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Olfactory Sensory-Specific Satiety in Humans

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ROLLS, E. T. AND J. H. ROLLS. *Olfactory sensory-specific satiety in humans.* PHYSIOL BEHAV **61**(3) 461–473, 1997.—It is shown that olfactory sensory-specific satiety, measured by ratings of the pleasantness of the odour of a food eaten relative to the change in pleasantness of other foods, can be produced by eating a food to satiety. It is also shown that olfactory and taste sensory-specific satiety can be produced by chewing samples of a food for approximately as long as the food would normally be eaten in a meal. It is further shown that partial olfactory sensory-specific satiety can be produced by smelling the food for approximately as long as it would be in the mouth during a meal. These sensory-specific changes in the pleasantness of a food do not appear to reflect changes in the intensity of the foods, which were small and not highly correlated with the changes in pleasantness. The results show that at least partial olfactory, as well as taste, sensory-specific satiety does not require food to enter the gastrointestinal system, and does not depend on the ingestion of calories. The implications for the control of food intake, and the way in which the brain computes sensory-specific satiety, are considered. © 1997 Elsevier Science Inc.

Feeding Food intake Smell Taste Pleasantness Appetite

SENSORY-specific satiety refers to the decrease in the pleasantness of a food after it has been eaten to satiety, and the smaller amount of that food, relative to other foods, that is subsequently eaten in a meal. Rolls and colleagues discovered that hypothalamic neurons stop responding to the sight and taste of food on which a monkey is fed to satiety, but remain responsive to other foods, and that the monkey's behavior reflects this by showing sensory-specific satiety (1,13,27,29). Soon after that, we initiated a series of investigations in humans of sensory-specific satiety. We showed that the pleasantness of the sight and of the taste of a food eaten to satiety decreased, and other foods not eaten to satiety remained relatively pleasant (13,26). We went on to show that this decrease in pleasantness was associated with less subsequent eating of that food relative to other foods in the meal, and [consistent with earlier findings of Le Magnen (9,10) in rats] that variety of food in a meal can lead to greater food intake (13,17). The taste, texture, and color of the food have been shown to be important factors in these effects (14). Because sensory factors such as similarity of color, shape, flavour, and texture are usually more important than metabolic equivalence in terms of protein, carbohydrate, and fat content in influencing how foods interact in this type of satiety, it has been termed ''sensory-specific satiety'' (8,13,14,16,19,20,21,26). It should be noted that this effect is distinct from alliesthesia, in that alliesthesia is a change in the pleasantness of sensory inputs produced by internal signals (such as glucose in the gut) (2–4). Sensory-specific satiety, on the other hand, is a change in the pleasantness of sensory inputs that is accounted for, at least partly, by the external sensory stimulation received (such as the taste of a particular food), in that, as shown above, it is at least partly specific to the external sensory stimulation received.

We have analysed the neural mechanisms of sensory-specific satiety. We have shown that, in primates (macaques), satiety effects on taste processing, including sensory-specific satiety, are implemented in the secondary taste cortex, in the caudolateral orbitofrontal cortex (31). Neuronal responses here to the taste of a food such as glucose are decreased to zero by feeding the monkey to satiety with glucose (6,31). There is no effect of satiety on taste processing in the primary taste cortex of primates (30,36). Thus, the identity of the taste is represented in the primary taste cortex, and the hedonic or affective quality of the taste is computed and represented in the secondary taste cortex (22–25). For effects of satiety on olfactory processing in primates, we have recently shown that satiety modulates the responses to olfactory stimuli of neurons in the secondary and tertiary olfactory cortical areas, which are in the caudal orbitofrontal cortex (6). We do not yet know if this is the first stage in the primate olfactory system where hunger modulates neuronal responses to olfactory stimuli.

These findings raise a number of issues that are investigated here. The first is whether olfactory sensory-specific satiety can be demonstrated in humans. To analyse this, we asked humans to rate the pleasantness of the smell of foods held in front of the nose before and after one of the foods was eaten to satiety. To provide an indication of whether or not the effects on pleasantness could be separated from an effect on the intensity of the odour (which, if true, would suggest that olfactory sensory-specific satiety might be implemented in the brain only after the identity and intensity of the odour has been analysed, and would be separable from peripheral sensory adaptation), the humans also rated the intensity of the odours. The second issue is on the mechanism of sensory-specific satiety. Sensory-specific satiety is

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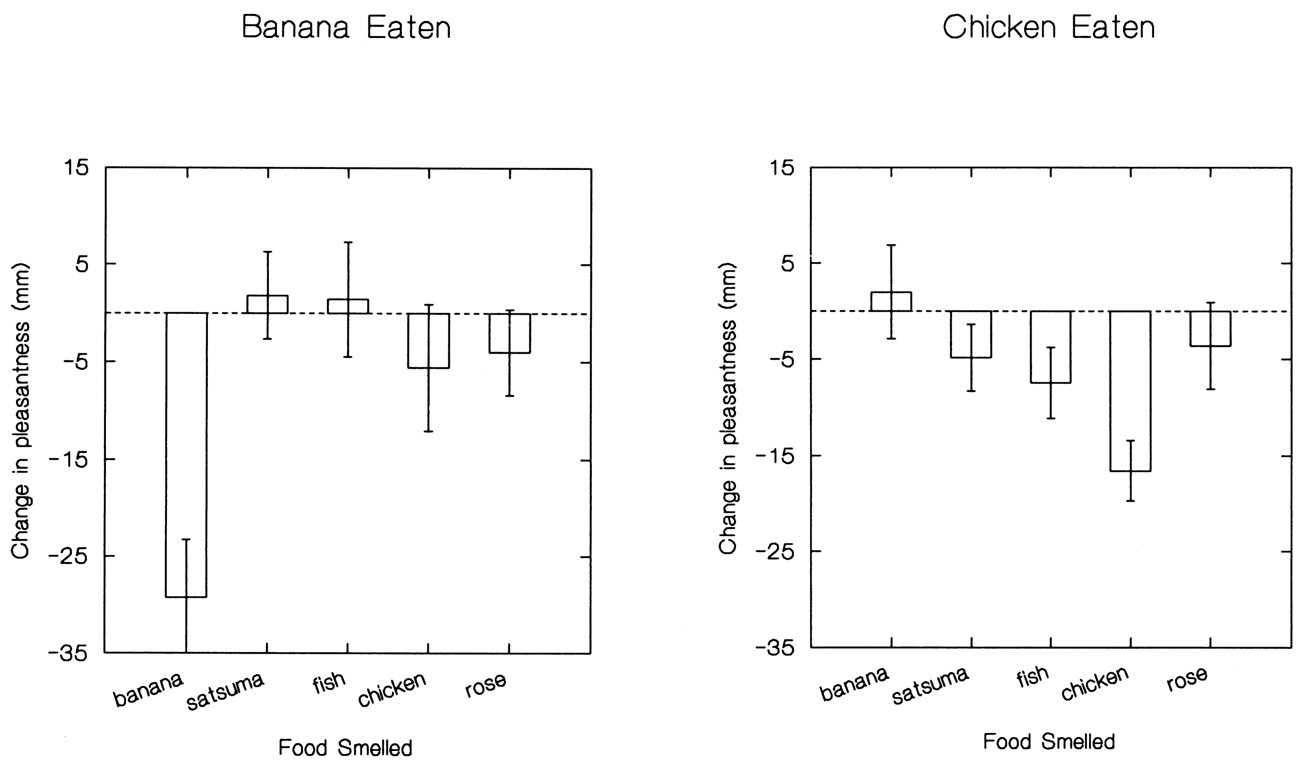

FIG. 1. The change in the pleasantness of the smell of 5 different odours after eating banana (left) or chicken (right) to satiety. The means and standard errors of the changes in rating on a 100-mm visual analog rating scale are shown in this and subsequent Figs.

strongly dependent on sensory aspects of the food, such as its taste and texture, rather than on the nutritional (protein, carbohydrate, fat, or energy content) of the food (13,18,34). This suggests that the mechanism is at least partly implemented as a function of activity in the high-order sensory pathways themselves, and is at least partly independent of the food in the gut. To be specific for, at least, taste, the hypothesis is that activity continuing for a few minutes in the part of the taste system where pleasantness is represented (the secondary taste cortex), leads to a decrease in the responsiveness of those neurons (21,24). Because the neurons here can be fairly sharply tuned, this could implement a sensory-specific decrease in pleasantness. The decline in responsiveness would occur during a period of several min of activation, such as occurs normally in a meal. Because there is no decrease in responsiveness in the primary taste cortex, the intensity of the taste, and the ability to identify the taste, would not decrease with satiety. To provide another type of evidence on this possibility, in Experiment 1, we allowed humans to merely chew samples of the food for several min, never swallowing it but always spitting it out, to determine if this would produce any sensory-specific satiety. We measured, for this purpose, the pleasantness separately from the taste and the smell of the food. We found that at least some sensory-specific satiety was produced in Experiment 1 merely by chewing the food.

