feed or water was available during the test.X

143 Intake was measured by calculating the difference between the initial and final weight of the 144pans during each preference and acceptability test. Usually, solution spillage was not significant and 145was not accounted when measuring consumption. Additionally, the behaviour of the pigs in term of 146consumption time and number of approaches to the pan was recorded simultaneously during the 147first 10 min of the acceptability test by focal continuous sampling using one video camera (IR 148Outdoor Cameras 700tvl 1/3 cmos Sony, SENKO SA, Santiago, Chile) placed in a central position 149on the ceiling of each pen. The CT/A was estimated based on study of Figueroa et al. (2019) as the 150total time in which the animal drinking at the pan (i.e. consumption time) divided by the number of 151times the pan was approached with a consumption result (i.e. number of approaches). For each pen, 152one video camera was used. Additionally, analyses of the first (0 to 5 min) and the final (6 to 10 153min) half of the period were performed to examine whether these sub-periods of the session would 154be more sensitive than the session as a whole in estimating palatability.

155

1562.1.3. Statistical analysis

157Consumption from each pen (pair of pigs) during the training sessions and at the preference, 158acceptability and palatability tests after training were analysed by mixed linear models with the 159MIXED procedure of the statistical package SAS 9.4 (SAS Inst. Inc., Cary, NC), taking into 160account for training sessions the solution consumed (CS+Suc or CS-), the flavour consumed (garlic 161or aniseed), the training session (1-4) and the interaction between factors. For preference and 162acceptability test the main factors considered were the solution consumed (CS+ or CS-), the flavour 163consumed (garlic or aniseed) and their interaction. Finally, to estimate palatability, CT/A were 164analysed for the total period (0 to 10 min) and in each sub-period (0 to 5 min and 6 to 10 min), 165considering as the main factors the solution consumed (CS+ or CS-) and the flavour consumed 166(garlic or aniseed) and the interaction between factors. Interactions that were not significant were 167 removed from the final model. Pen was included as a random effect. Each pair of pigs were 168considered as an experimental unit. Prior to ANOVA analysis, normality and homoscedasticity of 169dataset were analysed by using the UNIVARIATE procedure with the Shapiro Wilk and O'Brien's 170test, respectively. As no significant p-values were obtained for any of the specific factors, the 171 original hypothesis for normality and homogeneity of variance were accepted (P>0.10). Results are 172presented as LSMeans \pm SEM, considering a significance level of 5% adjusted by Tukey. A trend in 173the data was defined as $0.05 \le P \le 0.1$.

1742.2 Experiment 2: Flavour conditioned palatability after social learning

175

1762.2.1 Animals and housing

177 A total of 64 castrated male and female nursery pigs (PIC® genetics, Hendersonville, Tennessee, 178USA), weaned at 21 days of life and weighing 6.088 ± 0.209 kg were used. The origin of animals, 179transport, identification and husbandry conditions were the same as in Experiment 1 with the 180exception that pigs were allocated in groups of 4 to the 16 nursery pens.

181

1822.2.2 Experimental Procedure

Experimental procedures are summarized in **Figure 1.** After the acclimation period, two pigs 184from each pen (16 pig-pairs) were randomly selected to act as demonstrators (DEM) and were 185temporary removed and allocated to 16 pens (identical to their home pens in a neighbouring room). 186DEM were then *ad libitum* fed with a flavoured commercial diet (0.075% aniseed or garlic flavours 187(Floramatic ®, Santiago, Chile)) for 30 min; eight pairs were exposed to garlic flavour and the 188remaining eight to aniseed in order to balance the experimental design.

