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Habituation as an underlying mechanism for Sensory Specific Satiety: An assessment using flavor consumption and preference in rats

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ABSTRACT

Sensory specific satiety refers to a decline in the hedonic value of the sensory properties of a particular food as it is consumed. This phenomenon is characterized by a decrement in responding as a consequence of repeated exposure, is stimulus specific, and recovers after time. All these characteristics are shared with the habituation phenomenon and for this reason, habituation has been proposed as the underlying mechanism that explains this eating regulatory system. However, several studies conducted with human models have yielded mixed results. Using rats as experimental subjects, the present study tested the following three characteristics of habituation within a Sensory Specific Satiety (SSS) framework: spontaneous recovery, dishabituation and the distractor effect. Experiment 1 demonstrated the basic effect of SSS and its spontaneous recovery over time. In Experiment 2 we found that the presentation of a dishabituator after a pre-feeding procedure had no impact on the SSS effect. Finally, in Experiment 3 the presence of a distractor during a pre-feeding procedure did not alter the expression of SSS. These results challenge the idea that SSS constitutes a typical case of habituation, at least with the procedure used here.

1. Introduction

Sensory Specific Satiety (SSS) is the phenomenon that promotes the specific hedonic devaluation of the sensory properties of food by the time it is eaten, and which recovers after time (Rolls, Rolls, Rowe, & Sweeney, 1981). Although this phenomenon is specific to the consumed food, it can also generalize to other foods that share similar sensory properties to the devalued food (Rolls, Van Duijvenvoorde, & Rolls, 1984; Griffioen-Roose, Finlayson, Mars, Blundell, & de Graaf, 2010; Gonzalez, Recio, Sanchez, Gil & de Brugada, 2018).

SSS is a robust phenomenon and has been demonstrated in various animal species including rodents (e.g., González, Recio, Sánchez, Gil, & de Brugada, 2018), primates (e.g., Rolls, Murzi, Yaxley, Thorpe, & Simpson, 1986) and humans (e.g., Havermans, 2012). Most animal species need to eat a varied diet to obtain all the required nutrients (Ahn & Phillips, 2012), and SSS has thus been proposed as an adaptive mechanism that ensures the consumption of a varied diet in order to obtain such necessary nutrients. Therefore, animals do not only eat those foods that are more palatable or accessible in their natural environment (Reichelt, Morris, & Westbrook, 2014; Rolls, Rolls, et al., 1981). Furthermore, this feeding-adaptive mechanism, which has been recognized as a relevant factor in the cessation of food intake (Hetherington, 1996), is characterized by its sensory nature; SSS has been shown to occur independently (or at least partly), of post-absorptive factors. In this regard, several studies have shown how SSS is achieved by changing different sensory-related food attributes such as the smell (Rolls & Rolls, 1997) taste (Brondel, Lauraine, Van Wymelbeke, & Schaal, 2009a) texture (Guinard & Brun, 1998) and the sight or shape of foods, such as, for example different kinds of pasta (Rolls, Rowe, & Rolls, 1982). Moreover, SSS emerges just 2 min after the end of a meal (Hetherington, Rolls, & Burley, 1989) which implies that the shift in pleasantness of the food appears before the meal has been absorbed. Furthermore, evidence has shown that SSS can occur even in conditions of sham feeding; participants chew the food but do not swallow it (Nolan & Hetherington, 2009). Other evidence that supports the sensory nature of this phenomenon can be found in experiments that used stimuli that are iso-caloric but vary in different sensory attributes (Reichelt et al., 2014; González et al., 2018) or non-caloric stimuli such as sweeteners (Rogers et al., 2020).

Given all the features that characterize this eating regulatory system, it is essential to comprehend its nature and the underlying mechanisms through which it functions. In this regard, the mechanism that has been

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most widely used to explain the SSS effect is the habituation phenomenon. When considering the properties of SSS such as the decline in hedonic responding as a consequence of repeated exposure to food, stimulus specificity, and spontaneous recovery over time, it seems plausible to think that SSS could be a case of short-term habituation. However, the studies carried out to date (mainly with human subjects) with the intention of examining the different characteristics of habituation with an SSS paradigm have yielded contradictory results. Therefore, the purpose of the present study is to provide further evidence on this issue by using a rat model to demonstrate the spontaneous recovery of SSS and to test whether this phenomenon is sensitive to the effect of presenting a dishabituator and a distractor.

1.1. Habituation as an underlying mechanism of SSS

The habituation of responding to a stimulus is a non-associative learning process in which the repeated presentation of a target stimulus will produce a specific reduction in the original responses to that stimulus, which spontaneously recovers after time (Rankin et al., 2009). Due to its specificity, habituation differs from other basic changes in behavior such as muscular fatigue or sensory adaptation. Similar to habituation, SSS produces a decrement in hedonic responding as a consequence of repeated exposure to a particular food, which can recover after time and is specific to the eaten stimuli. Hence, the fact that the hedonic devaluation occurs specifically to the eaten stimuli and not to others can also be taken to indicate that SSS differs from other basic forms of behavior such as those mentioned above. In this respect, it has been shown that SSS is expressed within the secondary taste cortex by a specific reduction in neuronal activity in response to pre-feeding, and this activity recovers when other non-pre-fed foods are eaten (Rolls, 2005). Moreover, both phenomena have been proposed as adaptive mechanisms of behavioral regulation. On the one hand, the habituation phenomenon has been proposed as a general adaptive mechanism for ignoring non relevant stimuli within the environment and thus, avoiding a depletion of attentional resources in order to focus on other important stimuli. On the other hand, and as mentioned previously, SSS has been proposed as an adaptive mechanism by which animals are able to obtain all the required dietary nutrients, ignoring those that are no longer necessary.

Therefore, within the definition of SSS we can also observe some of the main features of habituation. In fact, Epstein, Temple, Roemmich, and Bouton (2009) in their review of the literature on habituation and food intake claim that both phenomena are sometimes used interchangeably in the literature. One way to test this hypothesis is to determine if SSS shows the same behavioral characteristics as habituation. In this regard, Epstein et al. (2009) proposed several paradigms for studying habituation, including dishabituation, stimulus specificity, distraction, variety, long-term habituation and sensitization. Some human studies have adapted the standard SSS procedure to some of these paradigms in order to explore the similarities between the features of habituation and SSS. The general SSS procedure in humans consists of asking participants to initially provide a subjective rating of the target foods (usually with liking and wanting measures), after which they consume one of the foods until satiety (pre-feeding). Finally participants again complete the original scales (pre-fed vs non pre-fed foods). On some occasions, this procedure is accompanied by a final choice test session in which participants are offered the pre-fed and non-pre-fed items to assess their intake patterns after pre-feeding. In the following section we will describe the most relevant results from these studies.