The olfactory sensory-specific satiety effect observed in Experiment 1 could have been due to activity in the unimodal olfactory pathways, before olfactory-taste convergence has occurred (see 33), or it could have been due to an effect of the taste in the mouth on olfactory processing. To determine where olfactory stimulation without taste could produce some sensory-specific satiety, in Experiment 2 we asked subjects to merely smell the food for as long as it would normally be eaten in a meal, without ever even placing the food in their mouths. Some olfactory sensory-specific satiety was found. The experiments have clear implications for the mechanisms of sensory-specific satiety, and also have implications for food-intake control.

EXPERIMENT 1

The aims of Experiment 1 were to determine if olfactory sensory-specific satiety occurs in humans, measured by whether or not the pleasantness of the smell of a food eaten to satiety decreases more than the pleasantness of the smell of other foods not eaten in the meal. Also we tried to determine if merely chewing a food, without swallowing it, for as long as it would be eaten in a meal, produces olfactory and taste sensory-specific satiety. The chewing condition excludes gastric, duodenal, and intestinal factors and nutrient feedback produced by swallowing the food. Intensity was also measured, to determine if the changes of pleasantness could be separated from any possible sensory adaptation. Sensory-specific satiety was measured by the decrease in the pleasantness of a food eaten to satiety. This correlates with and predicts the amount subsequently eaten in the meal (14).

METHODS

The design of the experiment was that subjects should rate the pleasantness and intensity of the odours and taste of 4 foods when hungry. Then they chewed 1 of the foods for 5 min, and performed the ratings again. Then, they ate as much of the same food as they wanted for lunch, until satiated, and performed the ratings again. Each subject was tested twice (in counterbalanced order), once when chewing, then eating, chicken for lunch, and once when chewing, then eating, banana for lunch. The chicken and banana were among the 4 foods rated for pleasantness and intensity.

The subjects were 12 normal weight nonsmoking people aged between 21 and 30 years (3 women and 9 men) who were not on any form of diet (to remove the possibility that some subjects might resist eating to full satiety). The subjects were screened to ensure that they liked the 2 main foods to be eaten, chicken and banana. They came to the laboratory in the same state of hunger (checked with a visual analog rating scale) for lunch, having eaten nothing since breakfast. Each test day was separated from the next by at least 1 full day. The tests were run at lunchtime so that the foods provided a reasonable replacement for a normal meal that might be eaten at that time.

The foods were presented in sealed cups to prevent the odours mixing. The 4 foods were banana, satsuma (a type of orange), fish paste, and chicken and, in addition, a fifth pleasant but non-food odour, rose water (phenylethylamine), was presented for comparison. The banana, satsuma, and freshly cooked cold chicken were cut into small pieces to maximise the surface area and the smell given off. The fish paste was bought preprepared. To make an olfactory rating, the subject removed the lid of the cup when it was close to the nose, took several large sniffs, closed the lid, and immediately made the pleasantness and intensity ratings. The olfactory ratings of all 5 stimuli were made in fixed sequence. Then, the taste ratings were made in the same fixed sequence. To make a taste rating, the subject placed a small sample (approximately 1 g) of 1 of the 4 foods in the mouth, immediately made the pleasantness and intensity ratings, and then swallowed the small sample. (Subjects were not asked to taste the rose water!)

The ratings were made on 100 mm visual analog rating scales (established for use in this type of research in previous studies) (14,15,17). For pleasantness, the line was marked at one end 'very unpleasant' and at the other 'very pleasant'. For intensity, the line was marked at one end 'very weak' and at the other 'very intense'. The subject was asked to make a mark at a position on the line that indicated the current pleasantness or intensity of the stimulus being rated. Only one rating scale could be seen at a time, so that comparisons with earlier ratings were not possible. The separate rating scales performed at the start of the experiment, after chewing and after eating, were provided in separate booklets that were collected at the end of each part of the experiment. The ratings made after chewing or eating to satiety were made immediately after the end of the chewing, as sensory-specific satiety is known to start to decrease after the end of a meal within a period of minutes. (Sensory-specific satiety lasts tens of min to a few h).

The chicken and banana to be eaten were weighed to make sure that the subjects ate a reasonable meal of, at the very least, 100 g. The mean ($\pm$ SD) amount of chicken eaten was 177 $\pm$ 44 g, and of banana 348 $\pm$ 90 g. Each subject was tested on 2 separate occasions, as noted, with the difference being the food that was consumed to satiety (chicken or banana). Subjects were tested under both conditions of food presentation, to permit a within-subjects analysis, and subjects were given the different conditions on different days. The order of presentation of meals to subjects was completely counterbalanced. Half were fed banana on the first day and half had chicken on the first day to control for an order effect. On the first test day, an initial set of ratings was performed by the subjects to provide them with experience of the range of pleasantnesses and intensities used in the experiment. The subjects were allowed to adjust their use of the visual analog rating scale at this point, in the light of the pleasantness and intensity of the foods in the experiment. The initial practice ratings were discarded.

RESULTS

Change in the Pleasantness and Intensity of the Smell of a Food Eaten to Satiety

It is shown in Fig. 1 that the pleasantness of the smell of banana decreased greatly when it was eaten to satiety (by 29.3 mm on the 100 mm visual analog scale), and that the other foods did not show large decreases in pleasantness (their means are not more than 2 standard errors from 0). It is also shown in Fig. 1 (right) that the pleasantness of the smell of chicken decreased considerably (by 16.6 mm) when it was eaten to satiety, and that this was a greater decrease than for the other foods not eaten. The change in rating shown is the difference between the initial pleasantness of the stimulus at the beginning of the experiment, and its pleasantness at the end of the experiment, immediately after the test food for that day had been eaten to satiety. A 2-way within-subjects ANOVA, in which the first factor was the food smelled and the second factor was the food eaten to satiety, showed a highly significant interaction ($F(4,44) = 7.03$, $p = 0.00034$), indicating that the olfactory sensory-specific satiety was highly statistically significant.

The first factor in the ANOVA just failed to reach significance, $F(4,44) = 2.56$, $p = 0.051$, indicating that there was little overall difference between the odours apart from the interaction. The second factor in the ANOVA also was not significant, $F(1,44) = 0.13$, $p = 0.72$, indicating that there was little overall decline in the pleasantness of the odours produced by eating one of the foods to satiety. These results emphasize the primary importance of the olfactory sensory-specific satiety effect observed in the experiment.

In contrast, it is shown in Fig. 2 that the changes in the intensity of the smell of the stimuli were much less specifically affected by eating one of the foods to satiety. Although there was some decrease in the intensity of the smell of banana when it was eaten to satiety, there was no specific decrease in the intensity of the smell of chicken when it was eaten to satiety and, overall, the interaction term in the 2-way ANOVA was not significant ($F(4,44) = 1.2$; $p = 0.32$). The first or sensory factor was significant, $F(4,44) = 2.96$; $p = 0.0296$, consistent with a small overall change in intensity of the odours, and the second or satiating factor was not significant, $F(1,44) = 0.89$, $p = 0.63$, indicating that the changes in intensity did not differ depending on whether banana or chicken was eaten. This result makes it likely that the change of pleasantness of the smell of a food eaten to satiety is not related just to a change in intensity.