DEM pigs were returned to their original pens to interact with pigs that remained there 190(observers; OBS) for 30 minutes. After the interaction period between DEM and OBS, DEM pigs 191were removed again and OBS were exposed to a pan-feeder with garlic feed for 30 minutes placed 192in the front of each pen. This was repeated 24 and 48h later in order to estimate the extinction of the 193expected change in observers' feeding behaviour. Before each test, animals underwent one hour of 194feed and water restriction. No commercial feed or water was available during the test. Feed intake 195was estimated by calculating the difference between the initial and final weight of the pans for each 196acceptability test. Feed waste was not significant and was not accounted when measuring 197consumption. As in experiment 1, OBS pigs were video recorded (16 Video-cameras, IR Outdoor 198Cameras 700tvl 1/3 cmos Sony, SENKO SA, Santiago, Chile) during the first 10 min. of their 199exposure to garlic diets and behaviour was analysed by focal continuous sampling in order to 200estimate CT/A (Figueroa et al., 2019). This was used as a possible indicator of changes in the 201hedonic perception for the flavoured food. Additionally, analyses of the initial (0 to 5 min) and the 202final (6 to 10 min) half of the period were performed to examine whether these sub-periods of the 203session would be more sensitive than the session as a whole to estimate palatability. Moreover, the 204time spent on oro-nasal contact between DEM and their respective OBS during the interaction 205period was measured to study possible correlations between interaction time and the magnitude of 206the expected effect on OBS feeding behaviour, reflected in animals' CT/A, consumption time and 207number of approaches during the complete period of the test (0-10 min), the initial (0 to 5 min) and 208the final (6 to 10 min) half of the test. In order to assess the time of oro-nasal contact more 209accurately between DEM and OBS, the video-cameras were installed on ceiling of each pen to 210capture from an upper view the physical contact between animals. The oro-nasal contact was 211defined when an observer pig touched the end of the snout of the demonstrator pig with the end of 212its own snout and vice versa.

213

2142.2.3. Statistical analysis

215 Consumption data of each DEM and OBS pairs and the palatability measures of OBS pairs were 216analysed by mixed linear models with the MIXED procedure of the statistical package SAS 9.4 217(SAS Inst. Inc., Cary, NC), taking into account in the case of DEM consumption the flavoured feed 218consumed (garlic or aniseed feed), and in the case of OBS consumption the flavoured feed 219consumed by their respective DEM (garlic or aniseed feed), the test day (1, 2 or 3) and the 220interaction between those factors. Finally to estimate OBS palatability, CT/A were analysed for the 221total period (0 to 10 min) and in sub-periods (0 to 5 min and 6 to 10 min), taking into account as the 222main factors the flavoured feed consumed by their respective DEM (garlic or aniseed feed), the test 223day (1, 2 or 3) and the interaction between those factors. Moreover, Spearman correlations were 224calculated between the oro-nasal interaction time of DEM and their respective OBS, and the CT/A 225and their components (consumption time and number of approaches to the pan) of those OBS 226during the complete period of the test and sub-periods. Before ANOVA analysis, normality and 227homoscedasticity of dataset were analysed by using the UNIVARIATE procedure with the Shapiro 228Wilk and O'Brien's test, respectively. As no significant p-values were obtained for any of the 229specific factors, the original hypothesis for normality and homogeneity of variance were accepted 230(P > 0.10). Results are presented as LSMeans \pm SEM, considering a significance level of 5% 231adjusted by Tukey. A trend in the data was defined as $0.05 \le P \le 0.1$.

232

2333. Results

234

2353.1 Results Experiment 1: Trial and error learning

236

2373.1.1 Training sessions

Animals increased their solution intake as the days increased [F(3, 15) = 21.29, P < 0.001]. 239Overall intake was higher for CS+Suc than CS- solutions [F(1, 15) = 16.44, P = 0.001]. Intakes of 240CS+Suc and CS- during the training sessions are shown in **Figure 2.** There was an interaction 241between testing days and solutions $[Day \times CS, F(3, 15) = 8.24, P = 0.002]$, were the intake of 242CS+Suc increased over training sessions exceeding the consumption of CS- only in session 4 (P = 2430.004; days 7 and 8) but not in the first 3 sessions, were a trend to consume more CS+Suc was 244observed in sessions 2 (P = 0.078) and 3 (P = 0.109) and no differences between solutions intake 245were observed during the first session (P = 0.228). The flavour used also had an effect on 246consumption (P < 0.001) irrespective of whether the solutions included sucrose [F(1, 15) = 28.39, P 247< 0.001]. Pigs drank more when garlic was added into solutions (292 vs. 210 g; SEM 15.36 g) The 248differences between flavour consumption also increased with time, reflected in a significant 249interaction between flavour and session day [F(3, 15) = 20.75, P < 0.001].