1.1.1. Spontaneous recovery from the hedonic devaluation produced by the SSS and long term SSS

Some studies have found that human participants who had consumed a food to satiety still express SSS with subjective ratings after 2, 20, 40 and 60 min (Hetherington et al., 1989; Rolls, Hetherington, & Burley, 1988), with the highest devaluation effect being observed 2 min after consumption (Hetherington et al., 1989). Regarding intake measures, Hetherington et al. (1989) showed that 1 h after the pre-feeding session, human participants showed no differences between their intake of pre-fed and non-pre-fed foods, and therefore on this occasion the SSS effect had disappeared when using a consumption test. Another study carried out by Havermans, Roefs, Nederkoorn, and Jansen (2012) found no effect of SSS recovery when using pleasantness ratings after 20 min of consumption in a sample of obese and healthy-weight female participants. Finally, a study conducted by Weenen, Stafleu, and De Graaf (2005) demonstrated that SSS was still expressed after more than 24hr of pre-feeding depending on the type of food consumed on the test. Therefore, at least for humans, it is not clear which variables modulate the recovery of the hedonic decline of SSS over time (e.g., individual differences, amount of orosensory exposure, or food category).

1.1.2. Dishabituation in SSS

Dishabituation is the phenomenon whereby the introduction of a different and salient stimulus will restore the original responding to the habituated stimulus (Epstein et al., 2009). Applying this paradigm to SSS, the introduction of a different stimulus after having eaten a food will reestablish the initial hedonic value of the latter through dishabituation. Some human studies have applied this paradigm to SSS by presenting a dishabituator after having eaten a meal to satiety, of either the same sensory modality (Havermans, 2012; Havermans, Siep, & Jansen, 2010; Meillon, Thomas, Havermans, Pénicaud, & Brondel, 2013) or different (a computer game, Havermans, 2012), and have found no dishabituation effect. These results contrast with those of a study conducted by Romer et al. (2006; Experiment 2) in which the authors found that the decay in the olfactory hedonic value of an ingested meal (SSS effect) could be restored after eating a second course of a different food. Furthermore, in Experiment 3, Romer et al. (2006) showed that the typical SSS food devaluation could be reversed by presenting the same pre-fed food altered with seasoning. In a similar vein, Epstein, Rodefer, Wisniewski, and Caggiula (1992) found that repeated presentation of a juice for a number of trials caused a reduction not only in hedonic but also in salivation measures, and in both cases this reduction was reversed when a dishabituator was presented (Experiment 1: different juice; Experiment 2: chocolate).

1.1.3. Distraction in SSS

The distraction procedure consists of presenting a different, novel stimulus while the habituation process is occurring. It is important to emphasize the differences between a dishabituator and a distractor, since sometimes these have been acknowledged to be the same. In particular, the differences between the two paradigms rely on the mechanism of action; while the dishabituator is presented at the end of the habituation procedure, the distractor interrupts the habituation process or in this case, the devaluation of the food stimulus through SSS. Distractors, as a regulatory mechanism, could be present in many everyday situations such as watching TV or being part of a social meeting whilst eating. Through a distraction process we might expect that these types of situations will promote a higher total intake due to the fact that the SSS process is being interrupted, thus slowing down or preventing the decay of the hedonic value of the food. In fact, several studies have focused on how being distracted while eating can affect other general intake-satiety processes such as feelings of fullness, total intake, or hunger, showing how distractors can promote an increase in total intake (Oldham-Cooper, Hardman, Nicoll, Rogers, & Brunstrom, 2011).

Whilst the results of human studies have shown that the use of a distractor such as a computer game can prevent wanting responses towards a specific satiated food to decrease, such distractors do not affect the decline in the hedonic value of food (Brunstrom & Mitchell, Experiment 2, 2006). Hetherington, Foster, Newman, Anderson, and Norton (2006), however, found that distracting participants during the SSS process by allowing them to taste other different foods promoted not only higher total intake but also led to a slowdown of the usual hedonic decline of pre-fed foods in comparison with a group that did not receive the distractor. Another study conducted by Brondel, Lauraine, Van Wymelbeke, Romer, and Schaal (2009) assessed whether multiple or single alternations of foods within a meal could increase total intake in comparison with a meal with no repetitions. The results revealed that single repetitions of foods within a meal increased total consumption when compared with the other two conditions, presumably through the disruption of habituation. However, in this study the pleasantness ratings of foods did not reveal any group differences in the pattern of hedonic decline of these foods. Finally, another study carried out by Epstein et al. (1992) showed how playing a computer game while tasting a juice on different trials slowed down the decrement in the salivation response to that juice, although in this study the hedonic value of the food was not measured.

1.2. Goals of the study

Thus, there appears to be mixed evidence for the notion that habituation is the underlying mechanism of SSS, at least with the methodology and procedures employed in existing studies in the literature. It is possible that the procedures employed within some human research could be critical when studying the mechanisms involved in SSS. For instance, human research has frequently made use of subjective ratings in order to assess the hedonic value (liking) or motivation to consume a food (wanting). Some authors, however, have pointed out that these types of measures can damage the validity of the constructs that are being assessed (Koranyi, Brückner, Jäckel, Grigutsch, & Rothermund, 2020). In particular, ratings can be altered by participants' supervision through the complete session such as the influence of recall on previous rating trials or perceiving food pleasantness to be a stable quality that does not change over time. For example, it is possible that even our own language can be a source of confusion with regard to what is really being assessed, since the concepts of liking and wanting are frequently used interchangeably in daily life situations regardless of their real meaning (Grigutsch, Lewe, Rothermund, & Koranyi, 2019). To complicate matters even further, it has been argued that liking and wanting components are not always consciously perceived. Thus, modifying the hedonic value or the appetite for a particular food can alter the real perception of these foods when participants have to rate the foods by introspection (Berridge & Kringelbach, 2008). Furthermore, ecological validity issues can also affect the procedure since humans could feel uncomfortable when required to consume food in unfamiliar surroundings instead of their natural or usual feeding environment. Ultimately, with human studies it is not possible to control prior experiences - and thus familiarity - with the target foods. For these reasons, the present study made use of a rat model to determine whether three characteristics of habituation are also shared by the SSS phenomenon, that is, spontaneous recovery, dishabituation and distraction. We have chosen these three characteristics from all those outlined in the previous literature (see Epstein et al., 2009; Rankin et al., 2009) since human studies on these variables have generated mixed results. To test this hypothesis, flavored fluids were used as stimuli in all the studies and SSS was assessed by total consumption of these flavors on a choice test.

