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 ORCID: <https://orcid.org/0000-0001-8069-5508> 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 file

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

9^cDepartamento 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: figueroa.jaime@uc.cl

16

17

1¹ Animal Behaviour & Welfare, Animal and Veterinary Sciences Research Group, Scotland's Rural

2College (SRUC), West Mains Rd., Edinburgh, EH9 3JG, United Kingdom

3² 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
27previously 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
33with 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).

62 Under commercial conditions, pigs are faced by nutritional challenges that may affect their
63subsequent 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 (Figuroa 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, Figuroa et al. (2020a) did not find hedonic changes in rats' flavour
83perception after interacting with a conspecific that recently consumed a flavoured solution.

84 The aim of this study was to investigate possible changes in pigs' responses (in terms of
85preference, acceptability and palatability) for flavours previously learnt during a training period by
86individual trial and error experiences (Experiment 1) and socially by a brief interaction (30 min)
87with 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
91facilities. The experimental procedures were approved by the Ethical Committee on Animal
92Experimentation of the Facultad de Ciencias Veterinarias y Pecuarias at the Universidad de Chile,
93certificate N° 252014.

94

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

972.1.1 Animals and housing

98 A total of 32 castrated male and female nursery pigs were used (PIC® genetics, Hendersonville,
 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
 108temperature ($27.3 \pm 2.70^\circ$ 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

116 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.

130 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

Outdoor Cameras 700tvl 1/3 cmos Sony, SENKO SA, Santiago, Chile) placed in a central position on the ceiling of each pen. The CT/A was estimated based on study of Figueroa et al. (2019) as the total time in which the animal drinking at the pan (i.e. consumption time) divided by the number of times the pan was approached with a consumption result (i.e. number of approaches). For each pen, one video camera was used. Additionally, analyses of the first (0 to 5 min) and the final (6 to 10 min) half of the period were performed to examine whether these sub-periods of the session would be more sensitive than the session as a whole in estimating palatability.

155

1562.1.3. Statistical analysis

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

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**

183 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.

189 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

estimate CT/A (Figueroa et al., 2019). This was used as a possible indicator of changes in the hedonic perception for the flavoured food. Additionally, analyses of the initial (0 to 5 min) and the final (6 to 10 min) half of the period were performed to examine whether these sub-periods of the session would be more sensitive than the session as a whole to estimate palatability. Moreover, the time spent on oro-nasal contact between DEM and their respective OBS during the interaction period was measured to study possible correlations between interaction time and the magnitude of the expected effect on OBS feeding behaviour, reflected in animals' CT/A, consumption time and number of approaches during the complete period of the test (0-10 min), the initial (0 to 5 min) and the final (6 to 10 min) half of the test. In order to assess the time of oro-nasal contact more accurately between DEM and OBS, the video-cameras were installed on ceiling of each pen to capture from an upper view the physical contact between animals. The oro-nasal contact was defined when an observer pig touched the end of the snout of the demonstrator pig with the end of its own snout and vice versa.

213

214 2.2.3. Statistical analysis

Consumption data of each DEM and OBS pairs and the palatability measures of OBS pairs were analysed by mixed linear models with the MIXED procedure of the statistical package SAS 9.4 (SAS Inst. Inc., Cary, NC), taking into account in the case of DEM consumption the flavoured feed consumed (garlic or aniseed feed), and in the case of OBS consumption the flavoured feed consumed by their respective DEM (garlic or aniseed feed), the test day (1, 2 or 3) and the interaction between those factors. Finally to estimate OBS palatability, CT/A were analysed for the total period (0 to 10 min) and in sub-periods (0 to 5 min and 6 to 10 min), taking into account as the main factors the flavoured feed consumed by their respective DEM (garlic or aniseed feed), the test day (1, 2 or 3) and the interaction between those factors. Moreover, Spearman correlations were calculated between the oro-nasal interaction time of DEM and their respective OBS, and the CT/A and their components (consumption time and number of approaches to the pan) of those OBS

during the complete period of the test and sub-periods. Before ANOVA analysis, normality and homoscedasticity of dataset were analysed by using the UNIVARIATE procedure with the Shapiro Wilk and O'Brien's test, respectively. As no significant p-values were obtained for any of the specific factors, the original hypothesis for normality and homogeneity of variance were accepted ($P > 0.10$). Results are presented as LSMeans $\pm$ SEM, considering a significance level of 5% adjusted by Tukey. A trend in the data was defined as $0.05 \leq P \leq 0.1$.