Change in the Pleasantness and Intensity of the Smell of a Food Chewed for 5 Min

It is shown in Fig. 3 that the pleasantness of the smell of banana decreased considerably when it was chewed and not swallowed (by 17.8 mm on the 100 mm visual analog scale), and that the other foods did not show large decreases in pleasantness. It is also shown in Fig. 3 (right) that the pleasantness of the smell of chicken decreased (by 10.7 mm) when it was chewed, and that this was a greater decrease than for the other foods not chewed. The change in rating shown is the difference between the initial pleasantness of the stimulus at the beginning of the experiment, and its pleasantness at the end of the chewing. A 2-way within subjects ANOVA, in which the first (sensory) factor was the food smelled and the second (satiating) factor was the food chewed, showed a highly significant interaction ($F(4,44) = 5.66$; $p = 0.001$), indicating that the olfactory sensory-specific satiety produced by chewing without swallowing was highly statistically significant. (The sensory and satiating main factors in

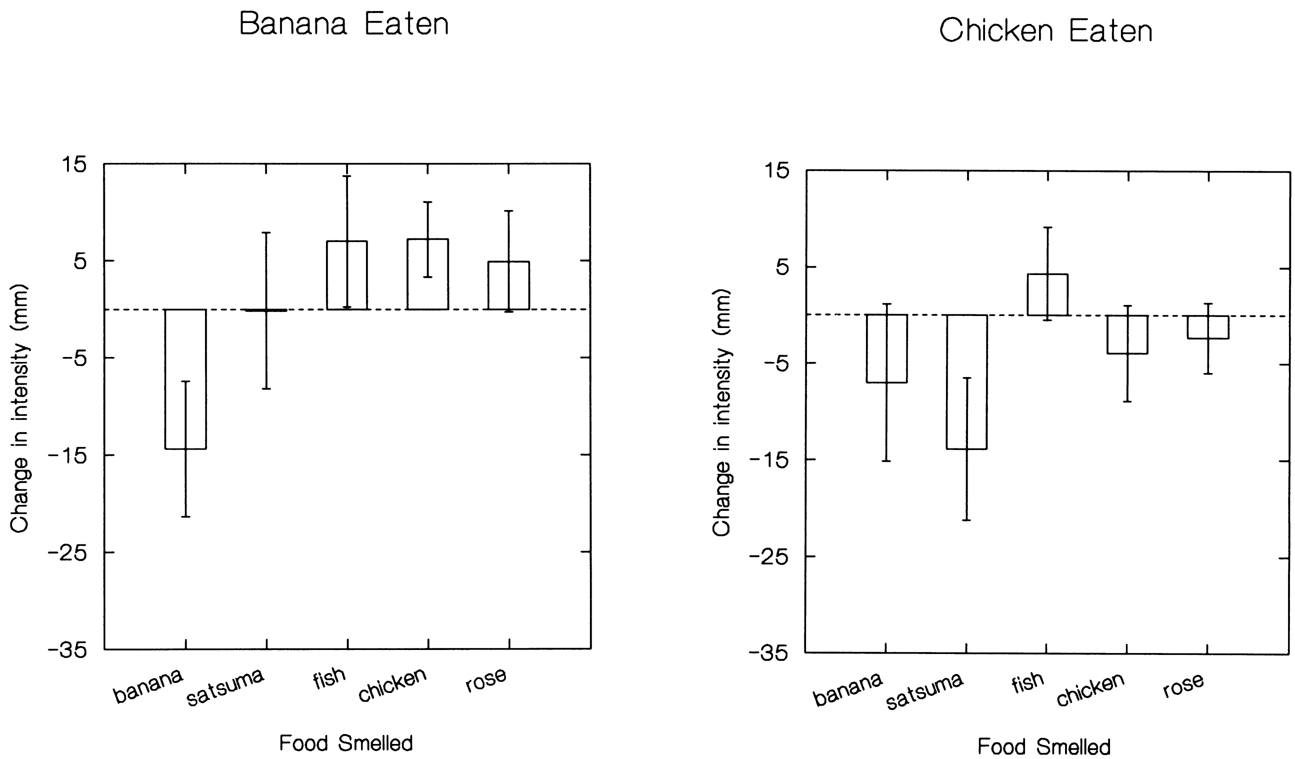

FIG. 2. The change in the intensity of the smell of 5 different odours after eating banana (left) or chicken (right) to satiety.

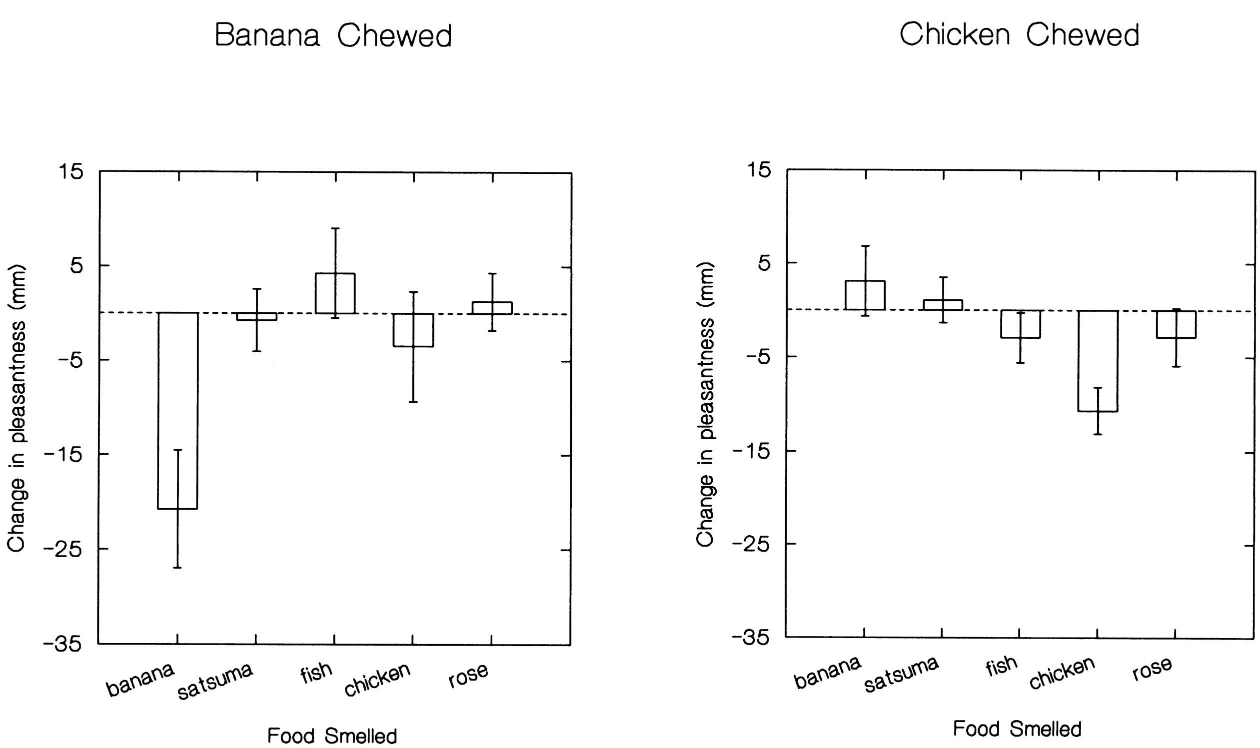

FIG. 3. The change in the pleasantness of the smell of 5 different odours after chewing banana (left) or chicken (right) for 5 min.

the ANOVA were not significant; p values 0.18 and 0.63, respectively.) These results show that olfactory sensory-specific satiety can be produced by chewing a food for 5 min without swallowing it, although the effect is, as might be expected, not as large as the change produced when the food is chewed and then eaten to satiety.

In contrast, it is shown, in Fig. 4, that although there was some decrease in the intensity of the smell of banana when it was chewed, there was no specific decrease in the intensity of the smell of chicken when it was chewed and, overall, the interaction term in the 2-way ANOVA was not significant ($F(4,44) = 1.36$; $p = 0.26$). (The sensory and satiating main factors in the ANOVA were not significant; p values 0.08 and 0.91, respectively.) This result makes it likely that the change of pleasantness of the smell of a food chewed for 5 min is not related just to a change in intensity.

Change in the Pleasantness and Intensity of the Taste of a Food Eaten to Satiety

It is shown, in Fig. 5, that a large sensory-specific satiety effect for the pleasantness of the taste of the food eaten was found. The interaction effect was highly significant ($F(3,33) = 12.07$; $p = 0.000054$). The change in rating shown is the difference between the initial pleasantness of the stimulus at the beginning of the experiment, and its pleasantness at the end of the experiment, immediately after the test food for that day had been eaten to satiety. This type of sensory-specific satiety replicates what has been seen many times previously, and is not dwelt on here, except to note that by ''taste'' here we refer to the rating given in response to the instruction ''rate the pleasantness of the taste of the food in your mouth now,'' which is in fact a combination of olfactory and gustatory stimuli, termed more strictly ''flavour'' (33).