2. Experiment 1: spontaneous recovery

In this experiment we examined the temporal recovery of the hedonic value (spontaneous recovery of SSS effect) across time with a between-subject design. Animals were familiarized with two flavored solutions for two days, after which they were pre-fed with one of the two solutions to obtain the SSS effect. Each group of rats was then tested for SSS after a specific time interval (0, 2, 5, 8 or 24 h) and by presenting a two-bottle test that contained both the pre-fed and non-pre-fed solution. If spontaneous recovery occurs, we should expect a direct relationship between the length of the time interval and recovery. A recovery of the SSS effect would be found when, after a certain amount of time has elapsed from the pre-feeding phase, total consumption of the pre-fed and non-pre-fed solutions do not differ.

2.1. Methods

2.1.1. Subjects and apparatus

A total of 30 male non-naïve Wistar rats with an average weight of 512 g (range: 420 g −610 g) were used in the present experiment. The rats were between 14 and 16 weeks old. The animals had received previous experience with other solutions and different procedures to those used in the present experiment. The rats were supplied by the Animal Production Unit of the University of Granada. Animals were randomly assigned to one of five groups matched for body weight (0hr: 539 g, 2-hr: 540, 5hr: 496, 8hr: 486 g, 24hr: 500 g).

Animals were individually housed in translucent plastic cages (35 × 12 × 22 cm) with wood shavings as bedding. A 12-h light/dark cycle was maintained for the whole procedure, beginning the light cycle at 8:00 a.m. Solutions were prepared everyday with tap water, and given to animals in centrifuge tubes (50 ml capacity) with stainless steel, ball-bearing-tipped spouts. All solutions were placed in the middle of the front metal cover of the cages on all the sessions in order to avoid the emergence of position preferences during the two-bottle tests. Consumption was measured by weighing the tubes before and after each procedure. The flavored solutions were prepared by diluting 0.05% vanilla aroma (Manuel Riesgo, Madrid) with 0.3% saccharin (Labortecnic) or 1% domestic soya sauce reduced in sucrose (Pearl River Bridge). All the procedures described in this paper were approved by the Comité de Ética en Experimentación Animal 06/06/2019/099 (Ethics Committee in Animal Research) at the University of Granada and were classified as low severity according to European guidelines. Animals were monitored daily by those responsible for animal welfare in the research center.

2.1.2. Procedure

The water bottles were removed one day before the beginning of the experiment, and access to water or experimental solutions was restricted to two daily sessions (10:00 a.m.- 4:00 p.m.). On the first two days of the experimental procedure, the rats received 30 min ad libitum access to water in the morning and afternoon sessions. These sessions were carried out in order to habituate animals to the schedule of the sessions and the tubes used, as well as to record baseline water consumption. The animals then began the familiarization phase (days 3–4), which consisted of two daily 20-min sessions (morning/afternoon) in which rats had access to 10 ml of one solution. These sessions were carried out so that rats had two previous exposures to each solution before the pre-feeding treatment in order to avoid neophobia. The order of presentation of each solution across the 4 sessions of familiarization was also counterbalanced. On the morning of the 5th day, animals started the pre-feeding phase, which consisted of 20 min access to 15 ml of one solution. After this procedure, each group of animals was tested for SSS with the following timings: immediately after (n = 6), 2 h after (n = 6), 5hr after (n = 6), 8hr after (n = 6) or 24hr after (n = 6) presentation of the solution. The SSS test consisted of a 10-min choice test in which animals were given free access to the pre-fed and non-pre-fed solution. The order and position in which the solutions were given on the test was counterbalanced to avoid any position preference. All rats received adlib access to water for 30 min in the afternoon sessions to rehydrate (4:00 p.m.). The rats from the 8hr group received this water session following the SSS test (6:00 p.m.). On the morning of Day 6, rats in the 24hr group received the SSS choice test while the rest of the groups had access to water. On the afternoon of Day 6 all rats again received 30 min access to water (4:00 p.m.). On Day 7–8 the same pre-feeding and SSS test cycles were carried out for all the groups but animals were pre-fed with the alternative solution to the one given on Day 5 (See Table 1).

Table 1
Design of Experiment 1.

Group	Familiarization	Pre-feeding	Choice test	Time of testing
0′	A/B	A/B	A vs B	Immediate
2hr				2hr interval
5hr				5hr interval
8hr				8hr interval
24hr				24hr interval

Note: A and B refer to the two solutions (vanilla + sucrose and soya, counterbalanced). "/" refers to alternate days of the counterbalancing, "vs" refers to the choice test between the two solutions (Pre-fed/Non-Pre-fed).

2.2. *Data analysis*

General linear model null hypothesis testing analyses were carried out, adopting a rejection level of $p < 0.05$, using Greenhouse–Geisser corrections for mixed factorial analysis of variance when needed. Partial eta squared and Cohen's d tests were used to measure effect sizes. The same statistical criteria were used for subsequent experiments.

2.3. *Results and discussion*

During the familiarization phase, consumption of the vanilla-saccharin solution was lower than that of the soya sauce solution, due to neophobia. However, two days of familiarization with the solutions was sufficient to produce an attenuation of neophobia. A repeated-measures ANOVA was carried out to assess consumption of the groups during the pre-feeding phase with Day (Day1/Day 2) as the within-subject factor and Group (0hr, 2hr, 5hr, 8hr, 24hr) as the between-subject factor. The analysis revealed no significant differences between days, groups or an interaction between these factors $Fs < 1$ (Mean consumption of both days of pre-feeding; 0hr: 11.41 SE = 0.91; 2hr: M = 11.11 SE = 0.96, 5hr: M = 11.74 SE: 0.40, 8hr: 11.43 SE = 0.65, 24hr: M = 11.30 SE = 0.76*)*.