3. Results

3.1 Results Experiment 1: Trial and error learning

3.1.1 Training sessions

Animals increased their solution intake as the days increased [$F(3, 15) = 21.29, P < 0.001$]. Overall intake was higher for CS+Suc than CS- solutions [$F(1, 15) = 16.44, P = 0.001$]. Intakes of CS+Suc and CS- during the training sessions are shown in **Figure 2**. There was an interaction between testing days and solutions [Day $\times$ CS, $F(3, 15) = 8.24, P = 0.002$], where the intake of CS+Suc increased over training sessions exceeding the consumption of CS- only in session 4 ($P = 0.004$; days 7 and 8) but not in the first 3 sessions, where a trend to consume more CS+Suc was observed in sessions 2 ($P = 0.078$) and 3 ($P = 0.109$) and no differences between solutions intake were observed during the first session ($P = 0.228$). The flavour used also had an effect on consumption ($P < 0.001$) irrespective of whether the solutions included sucrose [$F(1, 15) = 28.39, P < 0.001$]. Pigs drank more when garlic was added into solutions (292 vs. 210 g; SEM 15.36 g). The differences between flavour consumption also increased with time, reflected in a significant interaction between flavour and session day [$F(3, 15) = 20.75, P < 0.001$].

3.1.2 Flavour preference, acceptability and palatability

252 The preference, acceptability and palatability for CS+ and CS- solutions after training are
253 summarized 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 [$F(1, 14) = 6.69, P =$
256 0.022], (**Figure 3b**). Nevertheless, no differences were found between the CS+ and CS- CT/A [$F(1,$
257 $15) = 0.01, P = 0.913$] (**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
260 was not affected by the flavour tested [$F(1, 15) = 0.03, P = 0.856$].

261

262 3.2 Results Experiment 2: Social learning

263

264 3.2.1 Flavour acceptability

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

273

274 3.2.2 Flavour palatability

275 Palatability of observers for the garlic flavoured feed, expressed by CT/A is presented in **Figure**
276 **4b**. No effect of the flavour consumed by demonstrators (garlic or aniseed) [$F(1, 13) = 0.69, P =$
277 0.421], 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

285 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

299 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.

304

305 **4.1 Individual trial and error learning**

306 As in previous experiments, in the present study nursery pigs preferred flavours previously
307 conditioned with energy compounds such as sucrose (4%). Results suggest that both the palatable
308 taste and post-ingestive effects of sucrose contributed to the conditioned CS+ preference and
309 acceptability, 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
311 effect 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
314 maltodextrin (2.25%) were used as a reinforcement (Clouard et al., 2012). This could indicate that
315 post-ingestive effects might be sufficient to condition flavour preferences as several experiments
316 showed in rats (Lucas et al., 1997; Ackroff and Sclafani, 2010). Figueroa et al., 2012a also reported
317 protein-based flavour preference conditioning in pigs, where animals associated protein
318 concentrates (> 60% CP) with artificial flavours during nursery. They showed a clear preference
319 when those flavours were presented later in water solutions or commercial feed. Regarding
320 acceptability of previously conditioned flavours, in the present study we observed that animals
321 present a higher consumption of those flavours when only one option was offered. Despite the
322 existence of evidence in rats (Pérez et al., 1998), previous experiments in pigs did not explore the
323 effect 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.