Although this is usually not such a large effect, in this particular experiment, the rated intensity of the food eaten to satiety did decrease significantly relative to the intensity of the tastes of the other foods [see Fig. 6, interaction term in the ANOVA, $F(3,33) = 6.3$; $p = 0.002$].

Change in the Pleasantness and Intensity of the Taste of a Food Chewed for 5 Min

It is shown, in Fig. 7, that the pleasantness of the taste of banana decreased considerably when it was chewed and not swallowed (by 13 mm on the 100 mm visual analog scale), and that the other foods did not show large decreases in pleasantness. It is also shown in Fig. 7 (right) that the pleasantness of the taste of chicken decreased (by 11 mm) when it was chewed, and that this was a greater decrease than for the other foods not chewed. The interaction term in the ANOVA was significant ($F(3,33) = 3.97$; $p = 0.01$), indicating that sensory-specific satiety was found for the taste of a food chewed but not swallowed. The effect is not as great, however, as when the food was swallowed and eaten to satiety (Figs. 5 and 7). Factors that account for the larger effect when the food is swallowed (the ''eaten'' condition) are likely to include the second period of olfacto-gustatory stimulation after chewing when the food is actually eaten, and gastric distension and other postingestive consequences of food entering the gastro-intestinal system (see Discussion).

As in the later part of this particular experiment, the rated intensity of the taste of the food chewed did decrease significantly relative to the intensity of the tastes of the other foods (see Fig. 8); interaction term in the ANOVA, $F(3,33) = 11$, $p = 0.00011$.

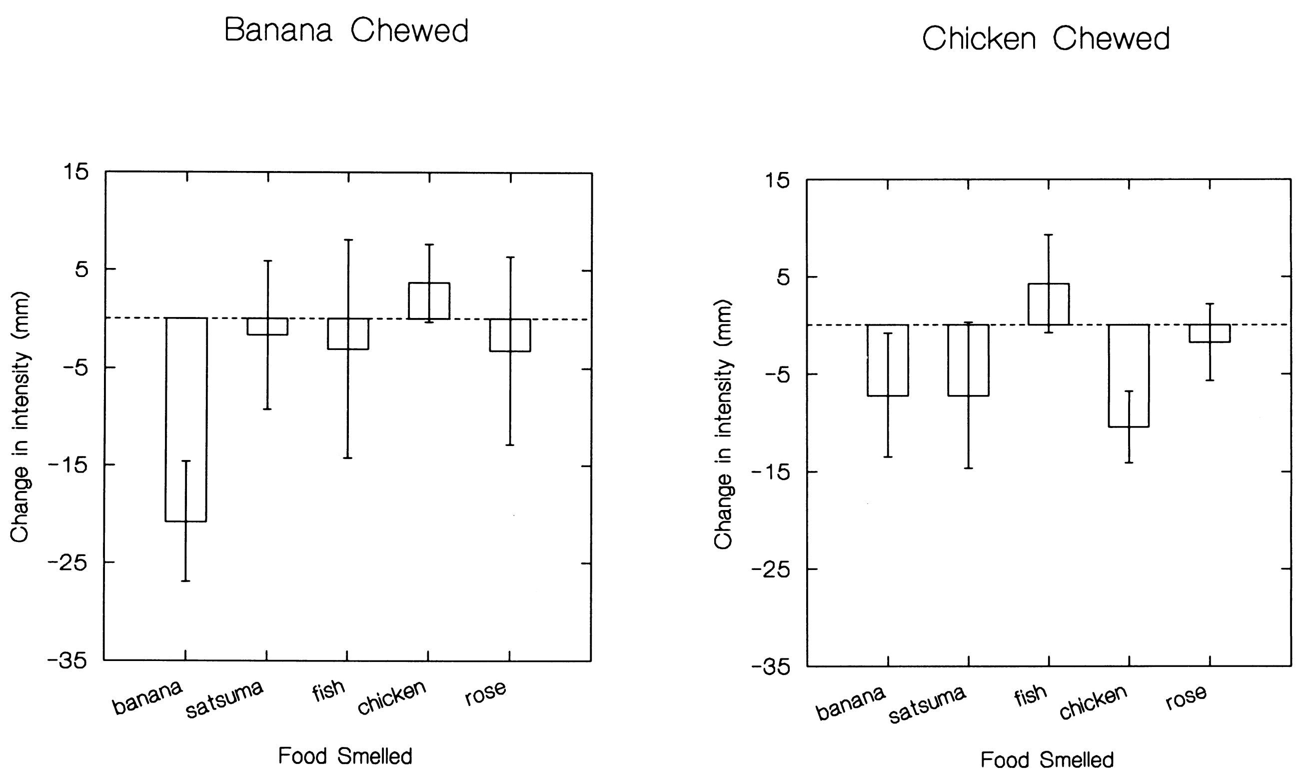

FIG. 4. The change in the intensity of the smell of 5 different odours after chewing banana (left) or chicken (right) for 5 min.

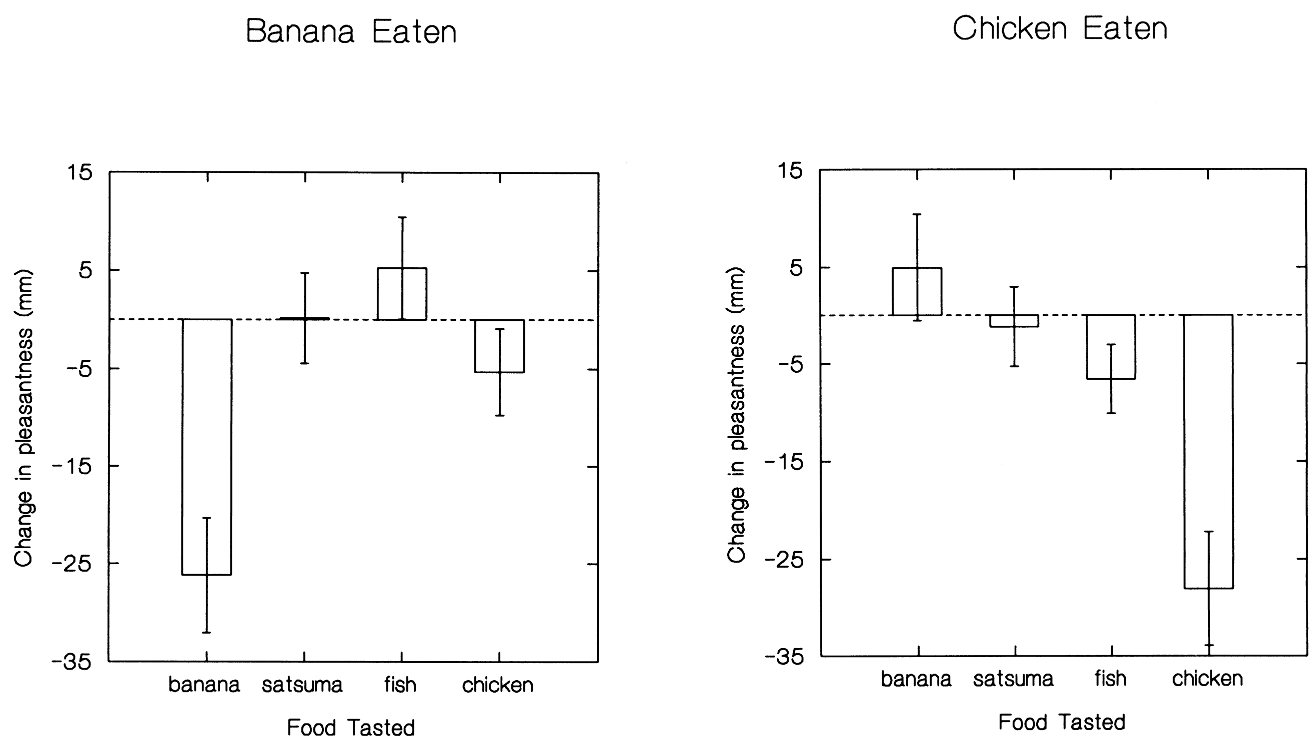

FIG. 5. The change in the pleasantness of the taste of 4 different foods after eating banana (left) or chicken (right) to satiety.