Fig. 1 shows the mean total consumption of the pre-fed and non-pre-fed solutions on the choice test across both days of testing. Inspection of this figure shows a clear SSS effect with the shorter time intervals, since subjects in these groups consumed less of the pre-fed solution than the non-pre-fed solution. This effect appears to be attenuated when animals are tested for SSS after a longer temporal interval. A repeated measures ANOVA conducted on these data with Pre-feeding as the within subject factor (Consumption of Pre-fed/Consumption of Non- Pre-fed solution) and Group as the between-subject factor revealed a main effect of Pre-feeding $F(1,25) = 5.54$, $p = 0.03$; $\eta_p^2 = 0.18$. Moreover, there was an interaction between Group and Pre-feeding $F(4,25) = 5.51$, $p = 0.003$; $\eta_p^2 = 0.47$, and a significant effect of Group, $F(4,25) = 4.95$, $p = 0.004$; $\eta_p^2 = 0.44$.

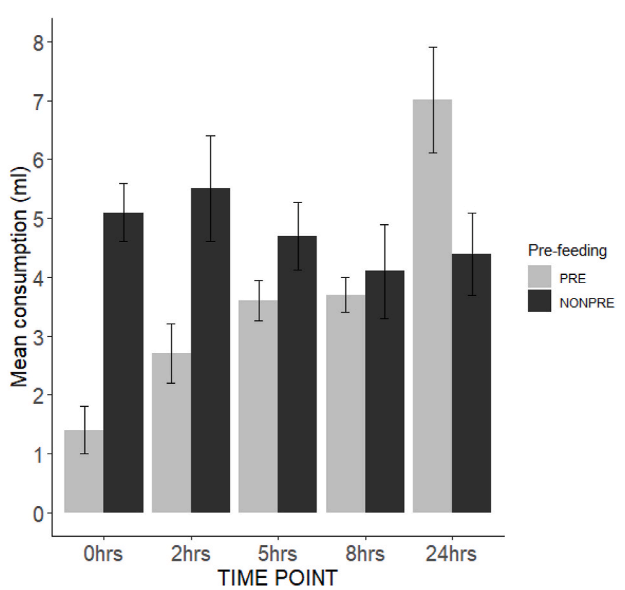

Fig. 1. The effect of SSS across the different experimental groups. "PRE": refers to the pre-fed solution whereas "NON-PRE" refers to the non-pre-fed solution.

As expected, the interaction between group and pre-feeding revealed that there were differences between the groups in the expression of the basic SSS effect. Thus, we conducted planned comparisons in order to observe the pattern of the SSS effect over time. A two tailed paired samples T-test was carried out on the consumption data for each group to compare direct consumption of the pre-fed solution with the non-pre-fed solutions between groups. Consumption of the solutions differed for the 0hr group $t(5) = -5.89$, $p = 0.002$; $d = -2.40$ and the 2hr group $t(5) = -2.57$, $p = 0.05$; $d = -1.05$. No SSS effect was found for the 5hr group $t(5) = -2.10$, $p = 0.09$; $d = -0.86$ the 8 h group $t(5) = -0.34$, $p = 0.75$, $d = -0.14$, or the 24hr group $t(5) = 1.65$ $p = 0.16$, $d = 0.67$ (See Fig. 1).

Therefore, and as expected, the present experiment provided evidence for an SSS effect immediately after the pre-feeding phase, since rats in the 0hr group showed significantly higher consumption of the non-pre-fed solutions than the pre-fed solutions. Moreover, rats tested within a 2-h time interval also showed a SSS effect, a finding that is consistent with other previous studies conducted with rats and using direct consumption tests (Reichelt et al., 2014; Parkes, Marchand, Ferreira, & Coutureau et al., 2016; González et al., 2018). In contrast, rats tested 5, 8 and 24 h after the pre-feeding session did not express a preference for the non-pre-fed solution, thus, the hedonic value of pre-fed solution was recovered. Interestingly, rats in the 24 h group showed a tendency to drink more of the pre-fed solution than the non-pre-fed solution. However, this effect was not significant and when this was tested again in our laboratory with a larger sample of experimental subjects (8 rats), this effect was not replicated.

3. Experiment 2: dishabituation

The aim of Experiment 2 was to assess the effects of presenting a dishabituator following the pre-feeding procedure. As in Experiment 1, following familiarization with two different solutions, rats were pre-fed with one of the solutions. After this, the Dishabituation Group was exposed to a bottle with a different solution (dishabituator) while the Control Group was presented with a bottle that contained water. Immediately after this, rats received a two-bottle test with the pre-fed and non-pre-fed solutions. If SSS is sensitive to the effect of dishabituation, rats presented with a different solution after the pre-feeding phase would be expected to show an absence or attenuation of the preference for the non-pre-fed solution over the pre-fed solution.

3.1. *Methods*

3.1.1. *Subjects and apparatus*

16 male non-naïve Long-Evans rats with a mean weight of 262.5 g (240 g –295 g) were used in this experiment. Rats were supplied by Janvier labs and were approximately 8–10 weeks old. Animals were randomly assigned to groups matched for body weight (Dishabituation group: 263.1 g; Control group: 262 g). All aspects of animal housing and the preparation and presentation of solutions were the same as Experiment 1. The flavored solutions were prepared by diluting 2% domestic vinegar with 10% domestic sucrose and 10% maltodextrin with 0.05% coffee aroma (Manuel Riesgo, Madrid). A solution of 0.9% domestic salt was used as the dishabituator for the Dishabituation group.

3.1.2. *Procedure*

The complete experimental procedure lasted for 6 days (See Fig. 1b). As in Experiment 1, animals were water deprived two days before the experimental procedure and water access was restricted to two 30-min sessions (10:00 a.m. and16:00 p.m.). In this experiment animals received 30 min of access to water during all the afternoon sessions in order to rehydrate. On Days 1–2 the animals were familiarized with the experimental sessions as in Experiment 1 and baseline water consumption was recorded. On Days 3–4 animals were familiarized with one of each solution in the morning sessions, with the order of presentation of each solution being counterbalanced. In this experiment, the animals were familiarized with each solution only once since they showed very little neophobia to the solutions. Each familiarization session lasted for 20 min and the animals were given 10 ml of each solution. The dishabituator was not familiarized in order to make this stimulus more salient and less familiar during the pre-feeding phase. On Days 5–6, the pre-feeding and test cycles took place; however, in this experiment, after the pre-feeding phase the animals in the Dishabituation group were given a salty solution (Dishabituator) and animals in the Control group were given plain water. The animals were given 20 min exposure to 12 ml of the solutions during pre-feeding and 5 min exposure to 4 ml of the salt or water. As in Experiment 1, the flavor of the solutions given during the pre-feeding phase was counterbalanced across both days. Immediately after the presentation of the dishabituator or the water solution, the rats were tested for SSS, as in Experiment 1 (See Table 2).

