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Selective Removal of a Target Stimulus Localized by Taste in Humans

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Abstract

Recent studies have shown that people can localize a punctate gustatory stimulus on the lingual epithelium in the absence of discriminative tactile cues. The present studies examined the human ability to localize taste sensations on the tongue and to use this information to remove selectively a target stimulus (a flavored, 1 cm³ gelatin cube) from the mouth when presented with non-target distractors that vary in number and taste. Findings indicate that humans are capable of localizing and removing either an aversive or an appetitive gustatory target from a field of tactile distractors via taste sensations alone, although this ability diminishes as the number of distractors increases (implicating serial searches, rather than parallel). In addition, humans can localize and selectively remove a target taste in the presence of distractors of another distinct taste quality. Under these conditions performance is either unaffected or reduced, which indicates that contrast with the distinct taste of the distractors does not enhance performance. Humans also are capable of removing a nearly tasteless cube from a field of flavored distractors, but this is clearly a more difficult task, suggesting that 'tactile capture' of taste occurs for the tasteless target cube and interferes with the localization of taste. Finally, perceived suprathreshold stimulus intensity did not seem to be related to the ability to localize and remove a target stimulus via taste sensations and failed to account for variations in performance across individuals.

Introduction

Humans selectively remove non-food portions of an oral bolus rather than expectorate it all and lose potential calories. For example, a bite of fish that contains a bone will most frequently result in the selective removal of the bone while retaining and swallowing the remaining flesh. In this case, localization of the offending item occurs via the tactile sense. Such behavior has obvious beneficial energetic consequences in that nutrition is maximized for effort expended to obtain the fish. We ask whether taste localization may similarly benefit humans by aiding in oral bolus manipulation, identification and intra-oral localization. To determine this we first must find out whether taste can be localized and selectively removed from people's mouths.

Early studies on human taste localization (Von Skramlik, 1924; Von Békésy, 1964), led researchers to believe that humans were capable of localizing taste sensations. However, these studies failed to account sufficiently for discriminative tactile cues and remain inconclusive by today's psychophysical standards. This, combined with clinical observations, has allowed others to argue that gustatory sensations are not themselves localizable and that localization is instead dependent upon the stimuli's accompanying tactile component (Miller and Bartoshuk, 1991; Todrank and Bartoshuk, 1991).

Recent studies have shown that people can indeed localize a punctate gustatory stimulus on the lingual epithelium in the absence of discriminative tactile cues. Shikata *et al.* (Shikata *et al.*, 2000) designed a yoked stimulator and an experimental procedure that controlled for tactile cues and presented one of four taste solutions (sodium saccharine, sodium chloride, citric acid, or quinine hydrochloride) and a blank solution simultaneously to the tip of the tongue. They found that in the absence of discriminative tactile cues, individuals could lateralize all four taste stimuli. Furthermore, their ability to localize the taste varied as a psychometric function of the stimulus concentration. Participants were unable to lateralize the highest tested concentrations of taste solutions presented under the lip (a non-gustatory surface), while lateralization performance was at 100% at the tip of the tongue (a gustatory surface). Other studies have indicated that people also are capable of lateralizing a target taste when a different taste solution, rather than a blank solution, is presented simultaneously (Shikata *et al.*, 1997; Breslin *et al.*, 1998).

To determine the potential functionality of such localization abilities, these studies investigated whether humans can use gustatory spatial information to identify and selectively remove a target taste stimulus from the mouth when simultaneously presented with distractors that are somatosensorily identical. We also investigated the effects of (i) taste quality (bitter compared to sweet), (ii) the presence of more than one taste quality, (iii) the perceived

intensity of the stimuli on people's ability to remove oral targets using taste cues and (iv) the influence of manipulation difficulties on response time.

Experiment 1: influence of number of distractors

The purpose of this experiment was to determine if information gained from the human ability to localize taste sensations on the tongue can be used to remove selectively a stimulus from the mouth when presented with one to three somatosensorily identical non-target distractors and if the number of distractors influenced this ability.