250

2513.1.2 Flavour preference, acceptability and palatability

The preference, acceptability and palatability for CS+ and CS- solutions after training are 253summarized in **Figure 3.** According to the preference test, pigs preferred the CS+ over the CS– 254[F(1, 15) = 8.60, P = 0.010] (**Figure 3a**). Moreover, when pigs were offered only one CS option 255(CS+ or CS- on different days), they consume more CS+ than CS- solutions [F(1, 14) = 6.69, P = 2560.022], (**Figure 3b**). Nevertheless, no differences were found between the CS+ and CS- CT/A [F(1, 25715) = 0.01, P = 0.913] (**Figure 3c**), at any of periods analysed (P > 0.05). Finally, the flavour tested 258(garlic or aniseed) had an effect on pigs acceptability [F(1, 14) = 6.58, P = 0.022] and preferences 259[F(1, 15) = 48.87, P < 0.001] observing a higher consumption of garlic over aniseed. Palatability 260was not affected by the flavour tested [F(1, 15) = 0.03, P = 0.856].

261

2623.2 Results Experiment 2: Social learning

263

2643.2.1 Flavour acceptability

The acceptability of garlic and aniseed flavoured feed by the DEM did not differ [137 vs. 166g, 266SEM 22.9g; F(1, 15) = 0.77, P = 0.394]. **Figure 4a** shows the acceptability of the garlic feed by the 267OBS on day 1, 2 and 3 according to the flavour consumed by their DEM. After the interaction with 268DEM pigs, the general consumption of garlic feed was higher in OBS pigs that had interacted with 269DEM who had consumed garlic [F(1, 13) = 5.12, P = 0.041]. Consumption did not show differences 270between days [F(2, 13) = 1.07, P = 0.371]. The interaction between the flavour consumed by the 271DEM and the day of the test did not have an effect on the consumption of garlic flavoured feed by 272the OBS [F(2, 13) = 0.13, P = 0.878].

273

2743.2.2 Flavour palatability

Palatability of observers for the garlic flavoured feed, expressed by CT/A is presented in **Figure** 2764b. No effect of the flavour consumed by demonstrators (garlic or aniseed) [F(1, 13) = 0.69, P =2770.421], day of the test [F(2, 13) = 2.13, P = 0.159] or the interaction of these factors [F(2, 13) = 2780.23, P = 0.796] were observed. The day of the test had an effect on CT/A in the first half of the test 279(0 – 5 min) [F(2, 13)=5.19, P = 0.022], increasing with time. However, no effect was observed 280during the second half of the test (6-10) [F(2, 13)=0.48, P = 0.629]. Finally, palatability was not 281affected by DEM flavour consumed or by the interaction between the day of the test and the flavour 282consumed by the DEM in any of the periods analysed (P > 0.05).

283

2843.2.3 Snout to snout interactions

The correlation between snout to snout interaction time between DEM and their respective OBS, 286and OBS' approaches, consumption time and CT/A for garlic feed during the sub-periods are shown 287in **Table 1.** This analysis was performed separately for the garlic and aniseed DEM groups. Most 288interestingly, when looking at the correlation between CT/A (palatability) and the DEM-OBS 289interaction, a positive but moderate correlation for observers that interacted with demonstrator that 290consumed garlic feed, over the first 5 min of the sessions (and a trend to the same effect over the 291whole 10 min analysis period), was observed. Critically, this relationship was entirely absent in 292observers interacting with demonstrators that consumed the aniseed flavour which was not used 293during the test sessions. Although not significant, results suggest that the correlation between DEM-294OBS interaction times and CT/A (consumption time/number of approaches) was driven by both a 295positive correlation with consumption time and a negative correlation with number of approaches 296(**Figure 5)**.

297

2984. Discussion

Pigs are able to acquire new flavour preferences by trial and error and social learning, allowing 300them to anticipate future oral and post-oral rewards. This was confirmed in Experiments 1 and 2, 301which also extended the analysis to the palatability of the learnt solutions. On the other hand, our 302results gives certain evidence for a change in palatability, finding little evidence of changes due to 303individual learning, but a suggestion of changes in palatability associated to social learning.