3.2. *Results and discussion*

During familiarization, all animals drank almost all of the fluid presented on both morning sessions. Consumption during the pre-feeding phase was analyzed to assess any possible group differences in taste preference or quantity of fluid ingested. The data of one rat from the Dishabituation group were excluded from the analysis due to consuming only 1 ml of the solution on the first day of pre-feeding. Furthermore, this rat was classified as an outlier in the choice test data by the JASP program. A repeated measures ANOVA was carried out with Day (Day1/Day2) as the within-subject factor and Group (Dishabituation or Control) as the between-subject factor. This analysis revealed no significant effect of Day, no effect of group, and no interaction between these factors, $F < 1$ (Mean consumption (ml) across both days of pre-feeding; Control: M = 8.26 SE = 0.34; Dishabituation: M = 7.67, SE = 0.75).

Fig. 2 displays the mean total consumption of the pre-fed and non-pre-fed solutions during the two choice tests for both groups. This figure shows that both groups seem to express the SSS effect, that is, the total consumption of the non-pre-fed solution was higher than that of the pre-fed solution. These data were analyzed using a repeated measures ANOVA to assess the effect of the dishabituator on the expression of SSS, with Pre-feeding (pre-fed or no-pre-fed) as the within-subject factor, and Group (Dishabituation or Control) as the between-subject variable. This analysis revealed a significant effect of Pre-feeding, $F(1,13) = 28.15$, $p < 0.001$; $\eta_p^2 = 0.68$, and no interaction $Fs < 1$ or effect of Group, $F(1, 13) = 1.51$, $p = 0.24$, $\eta_p^2 = 0.10$.

To analyze consumption of the salty solution (dishabituator) and water (control) a repeated measures ANOVA was carried out with Day (1–2) as the within-subject factor and Solution (Salt/Water) as the between-subject factor. The results revealed no significant effect of

Table 2
Design of Experiment 2.

Group	Familiarization	Pre-feeding→	Dishabituation→	Choice test
	Days 3–4		Days 5–6	
Control	A/B	A/B	Water	A vs B
Dishabituation			Y	

Note: A and B refer to the two solutions (Vinegar + sucrose and Coffee + Maltodextrin, counterbalanced). "Y" refers to the salt solution. "/" refers to alternate days of counterbalancing, "vs" refers to the choice test between the two solutions (Pre-fed/Non-Pre-fed). The arrow refers to different phases of a session.

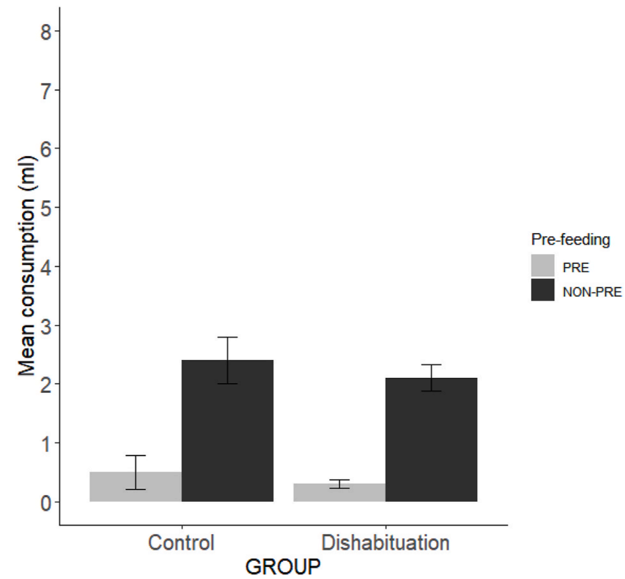

Fig. 2. The SSS effect in the different experimental groups. "PRE": refers to the pre-fed solution whereas "NON-PRE" refers to the non-pre-fed solution.

Solution $F(1,13) = 4.14$, p = 0.06 $\eta_p^2 = 0.24$, whilst no other effects or interactions reached significance $Fs < 1$. These data suggest a higher total intake of the salty solution in comparison with water (mean consumption in ml across both days; Salt: M = 1.94, SE = 0.36, Water: M = 1.01, SE = 0,28).

The present experiment investigated whether the presentation of a dishabituator following a pre-feeding procedure could restore the hedonic value diminished by the SSS effect when this is measured using a direct consumption test. The results of this experiment indicate that exposing rats to a dishabituator had no impact on the expression of SSS. Rats from both groups drank significantly less of the pre-fed solution than the non-pre-fed solution. If the dishabituator had disrupted the SSS effect, rats from the Dishabituator Group would have consumed more of the pre-fed solutions than those in the Control Group. However, in the present experiment, this effect was not demonstrated, at least when using a dishabituator of the same sensory modality as the pre-fed solution (liquid) and when using a direct consumption test to evaluate the hedonic value of this solution.

4. Experiment 3: distractor

In Experiment 3 we tested another property of habituation, that is, the effect of a distractor. Whilst the dishabituator is presented at the end of the habituation process, distractors act while the decrement in responding is occurring. To test this hypothesis, we used a within-subject design. The rats underwent different pre-feeding phases under two different conditions: distractor or control. The distractor condition involved the intermixed presentation of a different solution with the target solution, whilst in the control condition the subjects only received presentations of the target solution. After the pre-feeding phase, all rats received a two-bottle test containing the pre-fed and the non-pre-fed solution. If SSS is sensitive to the presentation of a distractor, we expect that the rats in the distractor condition will express a weaker (or absence of) SSS devaluation effect when consuming the pre-fed solution during the two-bottle test.

4.1. *Methods*

4.1.1. *Subjects and apparatus*

A total of 16 male naïve Wistar rats with a mean weight of 269 g (294g-230 g) were used in the present experiment. Rats were supplied by Janvier Labs and were approximately 8–10 weeks old. Animal housing was the same as described for Experiments 1 and 2. The flavored solutions were the same as those of Experiment 1 but in this experiment we also used a distractor solution composed of 1% squeezed lemon and 1% maltodextrin.