326 Experiments in rats support that flavours conditioned by the post-ingestive effects of nutrients
327 not only are better preferred and accepted, but also are perceived as more pleasant (Myers and
328 Sclafani, 2001). Diverse measures correlated with the palatability of a solution or feed, such as
329 licking 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
342intake, 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

356 acquisition of new feeding behaviours in the population that could remain dependent on the
357 immediate reinforcement generated by the consumption of that flavoured feed, other consumption
358 alternatives and population dynamics (Galef and Laland, 2005). Social learning could be a key
359 strategy in productive stages where pigs exhibit feed neophobia, such as at weaning (Pluske et al.,
360 2007). The interaction of the test day and flavour consumed by the DEM pigs did not show an
361 effect on the acceptability of the flavoured food, therefore, no extinction of learning was observed,
362 but rather, this was maintained (Galef and Whiskin, 1998).

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

373 While there was no reliable change in overall palatability due to social learning, a correlation
374 between palatability and the amount of snout to snout contact between OBS and DEM animals was
375 observed. According to Galef (for a summary see Galef, 2012) an OBS rat acquires a new feeding
376 behaviour by having a brief contact with an experienced DEM through its breath (Galef et al., 1988;
377 Munger et al., 2010). Based on this, interaction between individuals, more specifically the time and
378 number of oro-nasal interactions, is essential to generate changes in feed preferences in rats (Galef
379 and Stein, 1985). Although the specific components of pigs' breath were not isolated in the present
380 experiment, when studying the oro-nasal contact time between DEM and OBS, it was found that it
381 was positively 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

392 Learning based on individual experience or social exposure can change the feeding behaviour of
393pigs, presumably on the basis that previously novel flavours come to be associated with positive
394events 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
397interesting correlation between snout to snout contact time between DEM and OBS and the
398magnitude 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
402individual or social experiences) can lead in increases in the consumption of, and preference for,
403food 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.

407

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

410

4117. **Declarations of interest:** None.

412

4138. **Acknowledgments:** The authors are grateful for FONDECYT postdoctorado N° 3190048
414 supported by Agencia Nacional de Investigación y Desarrollo (ANID).

415

416References

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

420 Boughter, J.D., John, S.J., Noel, D.T., Ndubizu, O., Smith, D.V., 2002. A Brief-access Test for
421 Bitter 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
423 acquired via a beverage-induced conditioning and its transposition to solid food: Sucrose but not
424 maltodextrin or saccharin induced significant flavour preferences in pigs. *Appl. Anim. Behav. Sci.*
425 136, 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
427 flavour preference induced by oral and/or postoral administration of 16% sucrose in pigs. *Physiol.*
428 *Behav.* 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
430 movements of rats ingesting maltose and sucrose solutions. *Behav. Neurosci.* 106, 217-228. <https://doi.org/10.1037/0735-7044.106.1.217>.

432 Dwyer, D.M., 2008. Microstructural analysis of conditioned and unconditioned responses to
433 maltodextrin. *Learn. Behav.* 36, 149-158. <https://doi.org/10.3758/LB.36.2.149>.

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

437 Dwyer, D.M., Pincham, H.L., Thein, T., Harris, J.A., 2009. A learned flavor preference persists
 438 despite the extinction of conditioned hedonic reactions to the cue flavors. *Learn. Behav.* 37, 305-
 439 310. <https://doi.org/10.3758/LB.37.4.305>.

440 Figueroa, J., Frías, D., Solà-Oriol, D., Tadich, T., Franco-Rosselló, R., Nuñez, V., Dwyer, D.M.,
 441 2019. Palatability in pigs, the pleasure of consumption. *J. Anim. Sci.* 97, 2165-2174. [https://doi.org/](https://doi.org/10.1093/jas/skz085)
 442 10.1093/jas/skz085.

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

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

450 Figueroa, J., Solà-Oriol, D., Borda, E., Sclafani, A., Pérez, J. F., 2012a. Flavour preferences
 451 conditioned by protein solutions in post-weaning pigs. *Physiol. Behav.* 107, 309-316.
 452 <https://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
 454 conditioned by post-ingestive effect of sucrose and porcine digestive peptides in post-weaning pigs.
 455 *J. 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
 457 in pigs: Effects of neophobia and familiarity with the demonstrator conspecific. *Appl. Anim. Behav.*
 458 *Sci.* 148, 120-127. <https://doi.org/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.
 461[https:// doi: 10.1079/PAVSNNR20105052](https://doi.org/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](https://doi.org/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](https://doi.org/10.1002/wcs.1196).