3054.1 Individual trial and error learning

306 As in previous experiments, in the present study nursery pigs preferred flavours previously 307conditioned with energy compounds such as sucrose (4%). Results suggest that both the palatable 308taste and post-ingestive effects of sucrose contributed to the conditioned CS+ preference and 309acceptability, reflecting how attractive the sucrose is to pigs (Glaser et al., 2000). Figueroa et al. 310(2012b) associated a flavoured solution with sucrose (4%) observing that sucrose post-ingestive 311effect by itself may condition flavour preferences, noting a higher intake than flavours conditioned 312 with the same sweetness but a minor energy level (1% sucrose + 0.08% saccharine). Similar results 313 have been observed in pigs when other concentrations of sucrose (10%) or carbohydrates as 314maltodextrin (2.25%) were used as a reinforcement (Clouard et al., 2012). This could indicate that 315post-ingestive effects might be sufficient to condition flavour preferences as several experiments 316showed in rats (Lucas et al., 1997; Ackroff and Sclafani, 2010). Figueroa et al., 2012a also reported 317protein-based flavour preference conditioning in pigs, where animals associated protein 318concentrates (> 60% CP) with artificial flavours during nursery. They showed a clear preference 319when those flavours were presented later in water solutions or commercial feed. Regarding 320acceptability of previously conditioned flavours, in the present study we observed that animals 321present a higher consumption of those flavours when only one option was offered. Despite the 322existence of evidence in rats (Pérez et al., 1998), previous experiments in pigs did not explore the 323effect of learning on flavour acceptability. This information could be useful to extrapolate to real 324 commercial conditions where only one feed option is provided. However, the possible learning 325 extinction and long-term effect of flavour consumption still needs to be explored.

Experiments in rats support that flavours conditioned by the post-ingestive effects of nutrients 327not only are better preferred and accepted, but also are perceived as more pleasant (Myers and 328Sclafani, 2001). Diverse measures correlated with the palatability of a solution or feed, such as 329licking pattern, appetitive facial expressions and consumption in a brief period of time observing an

330increase when flavours are previously associated with the benefits of sucrose or maltodextrins 331(Forestell and LoLordo, 2003; Dwyer, 2008). However, palatability in pigs to date has not been 332systematically studied. Clouard et al. (2014) observed changes in behavioural activities, 333motivational responses and microstructure of CS intake in nursery pigs after they had been 334conditioned with 16% sucrose. Added to this, a non-significant higher duration of drinking episodes 335and a smaller number of drinking episodes were observed. This information could be extrapolated 336to lick cluster size analysis in rats (Davis and Smith, 1992) or CT/A in pigs (Figueroa et al., 2019), 337suggesting the importance of oral perception of the unconditioned stimulus (US) during training for 338possible hedonic changes for the CS+ in pigs. However, no changes in palatability were observed in 339the present experiment after conditioning flavours with 4% sucrose. A possible explanation could 340be that rather than acquiring the hedonic tone of the US, the CS+ acquires the incentive value of the 341US (perhaps because of the low concentration of sucrose used). This can maintain an elevated 342 intake, reflected in preferences and acceptability even in the absence of enhanced palatability 343(Myers and Sclafani, 2001). However, there is also evidence from rats that conditioned changes in 344palatability are relatively short-lived (e.g. Dwyer et al., 2009). Thus, learned changes in flavour 345palatability may have extinguished before because the palatability tests followed preference tests 346delivered without sucrose.

347

3484.2 Social learning

349 The changes in pigs' feeding behaviour induced by social learning through brief interactions 350have been previously studied in terms of preferences (Figueroa et al., 2013, 2020b). The present 351study explored the effects of social learning on pigs' flavour acceptability and palatability, 352highlighting the importance of oro-nasal contact in the acquisition of new feeding patterns, which 353has been previously reported by Galef and Stein (1985) in rats. Results show that, similar to rats, the 354acceptability of a flavoured feed increases after a brief contact with a familiar demonstrator that 355previously consumed that feed. This phenomenon could involve learning, establishing the 356acquisition of new feeding behaviours in the population that could remain dependent on the 357immediate reinforcement generated by the consumption of that flavoured feed, other consumption 358alternatives and population dynamics (Galef and Laland, 2005). Social learning could be a key 359strategy in productive stages where pigs exhibit feed neophobia, such as at weaning (Pluske et al., 3602007). The interaction of the test day and flavour consumed by the DEM pigs did not show an 361effect on the acceptability of the flavoured food, therefore, no extinction of learning was observed, 362but rather, this was maintained (Galef and Whiskin, 1998).

Regarding palatability, although changes have been described after associative learning in 364several species (Dwyer, 2008, 2009), little information exists on changes in feed palatability after a 365brief social contact (Figueroa et al., 2020a). In the present experiment interesting results were 366obtained when analysing the first half of the test, similar to results observed by Figueroa et al. 367(2019). This suggests that the first 5 minutes of exposure to a feed is most sensitive in assessing 368hedonic reactions after associative learning. Palatability, contrary to acceptability, showed no 369overall changes when the DEM consumed the same flavour as presented to the OBS (garlic 370flavour), and it did change according to the test day, increasing over the days. The latter could be 371attributed to the fact that neophobia modulates palatability, due to both a habituation effect and the 372perception of feed as familiar and safe (Lin et al., 2012).