Materials and methods

Subjects

Twelve paid volunteers (five men, seven women, 15–30 years old) were recruited from Monell Chemical Senses Center employees. They were instructed not to eat or drink anything but water for the hour preceding each session. All procedures were approved by the Human Subjects Committee, IRB at the University of Pennsylvania.

Materials

Gelatin cubes (1 cm^3) were cut from a 1 cm thick sheet of gelatin made from 116 g/l edible gelatin (bloom type B, Vyse Gelatin Co., Schiller Park, IL). For bitter-tasting gelatin cubes, 5 mM quinine hydrochloride dihydrate (Fluka, Milwaukee) and ~16 drops/l red and/or blue food coloring (Durkee Specialty Brands, San Francisco, CA) were added. In addition, an isotonic saline rinse (100 mM NaCl, Fisher Scientific, Fair Lawn, NJ) was used for rinsing during the interstimulus interval.

Test procedure

The participant received two to four gelatin cubes, only one of which was bitter flavored and colored (to allow for visual identification) on any trial. Stimulation was conducted in the following manner.

A flavored cube of gelatin (target) and one to three unflavored gelatin cubes (blanks) were presented in a disposable 1 oz. medicine cup. After shaking the covered cup, the participant placed all the cubes under the tongue while their eyes were closed to eliminate visual cues. At the experimenter's signal, ~1–2 s later, the participants slid the cubes out from beneath the tongue (a non-gustatory surface), pushed them forward simultaneously, gently pressed them into the inside surface of the front teeth with the leading edge of the tongue and held the cubes stationary. This process initiated gustatory stimulation at the tip of the tongue where the bitterness from the target cube was easily perceived. As quickly as possible, and in no more than 10 s, the participant spat the suspected 'bitter target' cube into another disposable cup. The use of movement-based strategies to select the target cube was forbidden.

The time it took the participant to respond was recorded to the nearest second, starting with the experimenter's signal and ending with the expectoration of the suspected target cube. By both minimizing the movement of the cubes across gustatory surfaces and by minimizing the time individuals retained the cubes in the mouth, the efficacy of movement-based strategies to taste localization was greatly reduced. In other words, participants did not have time to evaluate each individual cube with the very tip of the tongue, slide the cubes over the tongue one at a time, or adopt some other movement-based strategy for target identification that did not rely upon taste localization. Subjects were instead forced to hold the tongue still against the aligned cubes, as they had been instructed. In addition, by limiting the time the cubes were held in the mouth, complications from the gelatin melting and consequent taste diffusion were minimal, and remained so up to the 10 s maximum. The high stiffness of the gelatin, which remained firm even at room temperature, also helped to minimize melting and consequent taste diffusion.

After identification of the removed cube as either the flavored cube (colored) or an unflavored cube (uncolored), the participant then expectorated the remaining cubes. If no cubes had been expectorated after 10 s (which happened in only two trials throughout the 1080 experimental trials of Experiment 1), the participant was instructed to expectorate all the cubes and any cube selected was considered incorrect. To suppress the build up of bitterness, a 60 s interval passed between presentations, during which the participant rinsed at least three times with saline solution (Breslin and Beauchamp, 1995) and twice with distilled water, in that order.

In a given session, each person completed 30 experimental trials in ~45 min. Each individual participated in one training session (identical in structure to subsequent sessions) and three experimental sessions, resulting in 90 experimental trials. In the training session, in blocks of ten trials each, participants distinguished targets from one, two and three distractors, in that order. For the remaining three sessions, the order of the ten-trial blocks was counter-balanced. Of the 12 people tested, four began their first experimental session with one blank, four with two blanks and four with three blanks.