EXPERIMENT 2

The new findings of Experiment 1 were that olfactory sensory-specific satiety can occur, and that chewing a food without swallowing it can produce at least some olfactory and gustatory sensory-specific satiety. The aims of Experiment 2 were to determine if (at least some) olfactory sensory-specific satiety can be produced by olfactory stimulation alone, and to replicate the olfactory sensory-specific satiety produced by eating a food to satiety that was demonstrated in Experiment 1. The design of Experiment 2 was similar to that of Experiment 1 except that, instead of chewing the food, the subjects smelled the food without placing it in their mouths, for 5 min, that is, for a time period of about the same order as they took later to eat the food until they were satiated.

METHODS

The details of the Methods were as in Experiment 1, except in the following respects.

A new group of subjects was used. The subjects were 12 normal weight nonsmoking people aged between 18 and 21 years (9 men and 3 women) who were not on any form of diet.

After the initial ratings of the pleasantness and intensity of the smell of the stimuli, and then of their taste, the subjects were given the banana or chicken (in counterbalanced order on different days) to smell for 5 min, a time of the same order of magnitude as the time it later took them to eat the food to satiety. The olfactory stimulus for this 5-min period was presented in a plastic cup, the lid of which was removed while the cup was held close to the nose, and the subject smelled the food. The food was cut into small pieces, and was covered with a small piece of cotton wool, so that the subject could smell, but not see, the food. [We have demonstrated previously sensory-specific satiety for the sight of a food eaten to satiety (16), and wished to exclude that from this olfactory experiment.]

RESULTS

Change in the Pleasantness and Intensity of the Smell of a Food Eaten to Satiety

The results were similar to those in Experiment 1, with a highly significant sensory-specific satiety for the pleasantness of the food eaten to satiety [interaction $F(4,44) = 11.9$, $p = 0.000015$]. As before, there was no statistically significant decrease in the intensity of the food eaten to satiety [$F(4,44) = 2.5$; $p = 0.055$, not illustrated].

Change in the Pleasantness and Intensity of the Smell of a Food Smelled for 5 Min

It is shown in Fig. 9 that the pleasantness of the smell of banana decreased considerably when it was smelled for 5 min (by 12 mm on the 100 mm visual analog scale), and that the other foods did not show decreases in pleasantness. It is also shown in Fig. 9 (right) that the pleasantness of the smell of chicken decreased a little when it was smelled, and that this was a greater decrease than for any of the other foods. The change in rating shown is the difference between the initial pleasantness of the stimulus at the beginning of the experiment, and its pleasantness at the end of the smelling. A 2-way within-subjects ANOVA in which the first (sensory) factor was the test food smelled and the second (satiating) factor was the food smelled for 5 min showed a significant interaction, $F(4,44) = 3.76$, $p = 0.01$. This result shows that olfactory sensory-specific satiety can be produced by smelling a food for about as long as it is in the mouth in a meal, although the effect is, as might be expected, not as large as when the food is eaten to satiety.

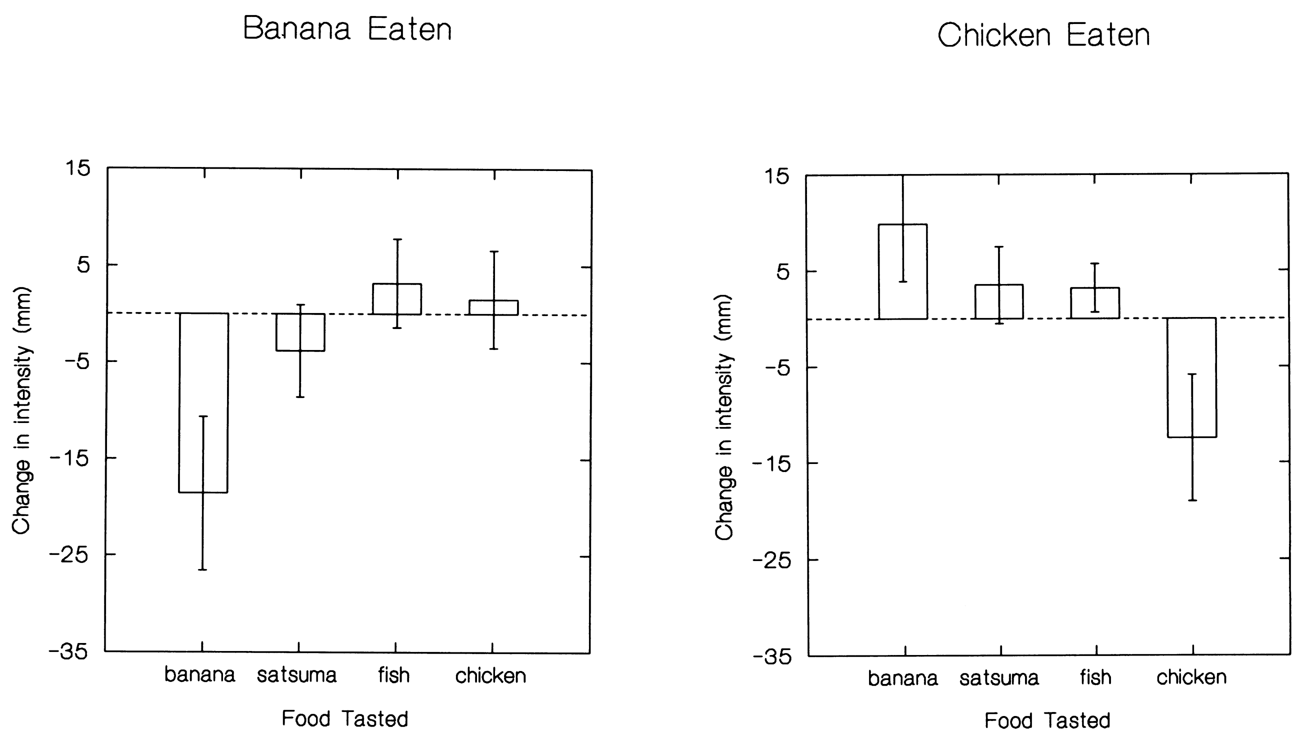

FIG. 6. The change in the intensity of the taste of 4 different foods after eating banana (left) or chicken (right) to satiety.

In contrast, it is shown in Fig. 10 that, although there was some decrease in the intensity of the smell of banana when it was smelled for 5 min, there was no specific decrease in the pleasantness of the smell of chicken when it was smelled for 5 min. Overall, the interaction term in the 2-way ANOVA was statistically significant, $F(4,44) = 3.06$, $p = 0.026$.