While there was no reliable change in overall palatability due to social learning, a correlation While there was no reliable change in overall palatability due to social learning, a correlation According to Galef (for a summary see Galef, 2012) an OBS rat acquires a new feeding According to Galef (for a summary see Galef, 2012) an OBS rat acquires a new feeding having a brief contact with an experienced DEM through its breath (Galef et al., 1988; Ar7Munger et al., 2010). Based on this, interaction between individuals, more specifically the time and Ar8number of oro-nasal interactions, is essential to generate changes in feed preferences in rats (Galef Ar9and Stein, 1985). Although the specific components of pigs' breath were not isolated in the present Br9and Stein, 1985). Although the oro-nasal contact time between DEM and OBS, it was found that it Br9and Steively correlated with the CT/A. Critically, this was only seen when the OBS animals were 382tested with the same flavour as consumed by the DEM animals (and thus the correlation cannot be 383due to animal temperament factors that would affect both snout to snout contact times and CT/A in 384the same way). This implies that the longer the oro-nasal contact time between OBS and DEM, the 385greater the subsequent palatability of the flavoured feed. This suggests that in pigs there would also 386be chemical compounds from their oro-nasal cavity that, in a given context (flavoured feed and 387presence of a conspecific), would be responsible for the changes in feeding behaviour described in 388this experiment. However, further studies are required to clarify the responsible mechanism of these 389changes in pigs' feeding behaviour.

390

3915. Conclusions

Learning based on individual experience or social exposure can change the feeding behaviour of 392 393pigs, presumably on the basis that previously novel flavours come to be associated with positive 394 events such as calories or social interaction. We conclude from our experiments that trial and error 395and social learning are important contributors to pigs' preferences and acceptability for flavours 396learnt. Nevertheless, only social learning modified the hedonic perception of flavours, with an 397 interesting correlation between snout to snout contact time between DEM and OBS and the 398 magnitude of OBS changes in their hedonic perception for those flavours. Therefore, the 399mechanisms that are involved in the oro-nasal-contact mediated social interaction in pigs, have to 400be further explored to better understand the changes of feeding behaviour observed in this study. 401Regardless of the exact mechanism of learning, it is clear that associative learning (based on either 402 individual or social experiences) can lead in increases in the consumption of, and preference for, 403 food flavours. Thus interventions based on associative learning about food flavours could be 404beneficial to implement on pig farms to help increase food consumption. This would be especially 405true around periods of change in the production stages (in particular weaning) because these are 406particularly stressful and associated with reductions in feed intake and welfare.

4086. Funding: The present study was financially supported by FONDECYT grant 11140576 headed409 by Jaime Figueroa.

410

4117. Declarations of interest: None.

412

4138. Acknowledgments: The authors are grateful for FONDECYT postdoctorado N° 3190048414supported by Agencia Nacional de Investigación y Desarrollo (ANID).

415

416References

417 Ackroff, K., Sclafani, A., 2010. Flavor preferences conditioned by post-oral infusion of
418monosodium glutamate in rats. Physiol. Behav. 104, 488-494.
419https://doi.org/10.1016/j.physbeh.2011.05.013.

Boughter, J.D., John, S.J., Noel, D.T., Ndubuizu, O., Smith, D.V., 2002. A Brief-access Test for
421Bitter Taste in Mice. Chem. Senses. 27, 133-142. https://doi.org/10.1093/chemse/27.2.133.

422 Clouard, C., Chataignier, M., Meunier-salaün, M.C., Val-Laillet, D., 2012. Flavour preference
423acquired via a beverage-induced conditioning and its transposition to solid food: Sucrose but not
424maltodextrin or saccharin induced significant flavour preferences in pigs. Appl. Anim. Behav. Sci.
425136, 26-36. https://doi.org/10.1016/j.applanim.2011.11.007.

426 Clouard, C., Loison, F., Meunier-Salaün, M.C., Val-Laillet, D., 2014. An attempt to condition
427flavour preference induced by oral and/or postoral administration of 16% sucrose in pigs. Physiol.
428Behav. 124, 107-115. https://doi.org/10.1016/j.physbeh.2013.10.025.