Data analysis

For the one, two and three distractor(s) conditions, the criteria for an individual to be regarded as capable of discriminating the target cube were set at 21, 15 and 12 correct rejections out of 30, respectively (one-tailed binomial test, $P < 0.05$). The group mean % correct (±SE) for each condition was calculated. The % correct value for each subject in each condition was converted to a d' value, a measure of stimulus distinguishability, by using the table in Hacker and Ratcliff (Hacker and Ratcliff, 1979). Comparisons of group performance across conditions were made using ANCOVA. When ANCOVA detected differ-

ences between conditions, Scheffe's test was used to evaluate which conditions were responsible. All data are reported as means ± SE.

Results

General findings

All participants performed significantly above chance (one-tailed binomial test, $P < 0.05$) when one or two distractors were presented, and 11 of 12 participants performed significantly above chance (one-tailed binomial test, $P < 0.05$) when three distractors were presented (see Figure 1, inset). People tended to make more errors with each increase in the number of cubes (see Figure 1, inset), but despite this there was no significant change in discriminability as measured by d' (ANCOVA, $P = 0.664$). However, as can be seen in Figure 1, response times significantly lengthened as the number of cubes increased (ANCOVA, $P < 0.01$; Scheffe's test, $P < 0.05$).

The influence of intensity

At the completion of the first experiment, the question of whether the perceived intensity of the bitter cubes had an influence on discriminatory ability was raised. Ten of the original 12 participants (three men, seven women) were able to return for a single session for the assessment of perceived intensity. Participants were given uncolored gelatin cubes, five of which were plain gelatin and ten of which contained 5 mM quinine–HCl, in a unique restricted random order (bitter cubes were not presented more than four times in a row, blanks were not presented more than twice in a row). The participants were asked to rate the intensity of bitterness of the cubes within the context of all the bitter sensations they had experienced in their life on the labeled magnitude scale (Green *et al.*, 1993, 1996). Although this is not the usual anchor for the top of the scale and consequently the ratings do not approximate magnitude estimation data, we felt that placing bitterness in the context of all bitters, rather than all oral sensations, would aid in determining relative (but not absolute) differences across individuals by expanding the portion of the scale used. A 60 s interval passed between ratings and the rinsing regime was matched to that used in the first experiment.

Bitter cubes were rated on average as moderately bitter (15.7 ± 2.9), while the neutral cubes were found to be barely detectable (0.4 ± 0.1). To control for any relative differences in scale usage or in scale anchoring due to personal experience or sensitivity, the average perceived signal strength and the average signal-to-noise ratio were calculated. Average perceived signal strength was calculated for each individual by subtracting the average bitterness intensity of the blanks from the average bitterness intensity of the bitter cubes. The average perceived signal-to-noise ratio was determined for each individual by dividing the average bitter intensity of the bitter cube by the average bitter intensity of the neutral cubes. No significant correlations were found between signal
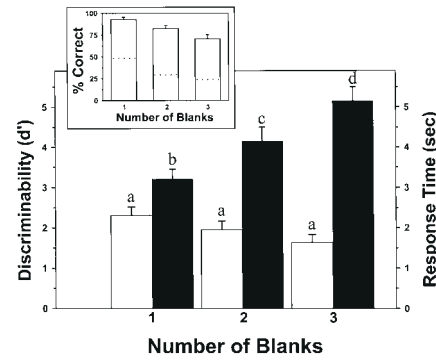

Figure 1 Main figure—average discriminability (d') and average response time (s), Experiment 1. The mean d' value ± SE (open bars) and the mean response time ± SE (closed bars) for each stimulus set (one, two and three blanks) was taken across all 12 participants. Values that are not significantly different from each other ($P > 0.05$, according to ANCOVA and Scheffe's test) are indicated by the same letter. Inset—average % correct, Experiment 1. The mean % correct (±SE) for each condition (one, two or three blanks) was taken across all 12 participants. The dotted lines indicate chance level performance for each condition.

strength or signal-to-noise ratio and number correct, d', or reaction time for any of the three conditions. Thus, it seems unlikely that individual differences in perceived intensity had a major influence on the discriminative ability of each person.