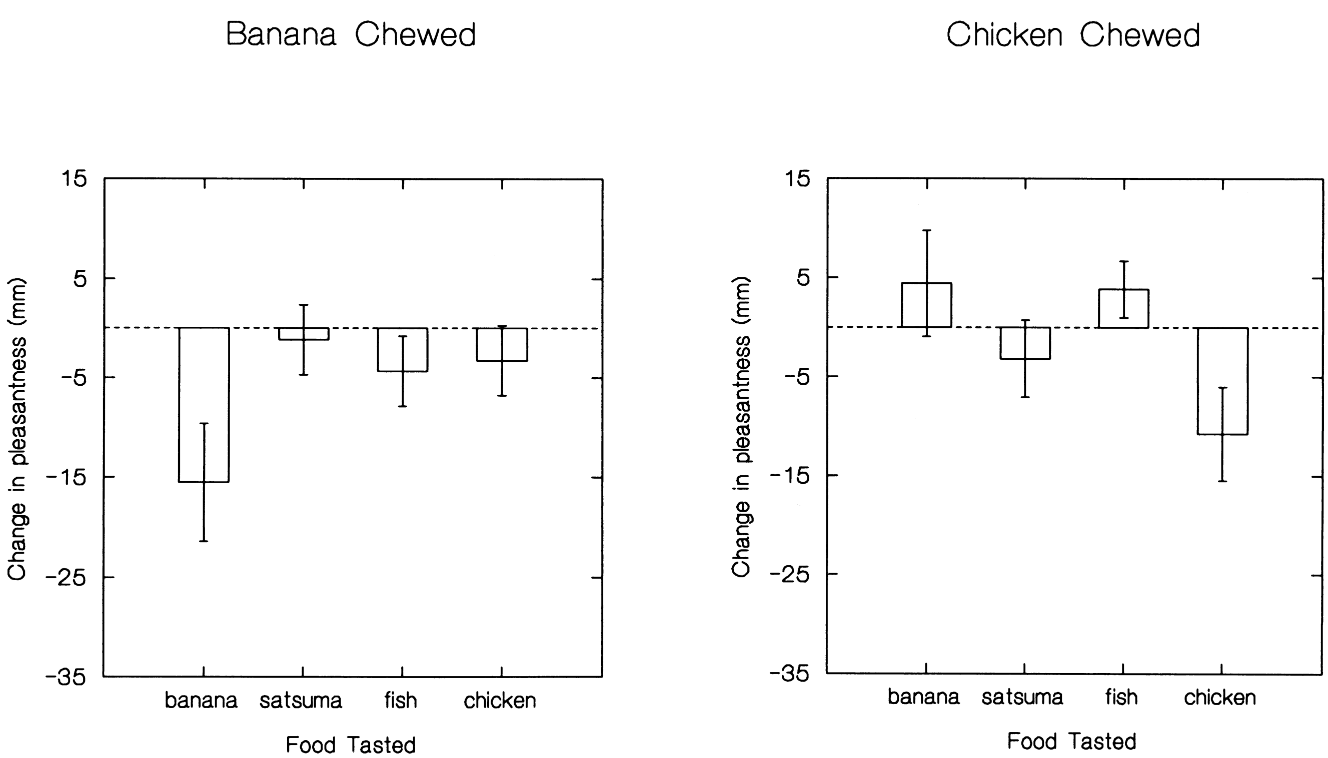

FIG. 7. The change in the pleasantness of the taste of 4 different foods after chewing banana (left) or chicken (right) for 5 min.

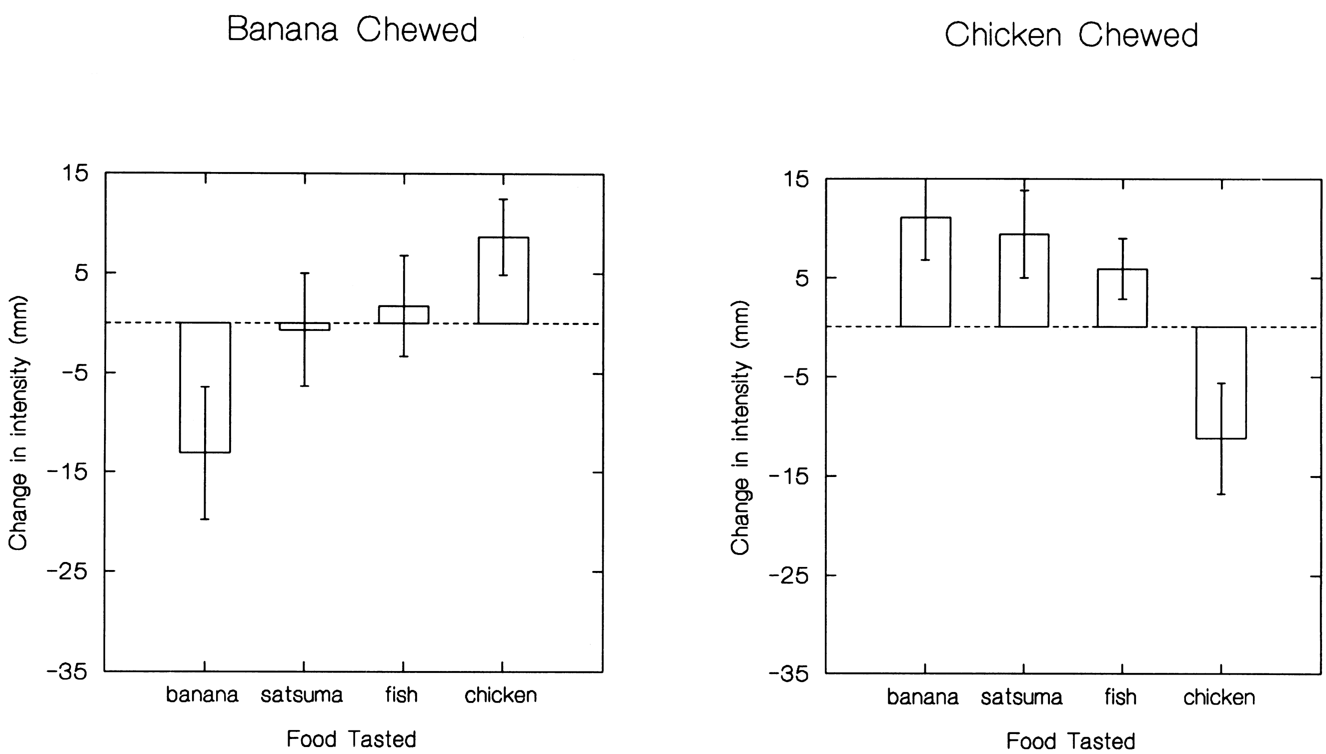

FIG. 8. The change in the intensity of the taste of 4 different foods after chewing banana (left) or chicken (right) for 5 min.

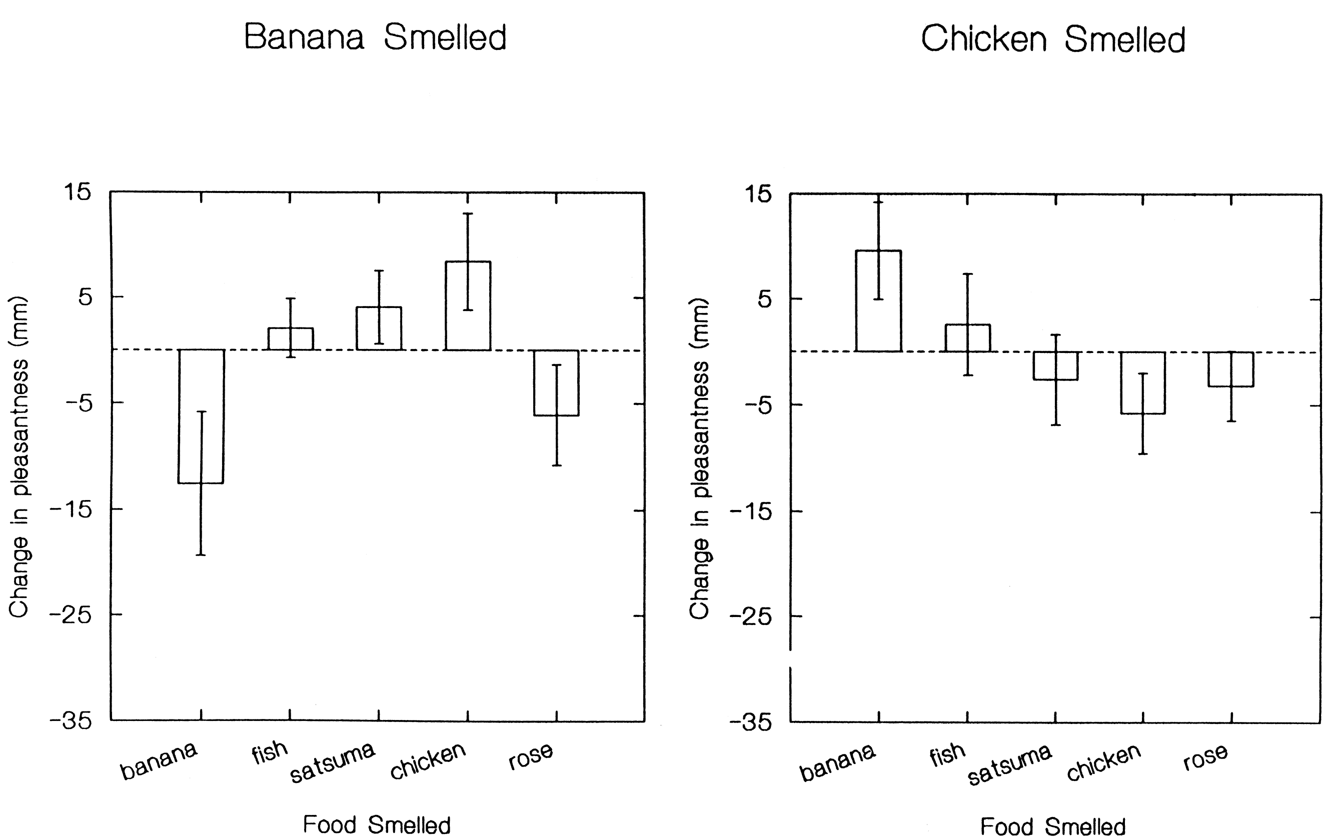

FIG. 9. Experiment 2: the change in the pleasantness of the smell of 5 different odours after smelling banana (left) or chicken (right) for 5 min.