429 Davis, J. D., Smith, G. P., 1992. Analysis of the microstructure of the rhythmic tongue
430movements of rats ingesting maltose and sucrose solutions. Behav. Neurosci. 106, 217-228. https://
431doi.org/10.1037/0735-7044.106.1.217.

432 Dwyer, D.M., 2008. Microstructural analysis of conditioned and unconditioned responses to433maltodextrin. Learn. Behav. 36, 149-158. https://doi:10.3758/LB.36.2.149.

434 Dwyer, D.M., 2009. Microstructural analysis of ingestive behaviour reveals no contribution of 435palatability to the incomplete extinction of a conditioned taste aversion. Q. J. Expo. Psychol. 62, 9-43617. https://doi.org/10.1080/17470210802215152.

437 Dwyer, D.M., Pincham, H.L., Thein, T., Harris, J.A., 2009. A learned flavor preference persists
438despite the extinction of conditioned hedonic reactions to the cue flavors. Learn. Behav. 37, 305439310. https://doi:10.3758/LB.37.4.305.

Figueroa, J., Frías, D., Solà-Oriol, D., Tadich, T., Franco-Rosselló, R., Nuñez, V., Dwyer, D.M.,
Palatability in pigs, the pleasure of consumption. J. Anim. Sci. 97, 2165-2174. https://doi.org/
44210.1093/jas/skz085.

Figueroa, J., Gasalla, P., Müller, M., Dwyer, D. 2020a. Socially conditioned flavor preferences
444with fluids: Transfer with solid foods, palatability, and testing constraints, Physiol. Behav.
445https://doi.org/10.1016/j.physbeh.2020.112976

Figueroa, J., Müller, M., Guzmán-Pino, S.A., Franco-Rosselló, R., Solà-Oriol, D., Borda, E.,
447Dwyer, D.M., Pérez, J.F., 2020b. Acquisition of flavor preferences in pigs through interactions with
448conspecifics that had previously consumed flavored protein solutions. Animal. 1-5.
449https://doi.org/10.1017/S1751731120000257.

450 Figueroa, J., Solà-Oriol, D., Borda, E., Sclafani, A., Pérez, J. F., 2012a. Flavour preferences
451conditioned by protein solutions in post-weaning pigs. Physiol. Behav. 107, 309-316.
452https://doi.org/10.1016/j.physbeh.2012.08.008.

453 Figueroa, J., Solà-Oriol, D., Guzmán-Pino, S., Borda, E., Pérez, J. F., 2012b. Flavor preferences
454conditioned by post-ingestive effect of sucrose and porcine digestive peptides in post-weaning pigs.
455J. Anim. Sci. 90, 381-383. https://doi.org/10.2527/jas.51308.

456 Figueroa, J., Solà-Oriol, D., Manteca, X., Pérez, J.F., 2013. Social learning of feeding behaviour
457in pigs: Effects of neophobia and familiarity with the demonstrator conspecific. Appl. Anim. Behav.
458Sci. 148, 120-127. https://doi:10.1016/j.applanim.2013.06.002

459 Forbes, J. M., 2010. Palatability: principles, methodology and practice for farm animals. CAB
460Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources. 5, 1-15.
461https:// doi: 10.1079/PAVSNNR20105052.

462 Forestell, C.A., LoLordo, V-M., 2003. Palatability shifts in taste and flavour preference 463conditioning. Q. J. Exp. Psychol-B. 56, 140-160. https://doi:10.1080/02724990244000232.

464 Galef, B.G., 2012. Social learning and traditions in animals: evidence, definitions, and 465relationship to human culture. Cogn. Sci. 3, 581-592. https:// doi: 10.1002/wcs.1196.

Galef, B.G., Laland, K.N., 2005. Social learning in animals: Empirical studies and theoretical
467models. Bioscience. 55, 489-499. https://doi.org/10.1641/0006-

4683568(2005)055[0489:SLIAES]2.0.CO;2.

Galef, B.G., Mason, J. R., Preti, G., Bean, N.J., 1988. Carbon disulfide: A semiochemical470mediating socially-induced diet choice in rats. Physiol. Behav. 42, 119-124.

471https://doi.org/10.1016/0031-9384(88)90285-5.

Galef, B.G., Stein, M., 1985. Demonstrator influence on observer diet preference: Analyses of
473critical social interactions and olfactory signals. Anim. Learn. Behav. 13, 31-38.
474https://doi.org/10.3758/BF03213362.