4.1.2. Procedure

The experimental procedure lasted for nine days (see Table 1). One day before the beginning of the experimental procedure, the rats were water deprived and access to water was restricted to two experimental sessions: 9:00 a.m. and 3:00 p.m. On the first and second day, the same procedure was carried out for assessing the baseline consumption and to familiarize the subjects with the experimental procedure. On the third day, all rats were familiarized with 10 ml of the distractor solution for 20 min in the morning session and received access to water for 30 min in the afternoon session. In this experiment we decided to provide the rats with an initial familiarization session with the lemon solution (distractor), given that the acidic properties of this flavor could elicit neophobia in the absence of previous exposure. Similarly, familiarization with the distractor was carried out on the first day of the procedure in order to maintain the salience or the novelty of the latter until the pre-feeding phase. On Days 4 and 5, all the rats were familiarized with the solutions in the morning and afternoon sessions, as in Experiment 1. From Day 6–9 the animals started the pre-feeding-choice test cycles in the morning and received 30 min access to water on all the afternoon sessions. During these four days, half of the animals received the Distractor treatment on the first two days (soya or saccharin counterbalanced) and the other half received this treatment on the last two sessions. In order to counterbalance the solution that they were given during pre-feeding (vanilla-saccharin/soya). The Distractor treatment lasted for 35 min. The animals were given full exposure to the target solutions for 20 min, whilst the distractor solution was presented for 15 min. The animals were presented with each of the stimuli for 5 min in an intermixed fashion (e.g., 5 min Soya/5 min distractor/5 min Soya … for 35 min). Animals in the Control condition received the target solution for 20 min without a distractor. During the pre-feeding phase, the animals were given 12 ml of the target solution and 6 ml of the distractor solution as appropriate. Given that the rats in the distractor condition will consume more than those in the control condition, both groups received the choice test 1 h after the end of the pre-feeding phase. The procedural details of the choice tests were the same as those described for the previous experiments (See Table 3).

4.2. Results and discussion

During familiarization with the distractor, the animals consumed almost all of the lemon-maltodextrin, soya and vanilla-saccharin solution. Animals showed neophobia to the vanilla-saccharin solution, but this effect disappeared on the last day of the familiarization phase. Two animals were excluded from the analysis due to the fact that they showed higher levels of neophobia to the saccharin solution during the entire familiarization procedure (consuming less than 2.5 of the 10 ml available on both days).

Table 3
Design of Experiment 3.

Familiarization	Pre-feeding/Distraction→	Choice test
Days 3–5	Days 6–9	
Y- A/B	A/B/A + Y/B + Y	A vs B

Note: A and B refer to the two solutions (vanilla + sucrose and soya, counterbalanced). "Y" refers to the lemon-maltodextrin solution. "/" refers to alternate days of counterbalancing, "-"refers to separate days. "vs" refers to the choice test between the two solutions (the Pre-fed and the non-Pre-fed). "+" denotes the presentation of two different solutions within the same session. The arrow refers to different phases of a session.

The data for consumption of the target solutions during the pre-feeding phase were analyzed with a repeated measures ANOVA with condition (Distractor/Control) and Day (Day 1/Day 2) as within subject factors. This analysis revealed no significant effects of the Day factor $F < 1$, the Condition factor $F(1,13) = 2.13$, $p = 0.17$; $\eta_p^2 = 0.14$ or the interaction Day*Condition $F < 1$ (mean consumption of both days across both conditions; Distractor: M = 10.64, SE = 0.20/Control: M = 10.25, SE = 0.33).

Consumption of the distractor solution showed that all animals drank the lemon-maltodextrin solution during the pre-feeding phase in this condition (M = 3.98, SE = 0.34; min = 1.4, Max = 5.4).

Fig. 3 shows the mean total consumption of the pre-fed and non-pre-fed substances for the distractor and control conditions during the 4 days of testing. These results suggest no group differences in the expression of SSS, with the consumption of the pre-fed solution being lower than the non-pre-fed solution in both cases. These data were analyzed using a repeated measures ANOVA with Condition (Distractor/Control) and Pre-feeding (Pre-fed/Non-Pre-fed) as the within-subject factor. This analysis revealed a significant effect of Pre-feeding $F(1,13) = 20.43$ $p < 0.001$, $\eta_p^2 = 0.61$ and a significant effect of Condition $F(1,13) = 7.91$, $p = 0.01$,; $\eta_p^2 = 0.38$, but no significant interaction between these factors, $F < 1$.

The results of this experiment have demonstrated that rats in both conditions show an effect of SSS by drinking less of the pre-fed solution than the non-pre-fed one. Animals in the distractor condition, however, consumed less overall during the two-bottle test. This might be expected, given the fact that animals in the distractor condition had an additional solution to drink before the choice test and therefore, were less thirsty. Thus, these results show that the presentation of a distractor of the same sensory modality did not impair the SSS effect.

5. General discussion

Using a rat model, this study set out to assess whether habituation is the underlying mechanism of SSS by testing whether the latter phenomenon shares the following three characteristics of habituation: spontaneous recovery, dishabituation and distraction. The results of Experiment 1 confirmed the SSS effect when two flavored solutions were used as the target stimuli and the effect was measured using a direct consumption test (see also González et al., 2018). Moreover, these findings revealed a spontaneous recovery of the relative preference of

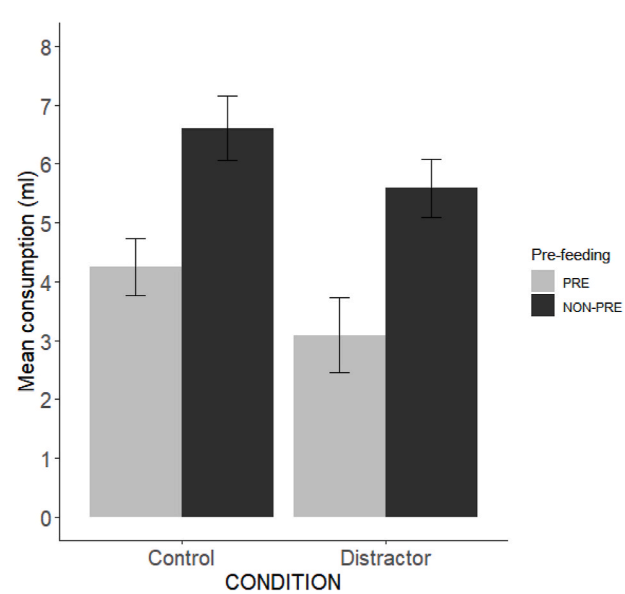

Fig. 3. The SSS effect in the different experimental conditions. "PRE": refers to the pre-fed solution whereas "NON-PRE" refers to the non-pre-fed solution.