466 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-](https://doi.org/10.1641/0006-4683568(2005)055[0489:SLIAES]2.0.CO;2)
 4683568(2005)055[0489:SLIAES]2.0.CO;2.

469 Galef, B.G., Mason, J. R., Preti, G., Bean, N.J., 1988. Carbon disulfide: A semiochemical
 470mediating socially-induced diet choice in rats. Physiol. Behav. 42, 119-124.
 471[https://doi.org/10.1016/0031-9384\(88\)90285-5](https://doi.org/10.1016/0031-9384(88)90285-5).

472 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.
 474<https://doi.org/10.3758/BF03213362>.

475 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>.

477 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.
 479<https://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.
 482[https://doi.org/10.1016/S0308-8146\(99\)00212-5](https://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.
 485[https://doi.org/10.1016/0006-8993\(78\)90569-3](https://doi.org/10.1016/0006-8993(78)90569-3).

486 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/](https://doi.org/10.1006/anbe.1999.1322)
 488anbe.1999.1322.

489 Laland, K.N., 2004. Social learning strategies. *Anim. Learn. Behav.* 32, 4-14.
 490<https://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](https://doi.org/10.1016/S0031-9384(97)00364-8).

496 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.
 498<https://doi:10.2527/2004.8251499x>.

499 Munger, S.D., Leinders-Zufall, T., McDougall, L.M., Cockerham, R.E., Schmid, A.,
 500Wandernoth, P., Wennemuth, G., Biel, M., Zufall, F., Kelliher, K. R., 2010. An Olfactory
 501Subsystem that Detects Carbon Disulfide and Mediates Food-Related Social Learning. *Curr. Biol.*
 50220, 1438-1444. <https://doi:10.1016/j.cub.2010.06.021>.

503 Myers, K.P., Sclafani, A., 2001. Conditioned enhancement of flavor evaluation reinforced by
 504intragastric glucose: II. Taste reactivity analysis. *Physiol. Behav.* 74, 495-505.
 505[https://doi.org/10.1016/S0031-9384\(01\)00596-0](https://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.

508 Nicol, C.J., 1995. The social transmission of information and behaviour. *Appl. Anim. Behav.*
509 *Sci.* 44, 79-98. [https://doi.org/10.1016/0168-1591\(95\)00607-T](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
511 mom how to eat like a pig’ to improve welfare of piglets around weaning. *Appl. Anim. Behav.*
512 *Sci.* 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
514 conditioned by the postingestive actions of glucose. *Physiol. Behav.* 64, 483-492.
515 [https://doi.org/10.1016/S0031-9384\(98\)00104-8](https://doi.org/10.1016/S0031-9384(98)00104-8).

516 Pluske, J.R., Kim, J.C., Hansen, C.F., Mullan, B.P., Payne, H.G., Hampson, D.J., Callesen, J.,
517 Wilson, R.H., 2007. Piglet growth before and after weaning in relation to a qualitative estimate of
518 solid (creep) feed intake during lactation: a pilot study. *Arch. Anim. Nutr.* 61, 469-480. [https://doi:](https://doi.org/10.1080/17450390701664249)
519 [10.1080/17450390701664249](https://doi.org/10.1080/17450390701664249).

520 Sclafani, A., 2004. Oral and postoral determinants of food reward. *Physiol. Behav.* 81, 773-
521 779. <https://doi.org/10.1016/j.physbeh.2004.04.031>.

522

Table 1. Spearman's correlation between snout to snout interaction time of demonstrators (DEM) pigs that previously consumed garlic or aniseed flavoured feed with their respective observers and consumption time (CT), the number of approaches (A), and CT/A of those observers against garlic flavoured feed analysed during the complete period of the observer test (0-10 min), the first half (0-5 min) and the last half (6-10 min).

	Garlic DEM		Aniseed DEM	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
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

532

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

538

539

540**Figure 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.

544

545

546

547

548

549

550

551

552

553**Figure 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.

557

558

559

560

561

562

563**Figure 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.

568

569

$r = -0.518$
 $p = 0.084$

571**Figure 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.

575