Galef, B.G., Whiskin, E.E., 1998. Determinants of the longevity of socially learned food
476preferences of Norway rats. Anim. Behav. 55, 967-975. https://doi.org/10.1006/anbe.1997.0672.

Galef, B.G., Whiskin, E.E., 2008. Effectiveness of familiar kin and unfamiliar nonkin
478demonstrator rats in altering food choices of their observers. Anim. Behav. 76, 1381-1388.
479https://doi.org/10.1016/j.anbehav.2008.07.004.

480 Glaser, D., Wanner, M., Tinti, J.M., Nofre, C., 2000. Gustatory responses of pigs to various 481natural and artificial compounds known to be sweet in man. Food Chem. 68, 375-385. 482https://doi.org/10.1016/S0308-8146(99)00212-5. 483 Grill, H.J., Norgren, R., 1978. The taste reactivity test. II. Mimetic responses to gustatory stimuli
484in chronic thalamic and chronic decerebrated rats. Brain Res. 143, 281-297.
485https://doi.org/10.1016/0006-8993(78)90569-3.

Held, S., Mendl, M., Devereux, C., Byrne, R.W., 2000. Social tactics of pigs in a competitive
487foraging task: the 'informed forager' paradigm. Anim. Behav. 59, 569-576. https://doi.org/10.1006/
488anbe.1999.1322.

489 Laland, K.N., 2004. Social learning strategies. Anim. Learn. Behav. 32, 4-14.490https://doi.org/10.3758/BF03196002.

491 Lin, J.Y., Amodeo, L.R., Arthurs, J., Reilly, S., 2012. Taste neophobia and palatability: The 492pleasure of drinking. Physiol. Behav. 106, 515-519. https://doi:10.1016/j.physbeh.2012.03.029.

493 Lucas, F., Azzara, A.V., Sclafani, A., 1997. Flavor preferences conditioned by intragastric 494polycose in rats: more concentrated polycose is not always more reinforcing. Physiol. Behav. 63(1), 4957-14. https://doi.org/10.1016/S0031-9384(97)00364-8.

Main, R.G., Dritz, S.S., Tokach, M.D., Goodband, R.D., Nelssen, J.L., 2004. Increasing weaning
497age improves pig performance in a multisite production system. J. Anim. Sci. 82, 1499-1507.
498https://doi:10.2527/2004.8251499x.

Munger, S.D., Leinders-Zufall, T., McDougall, L.M., Cockerham, R.E., Schmid, A.,
S00Wandernoth, P., Wennemuth, G., Biel, M., Zufall, F., Kelliher, K. R., 2010. An Olfactory
S01Subsystem that Detects Carbon Disulfide and Mediates Food-Related Social Learning. Curr. Biol.
S0220, 1438-1444. https://doi:10.1016/j.cub.2010.06.021.

503 Myers, K.P., Sclafani, A., 2001. Conditioned enhancement of flavor evaluation reinforced by504intragastric glucose: II. Taste reactivity analysis. Physiol. Behav. 74, 495-505.

505https://doi.org/10.1016/S0031-9384(01)00596-0.

506 National Research Council (NRC.)., 2012. Nutrient requirements of swine. National Academy 507Press: Washington (DC), USA.

Nicol, C.J., 1995. The social transmission of information and behaviour. Appl. Anim. Behav.
509Sci. 44, 79-98. https://doi.org/10.1016/0168-1591(95)00607-T.

510 Oostindjer, M., Kemp, B., van den Brand, H., Bolhuis, J. E., 2014. Facilitating 'learning from
511mom how to eat like a pig' to improve welfare of piglets around weaning. Appl. Anim. Behav.
512Sci. 160, 19-30. https://doi.org/10.1016/j.applanim.2014.09.006.

513 Pérez, C., Lucas, F., Sclafani, A., 1998. Increased flavor acceptance and preference 514conditioned by the postingestive actions of glucose. Physiol. Behav. 64, 483-492. 515https://doi.org/10.1016/S0031-9384(98)00104-8.

Pluske, J.R., Kim, J.C., Hansen, C.F., Mullan, B.P., Payne, H.G., Hampson, D.J., Callesen, J.,
517Wilson, R.H., 2007. Piglet growth before and after weaning in relation to a qualitative estimate of
518solid (creep) feed intake during lactation: a pilot study. Arch. Anim. Nutr. 61, 469-480. https://doi:
51910.1080/17450390701664249.