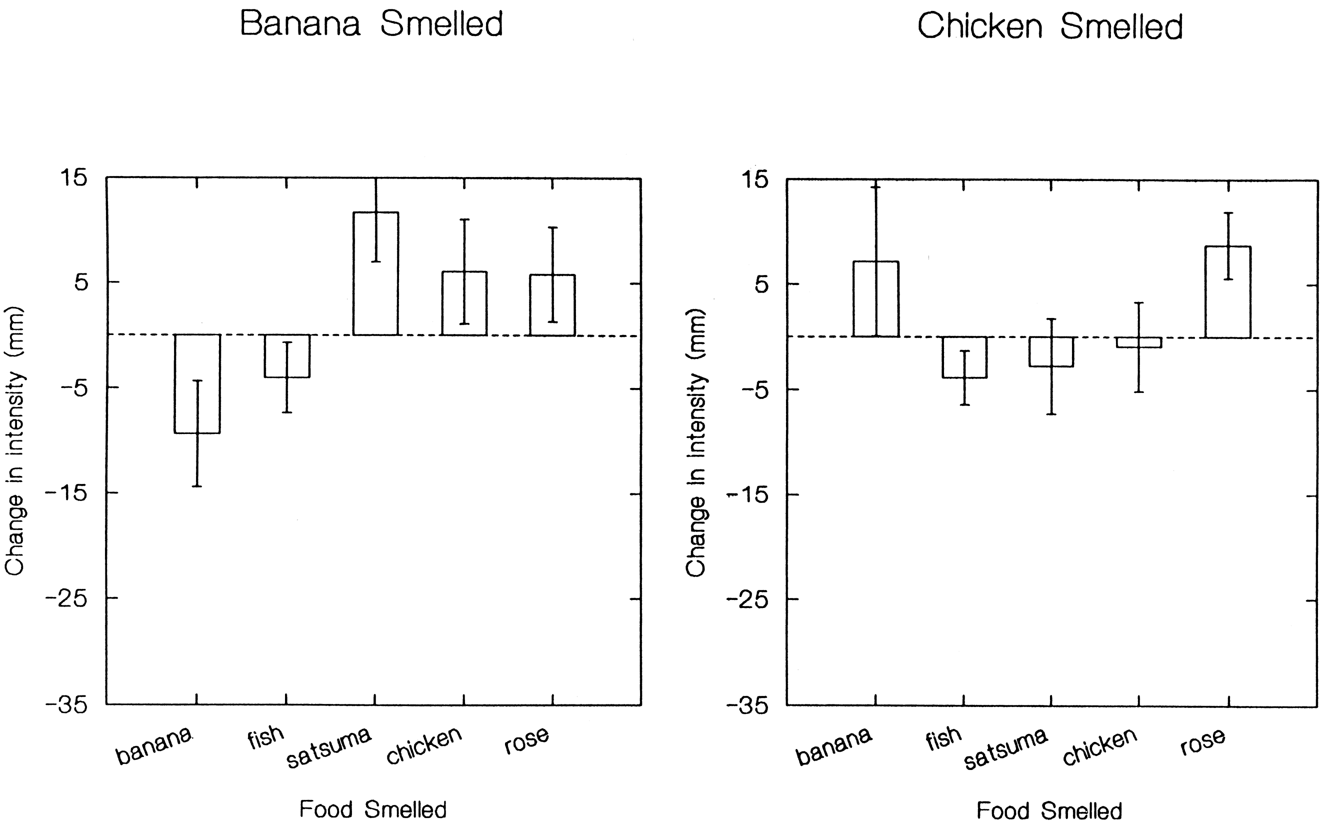

FIG. 10. Experiment 2: the change in the intensity of the smell of 5 different odours after smelling banana (left) or chicken (right) for 5 min.

Change in the Pleasantness and Intensity of the Taste of a Food Eaten to Satiety

The results for pleasantness were very similar to those of Experiment 1, and are shown in Fig. 11. The interaction term was highly significant, $F(3,33) = 8.861$ $p = 0.0004$). The reason for illustrating this is that, for comparison, in Fig. 12 the more usual result in this type of experiment for the intensity of taste is shown. In Fig. 12, it is seen that there is no specific decrease in the intensity of the food eaten to satiety, and the interaction term in the ANOVA was not significant, $F(3,33) = 1.56$; $p = 0.22$.

Change in the Pleasantness and Intensity of the Taste of a Food Smelled for 5 Min

The data shown in Fig. 13 show that simply smelling a food for 5 min was not sufficient to produce sensory-specific satiety for the rated pleasantness of the taste of the food. The interaction term in the ANOVA was not significant, $F(3,33) = 2.15$; $p = 0.11$. There was, similarly, no effect on the rated intensity of the taste (not illustrated).

GENERAL DISCUSSION

The results of Experiment 1 show that olfactory sensory-specific satiety can be produced by eating a food to satiety. The experiment showed that it was a change in the pleasantness of an olfactory stimulus by asking the subject to rate the odour that was sniffed from a cup, and not placed in the mouth.

The results of Experiment 1 also show that olfactory sensory-specific satiety can be produced by placing samples of the food in the mouth without swallowing for approximately as long as it would have been in the mouth when it was eaten to satiety. Further, the results of Experiment 2 show that partial olfactory sensory-specific satiety can be produced by smelling the food for approximately as long as it would have been in the mouth when it was eaten to satiety. These results show that, at least partial, olfactory sensory-specific satiety does not require food to enter the gastrointestinal system, and does not depend on the ingestion of calories.

The olfactory sensory-specific satiety is larger after eating to satiety than after chewing the food for 5 min. We remind the reader that the measure of the change of pleasantness after eating to satiety is the difference between the initial rating at the start of the experiment, and that after eating to satiety which, of course, took place after chewing for 5 min. Thus, the larger effect measured after eating to satiety than after only chewing for 5 minutes is likely to be larger partly due to the fact that the food is in the mouth producing olfactory and taste stimulation a second time, and partly because food does then enter the gut, allowing factors such as gastric distension and intestinal stimulation by food to add to the sensory stimulation-mediated satiety to produce full satiety. It was not a primary aim of this experiment to compare directly the magnitude of just eating to satiety vs. just chewing for 5 min: the experiment was designed to allow measurement of whether chewing alone or smelling alone could produce any sensory-specific satiety. It is known that, in primates, full satiety requires both gastric distension and intestinal stimulation by food (7). The olfactory sensory-specific satiety also appears to be larger when the food is placed in the mouth, so that it can be tasted and smelled, than when it is only smelled (as in Experiments 1 and 2, food-chewed and food-smelled conditions). This may be because the olfactory stimulation is more

FIG. 11. Experiment 2: the change in the pleasantness of the taste of 4 different foods after eating banana (left) or chicken (right) to satiety.

FIG. 12. Experiment 2: the change in the intensity of the taste of 4 different foods after eating banana (left) or chicken (right) to satiety.