the pre-fed solutions over time. Animals expressed a SSS effect both immediately and 2 h after pre-feeding, consuming more of the non-pre-fed solution then the pre-fed solution on a choice test. After 5 h, the recovery of the preference was apparent, with no differences in consumption between the two solutions. Interestingly, this result contrasts with that reported by Parkes, Marchand, Ferreira, and Coutureau (2016) who measured the SSS effect in rats across various time intervals and by measuring both the patterns of intake and instrumental responses towards pre-fed and non-pre-fed flavored pellets. In this study, after an interval of 5 h, rats still consumed less of the pre-fed than the non-pre-fed flavored pellets. However, there are two main procedural differences between our study and that of Parkes et al. (2016) that could possibly explain these discrepant findings. First, the different pattern of results could be explained by the type of pre-feeding procedure used, since in the present study, the pre-feeding session was shorter (20 min exposure compared with 60 min in Parkes et al., 2016). Second, in our study all the stimuli were liquid solutions as opposed to solid stimuli (flavored pellets). Some authors argue that satiety processes are weaker with liquid stimuli in comparison with solid stimuli since with the former sensory modality, oro-sensory exposure is weaker (Bilman, Ellen van Kleef & Hans van Trijp, 2015). Thus, it is reasonable to suppose that with liquid stimuli the SSS processes could decay earlier in comparison with solid stimuli.

Experiment 2 showed that the SSS effect is not restored after the presentation of a dishabituator; on the choice test both groups consumed higher amounts of the non-pre-fed solution than the pre-fed solution. This finding is consistent with the results of many other human studies that tested this hypothesis although it contrasts with the results reported by Romer et al. (2006). In Experiment 2, these authors showed that after eating a first course, introducing a different meal in a second course reversed the devaluation effect when using measures of olfactory pleasure to evaluate the SSS effect. Moreover, Experiment 3 of the same study showed how presenting the same pre-fed food in a second course with seasoning could restore the decrement in the hedonic value of this food (see also Brondel, Romer, et al., 2009 for a similar result). Whilst the results of this third experiment could be interpreted as evidence for dishabituation, these findings are open to an alternative interpretation in terms of positive hedonic contrast. In fact, Yeomans, Morris, and Armitage (2020) have shown that the typical decrement in hedonic value that characterizes SSS can be reversed after presenting a more palatable version of the same meal (by adding more salt). Thus, comparison with a previous meal that is more or less valuable can, over time, modify the current value of the same food in a positive or negative way. If a food is eaten to satiety and is then presented in a more palatable format, any recovery in hedonic pleasure could be attributed to hedonic contrast rather than dishabituation.

Experiment 3 showed that the presence of a distractor during the SSS process did not alter the SSS effect since there were no significant group differences in consumption on the choice test. This finding contrasts with those of other studies conducted with human participants that found a disruption of the SSS effect as measured by wanting (Brunstrom & Mitchell, Experiment 2, 2006), liking (Hetherington et al., 2006) or intake patterns (Brondel, Lauraine, et al., 2009; Hetherington et al., 2006). A notable difference between the procedures conducted with human subjects and the one presented in this study is the way in which the distractor is presented during the procedure. In human studies, the distractor is presented simultaneously with the target stimuli, similar to the way it occurs in day-to-day life. In the present experiment, the distractor was not presented simultaneously with the target solution, but in an intermixed fashion. This procedure was carried out to ensure that consumption of the target and the distractor solution were equally distributed during pre-feeding, thus preventing rats from consuming their preferred substances first. In view of this situation, one could question whether this manipulation did not succeed in distracting the experimental subjects (as it would be expected to do in everyday life when talking with people or watching television, etc.). However, according to Epstein et al. (2009) for the distractor to be effective, it is sufficient that it interrupts the processing of the habituating stimulus. In this way, the intermixed presentation of the distractor would remove the pre-fed solution from working memory, disrupting its processing and thus, its habituation.

This study produced results which confirm the findings of many previous studies conducted in this field, questioning the possibility that habituation is the only mechanism underlying SSS, at least with the experimental procedures used here. However, the study of the mechanisms involved in this SSS is of great interest for better understanding our eating behavior within so-called obesogenic environments. Such obesogenic environments are characterized by Cafeteria diets that include a wide variety of caloric foods within a meal, which have been proposed to increase total intake, at least in part due to the Buffet or Variety Effect. The Variety Effect predicts that the greater the variety of different foods within a meal, the higher the total intake within that meal (Brondel, Lauraine, et al., 2009; Brondel, Romer, et al., 2009; Epstein, Robinson, Roemmich, Marusewski, & Roba, 2010; Raynor & Wing, 2006; Rolls, Rowe, et al., 1981; Rolls, Van Duijvenvoorde, & Rowe, 1983). SSS has been proposed as the main explanatory phenomenon for the Variety Effect (Norton, Anderson, & Hetherington, 2006; Reichelt et al., 2014). One way in which SSS could promote this increase in consumption is through a dishabituation (when meals are presented sequentially) or distraction process (when meals are presented simultaneously).

However, there is also evidence to suggest that presenting different foods in a simultaneous or a sequential fashion during a meal does not reverse the hedonic devaluation that is characteristic of the SSS effect (Meillon et al., 2013). Thus, an alternative explanation of the Buffet effect involves the rate of exposure to the different foods within a meal. In contrast to the habituation approach, from this point of view, rather than variety, the amount of exposure to each food item during a meal is crucial. Thus, the SSS process occurs independently for each food stimulus and there are no interactions between food items. If we are given many food choices (high variety condition, Buffet Effect) oro-sensory exposure to each component of the meal is shared between many food items and the course of SSS is weaker for each stimulus. In a monotonous diet (low variety condition) there are relatively few options to choose from, so that exposure to each stimulus is higher, allowing for a rapid and strong sensory devaluation of all foods. Hendriks, Havermans, Nederkoorn, and Bast (2019) found evidence for the latter proposal by manipulating the number of exposures to food stimuli as well as the level of variety within the presentations of the target foods. In this study they assessed SSS expression by measuring both hedonic and motivational responses. These authors found that whilst the most relevant factor for observing the SSS effect was the amount of exposure to the foods, alternation between different foods within a meal had no impact on SSS. Again, the latter study constitutes further evidence to suggest that SSS does not share all of the properties of the habituation phenomenon.