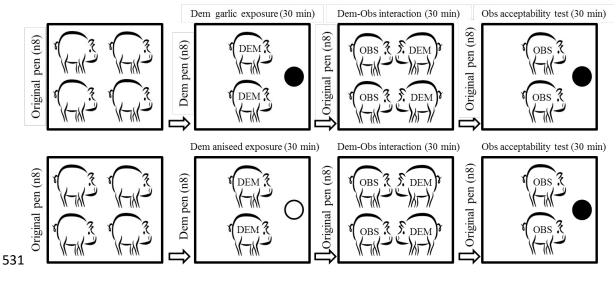
Sclafani, A., 2004. Oral and postoral determinants of food reward. Physiol. Behav. 81, 773521779. https://doi.org/10.1016/j.physbeh.2004.04.031.

523**Table 1.** Spearman's correlation between snout to snout interaction time of demonstrators (DEM) 524pigs that previously consumed garlic or aniseed flavoured feed with their respective observers and 525consumption time (CT), the number of approaches (A), and CT/A of those observers against garlic 526flavoured feed analysed during the complete period of the observer test (0-10 min), the first half (0-5275 min) and the last half (6-10 min).

528

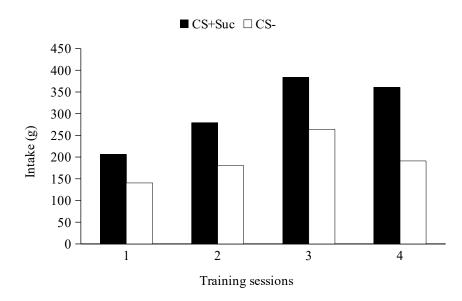
	Garlic DEM		Aniseed DEM	
	r	р	r	р
Consumption time (CT, s)				
0-5 min period	0.388	0.211	0.151	0.638
6-10 min period	0.302	0.334	-0.129	0.688
0-10 min period	0.410	0.185	0.000	1.000
Number of approaches (A)				
0-5 min period	-0.475	0.118	0.390	0.210
6-10 min period	-0.227	0.477	0.529	0.076
0-10 min period	-0.518	0.084	0.422	0.172
CT/A				
0-5 min period	0.626	0.029	0.000	1.000
6-10 min period	0.388	0.211	-0.259	0.416
0-10 min period	0.497	0.100	-0.194	0.545

529



532

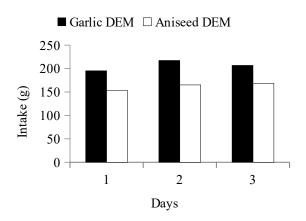
Figure 1. Experiment 2: Layout of the social learning procedures between observers (OBS) and 534demonstrators (DEM) pigs. Closed circles represent the garlic flavoured feed given to half of 535demonstrators (8 pig pairs) and the open circles the aniseed flavoured feed given to the other half of 536demonstrators (8 pig pairs). Observer animals were tested with an acceptability test where they 537were offered garlic flavoured feed.



540Figure 2. Experiment 1: Mean solution intake (+ SEM) of nursery pigs' pairs after 30 min. during 541training session for flavoured solutions (garlic or aniseed; 0.075%) with the inclusion of 4% of 542sucrose (CS+Suc) or without sucrose inclusion (CS–). No feed or other fluids were available during 543training sessions. †P < 0.1; *P < 0.05.

545	
546	
547	
548	
549	
550	
551	

553Figure 3. Experiment 1: Mean intake of CS+ and CS- solutions (+ SEM) during 30 min. non-554reinforced two-choice test (a), during 30 min. non-reinforced one-pan acceptability test (b), and 555palatability estimated during the first 10 minutes (c) [consumption time (CT)/number of approaches 556(A)]. No feed or other fluids were available during the tests. *P < 0.05.



563Figure 4. Mean consumption for garlic flavoured feed by observer nursery pigs that previously
564interacted during 30 min. with demonstrators (DEM) that consumed garlic (Garlic DEM) or aniseed
565(Aniseed DEM) flavoured feed (a) and palatability estimated during the first 10 minutes (c)
566[consumption time (CT)/number of approaches (A)]. Results are expressed by the day of the test.
567Flags: + SEM.

r = -0.518 p = 0.084

571Figure 5. Experiment 2: Scattergrams of the number of approaches (a), consumption time (b) and 572consumption time per approach (c) of observers with garlic flavoured feed after interaction with 573demonstrators that previously consumed garlic flavoured feed, against snout to snout interaction 574times.