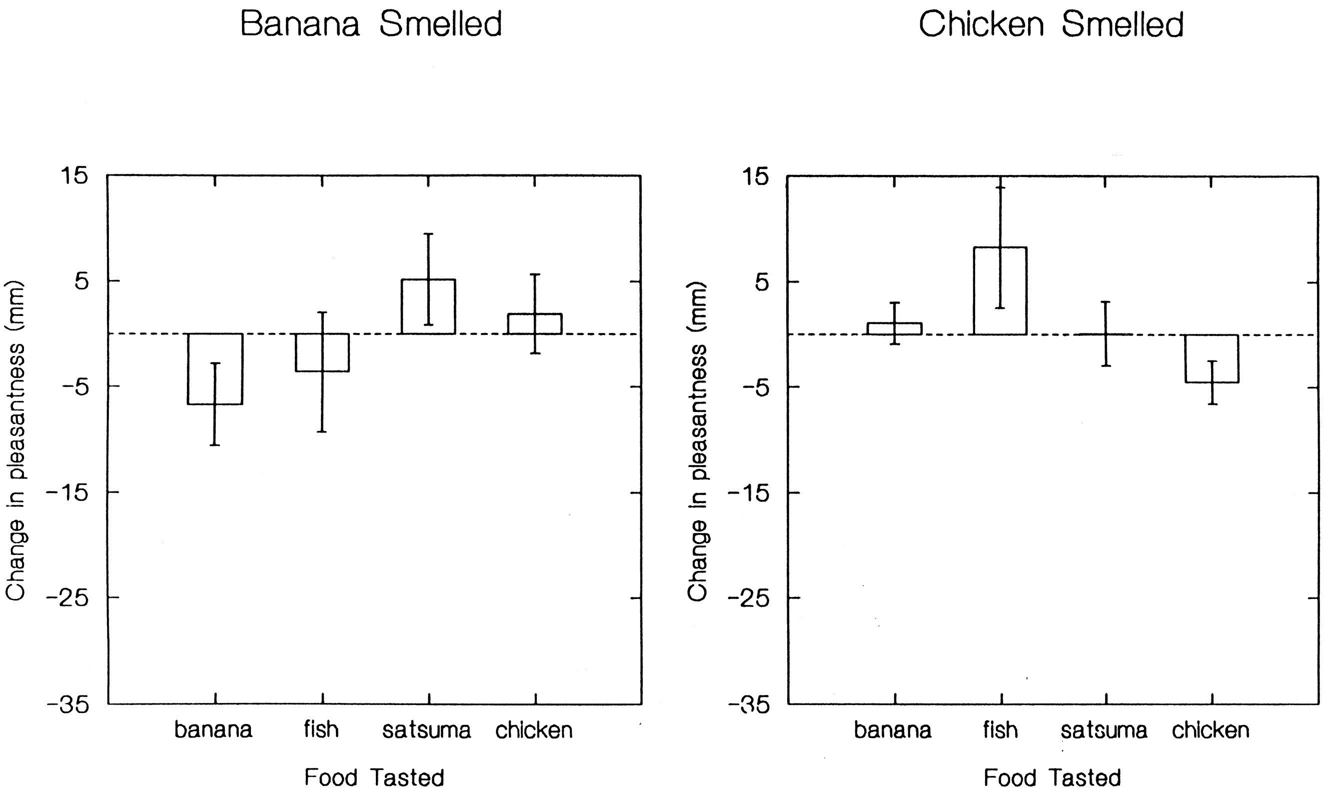

FIG. 13. The change in the pleasantness of the taste of 4 different foods after smelling banana (left) or chicken (right) for 5 min.

effective when the food is in the mouth. It may also be because bimodal olfactory and taste neurons that are known to be present in the orbitofrontal cortex (33) may be affected by purely gustatory inputs (35), so that the olfactory response of these neurons may be reduced as part of the process by which they become less responsive after satiety to a taste. An implication of these results is that the mechanism that produces sensory-specific satiety may be dependent primarily on activity in the processing systems for olfactory and taste information in the brain, rather than depending on interaction with gastrointestinal feedback or energy monitoring signals for the computations, which are considered below.

One novel aspect of the present experiments was that we ensured that it was an olfactory stimulus that was being rated to assess sensory-specific satiety for olfactory processing, by asking subjects to rate the odour produced by the food being smelled in a cup. Another novel aspect was that the contributions of oropharyngeal factors to the olfactory and taste sensory-specific satiety were assessed by the chewing and smelling conditions in Experiments 1 and 2, respectively. We can add to the findings described here in the following way, based on experiments run with a similar experimental design, but different stimuli and different subjects. First, sensory-specific satiety for the flavour of liquid stimuli, such as coffee and orange juice, can be produced not only by ingestion of them to satiety [10 subjects, $F(1,9) = 38$; $p = 0.003$], but also by rinsing the mouth with changing aliquots for 5 min and not swallowing, $F(1,9) = 12.4$; $p = 0.007$. Moreover, in this experiment we ran an unexpected second course after the rinsing, and found that more was ingested if the second course was different from what had been rinsed, $F(1,9) = 8.54$; $p = 0.016$, thus demonstrating that the sensory-specific satiety we describe here measured by pleasantness changes can influence also the amount consumed. (The intake in the ''variety'' condition was 137% of that in the ''same'' condition.)

The results show that, for taste (or flavour, that is a rating of ''taste'' when the food is in the mouth producing both olfactory and gustatory inputs), the decrease in pleasantness can occur without much change in intensity (Experiment 2), or may be associated with a significant change in intensity. Part of the variability of the intensity results may be due to how well the subjects are able to rate pleasantness separately from intensity. Most of our subjects are able to do this (28), but some who can rate pleasantness well may tend to rate the intensity as less when the pleasantness moves towards neutral. What is clear is that the changes in pleasantness are highly reliable and replicable in these experiments, whereas any changes in intensity are smaller and not very reliable. This implies that the change in pleasantness is not due to any change in intensity that may occur, and where the change in intensity might be produced, for example, by peripheral sensory adaptation. Further evidence for the view that altered representation of intensity does not produce the change in pleasantness is that the correlation between the change in pleasantness and the change in intensity was low (0.238 for the banana and chicken ratings). Further evidence is that, in any case, the relation between pleasantness and intensity for different concentrations of tastants is not very close, with pleasantness remaining relatively unaffected despite large changes in concentration that produce large differences in intensity ratings (28).

For olfactory sensory-specific satiety, some decrease in the intensity of the odour eaten to satiety was found, but was, again, not as large as, nor as reliable as the change in pleasantness (see, for example Figs. 1–4). This implies that also in the olfactory system the computation of the pleasantness of an odour is separate from the computation of its intensity and identity.

For taste, the actual computation of the pleasantness of a taste appears to be performed in the caudolateral orbitofrontal cortex. The evidence for this is that in the primary taste cortex of primates (in the rostral insula and adjoining frontal operculum), neurons respond to tastes independently of hunger and of sensory-specific satiety. Here, the intensity of a taste could be represented, but not its pleasantness (29,36). In contrast, one synapse further on in the secondary taste cortex, the responses of taste neurons decrease to zero to the food with which the monkey is fed to satiety, and this is a sensory-specific effect (21,24). One reason for keeping these computations separate is that it may be biologically adaptive to recognise a taste even if we are not hungry. We have suggested a simple neurophysiological mechanism elsewhere for this computation of gustatory sensory-specific satiety, involving declining activity of orbitofrontal neurons but not earlier neurons in the pathway over a period in the order of 5 min of continuing sensory stimulation by the tastant (21,24,32).

For smell, the evidence from neurophysiology is less complete than for the taste system. It is now clear that olfactory sensory-specific satiety is represented in the orbitofrontal cortex, where the secondary and tertiary olfactory cortices are located (5,6,21,24), because the responses of many orbitofrontal cortex neurons show a sensory-specific decrease in responsiveness to the odour of the food with which the monkey has been fed to satiety (6). What is less clear is whether or not this effect occurs earlier in sensory processing in primates in, for example, the primary olfactory (pyriform) cortex, or even earlier in processing, in the olfactory bulb, as has been suggested in rats (11,12). The experiments described here do at least indicate that, in primates, the intensity of an odour can be rated relatively normally even when the pleasantness has been reduced to neutral, and this would be consistent with processing of the identity and intensity of odours before the motivation-related pleasantness or hedonics of the odour is computed.

The experiments described here have implications for understanding the mechanisms that control food intake, and how to control food intake. One implication, already addressed, is that one contribution to the mechanisms of satiety is a sensory-specific decrease in neuronal activity produced by a food in a part of the system in which the pleasantness of the taste or smell is represented. This contribution can be computed independently of gut feedback from food entering the stomach and beyond. Another implication is that, at least within the single-meal condition, the intake of foods can be limited by presenting the same odour for a period of at least several min. (This could occur before eating starts, or during the initial part of the meal. Of course, the initial reaction is well known to be incentive motivation, but it is suggested that that effect turns to a sensory-specific decrease in pleasantness after a number of minutes.) An implication of this point is that slow eating, by allowing olfactory and gustatory sensory-specific satiety time to build up, may tend to reduce meal size. Conversely, odour variety in a meal can be expected to enhance intake, because of the operation of the mechanism that is at least partly sensory-specific. A final point to be considered and evident in many of the Figures in this paper is that, although eating one food to satiety can decrease its pleasantness, this can not only decrease the pleasantness of similar foods, but also increase the pleasantness of dissimilar foods (13).

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