Havermans (2012) and Meillon et al. (2013) have argued that the fact that SSS does not share all of the properties of habituation does not necessarily mean that SSS does not reflect the expression of this phenomenon. In fact, Havermans (2012) argues that SSS is a special form of habituation in which stimuli specificity is expressed but dishabituation does not occur. Moreover, Meillon et al. (2013) suggested that SSS is composed of two main phases that are critical in determining whether or not the SSS effect can be disrupted. In the first stage, SSS is developing and can still be modified whilst in the second stage it is fully complete and this sensory devaluation cannot be disrupted or reversed. These authors argue that the very nature of SSS as an eating behavior mechanism is the property that distinguishes it from other types of behavior that can be habituated. As foods are ingested, it is not only the sensory input but also the feelings of fullness or satiety that make SSS impossible to dishabituate. Thus, according to this hypothesis, SSS can only be disrupted when it is in the development stage. However, in Experiment

3, animals were exposed to a distractor within 5 min, that is, when the SSS process was still developing, and no attenuation of the effect was found. On the other hand, SSS is defined as a specific devaluation of the sensory properties of food which occurs independently (or at least partly) of post-absorptive factors. Thus, if any physical input (feeling of fullness) affects the expression of SSS then this would operate by decreasing the total consumption of all the available foods (eaten and uneaten meals) leaving intact the preferences, or the value of the foods (Pre-fed: devalued vs Non-Pre-fed: non devalued). This pattern of results was found in Experiment 3 when rats in the distractor condition, which drank more in total during the pre-feeding phase due to the additional presence of the distractor, consumed less on the consumption test whilst still showing the SSS effect.

Another tentative explanation of the SSS suggested by Hetherington and Havermans (2013) is in terms of stimulus satiation. What underlies this idea, which is based on the research of Glanzer (1953), is that after SSS, subjects experience a state of boredom in response to the exposed stimuli. Thus, in contrast to habituation, the eaten food does not become irrelevant, but aversive in such a way that a stimulus changes from positive to negative valence. This notion is based on the idea that SSS does not occur due to a decrease in responding but a qualitative change in responding from approach to avoidance behavior. However, there is evidence that runs counter to this hypothesis. Berridge (1991) found that after an SSS procedure rats reduced their orofacial appetitive responses to the consumed solution, but in no case did aversive responses increase. This evidence does not support an explanation in terms of a qualitative change of stimulus valence.

Finally, other attempts to explain SSS have been presented from a top-down process perspective. For instance, Wilkinson and Brunstrom (2016) hypothesized that SSS could be modulated by the perceived availability of food items. These authors argued that when a food stimulus is not available, its subjective value increases. Hence, when in some of the typical SSS experimental procedures, human participants are asked to rate the hedonic value of eaten and uneaten foods, the latter should be perceived as unavailable items, inaccessible during the whole procedure, and, as a consequence, more valuable. Furthermore, these authors suggest that eaten (available) foods would be perceived as less valuable due to negative contrast, when compared with uneaten (unavailable) foods. However, the results of their study did not support this interpretation of the SSS phenomenon (Wilkinson & Brunstrom, 2016). With regard to the buffet effect, Havermans and Brondel (2013) suggested that this phenomenon occurs not as a consequence of eating different foods that could undermine SSS expression (presumed dishabituation/distraction or rate of exposure to foods), but is due to the mere perception of variety. This implies that variety itself has reinforcing properties and therefore can disrupt SSS, thereby preventing the normal course of food devaluation from occurring. Again, the results of their study did not support their hypothesis; mere perception of food variety did not disrupt the SSS effect. These suggestions, which are based on more complex cognitive processes, can be contrasted with the results of a study by Higgs, Williamson, Rotshtein, and Humphreys (2008) who showed how this eating regulatory mechanism was present in two amnesic patients when SSS was assessed by hedonic scales. These authors argue that the SSS effect is a basic process in which explicit memory for recent eaten meals is not necessary, suggesting that the mechanism responsible for this is habituation. Thus, the behavioral evidence seems to suggest that SSS is a phenomenon that operates through a basic mechanism in which the explicit memory of recently eaten meals is not critical (Higgs et al., 2008) and which is similar to habituation due to its stimulus specificity (Havermans, 2012).

A number of caveats need to be noted regarding the present study. First, although the present study did not show evidence for a habituation-based account of SSS, it should be noted that all the procedures carried out in this experiment measured preferences during consumption. This measure, however, fails to completely capture what was originally assumed to occur in SSS, that is, a change in the relative preference for the target stimulus. Thus, we have to presume that any change in direct consumption of the target stimuli can be taken to indicate a change in the pleasantness of the solutions. Second, all the stimuli used in the three experiments were fluids. It is possible that using stimuli of the same sensory modality as the distractors and dishabituators could weaken the effects as a consequence of generalization to the target stimuli. Furthermore, we have no prior evidence to suggest that the distractor/dishabituator solutions have the capacity to dishabituate/distract the habituation process. Therefore, it remains possible that these processes are still occurring with this procedure but that the stimuli used here failed to detect them. Finally, in the present study we only tested three properties of habituation. Future research should be conducted using an animal model focusing on whether other characteristics of habituation can be demonstrated with this SSS procedure (Rankin et al., 2009) such as long-term habituation, potentiation of habituation, or the effects of the intensity or frequency of stimulation on SSS expression.

6. Conclusion

In summary, the presentation of a dishabituator after establishing SSS did not restore the value of the pre-fed solution. Furthermore, we found no evidence to suggest that the presence of a distractor during pre-feeding disrupts the SSS process and attenuates the hedonic devaluation of the pre-fed solution. These results suggest that with the paradigm used here, the SSS effect cannot be explained in terms of a typical case of response habituation, at least when considering the idea that all habituated responses can be re-established after the presentation of a dishabituator or a distractor**.** Further studies should be conducted with other techniques such as the oro-facial reactivity test or an assessment of licking clusters to ascertain whether the use of dishabituator or distractor stimuli of sensory modalities different from the target stimuli could impair or attenuate the observed SSS effect.

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Ethical statement

All the procedures described in this paper were approved by the Comité de Ética en Experimentación Animal, number reference: 06/06/2019/099 (Ethics Committee in Animal Research at the University of Granada and Junta de Andalucia, (Spain), and were classified as low severity according to European guidelines.

Declaration of conflicting interest

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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