The influence of manipulation difficulties

To check whether the increase in response time with cube number was due simply to increased difficulty in cube manipulation, a single control session was conducted with six of the 12 original subjects (one man, five women). Here, subjects were presented with two, three or four unflavored cubes (1 cm^3) in the same fashion as before, but instead of spitting out the bitter target cube, they were asked to spit out the unflavored cube from a designated position. Positions were labeled in ascending order from left to right, with two, three or four positions being possible, depending upon the condition; an illustration of these positions was placed in front of subjects during the procedure. Subjects began as before by placing the cubes under the tongue. At the experimenter's signal, which was to simply state the position from which the subject was to remove the stimulus, the timer was started. The subject would then line the cubes up on the inside of the teeth as before and expectorate the cube from the indicated position. The time it took the subject to accomplish the task was recorded. The position indicated by the experimenter was counter-balanced across the 12 trials for each condition, and the starting condition was counter-balanced across subjects.

As can be seen in Figure 2, response time was significantly longer for the four-cube condition, although there was no significant difference between the two- or three-cube conditions (ANOVA, $P < 0.01$; Scheffe's test, $P < 0.05$). The increase in response time with cube number suggests that
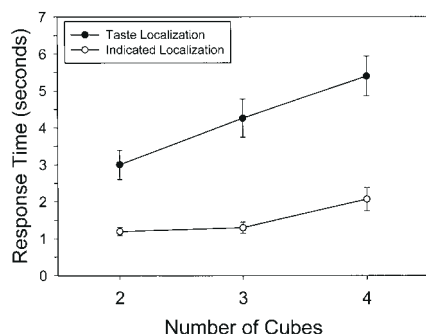
Figure 2 Average response time and number of cubes, Experiment 1. The mean response time ± SE for each condition (two, three and four cubes) was taken across six of the 12 original participants when the subjects selected the target cube via taste localization (closed circles) and via indicated location (open circles).

subjects were following instructions and expectorating the designated target rather than expectorating a random cube. This small increase in response times, however, does not account for the larger differences found when subjects were using taste localization to select the target cube, and significant increases in response times with increasing cube number were still found after this covariance was taken into consideration (ANCOVA, $P < 0.05$; Scheffe's test, $P < 0.05$).

Experiment 2: influence of taste quality

This experiment investigated multiple hypotheses using different sets of flavored gelatin cubes. First, we investigated whether people could selectively reject an appetitive (sweet), as opposed to an aversive (bitter), stimulus from the mouth when presented with non-target distractors. Second, we investigated if individuals would be able to localize a target taste in the presence of distractors of another distinct taste, and selectively reject (i) a less palatable target (a bitter cube from three salty cubes) or (ii) a more palatable target (a sweet cube from three bitter cubes). Finally, the role of 'tactile-capture' of taste (Todrank and Bartoshuk, 1991) on localization performance was investigated by having participants attempt to localize and remove a blank target cube from three sweet distractor cubes.

Materials and methods

Subjects

Twelve paid volunteers (six men, six women, 16–31 years old) were recruited from Monell Chemical Senses Center employees. Seven of the subjects (five women, two men) had participated in the first experiment. As in the first experiment, they were instructed not to eat or drink anything but water for the hour preceding each session. All procedures were approved by the Human Subjects Committee, IRB at the University of Pennsylvania.

Materials

As in Experiment 1, 1 cm³ gelatin cubes (116 g/l edible

gelatin, bloom type B, Vyse Gelatin Co., Schiller Park, IL) were cut from 1 cm thick gelatin sheets. The blank and bitter cubes were identical to those used in the previous experiment. The sweet cubes were made by adding 75 mM sodium cyclamate (Sigma, St Louis, MO), while the salty cubes were made by adding 75 mM sodium chloride (Fisher Scientific, Fair Lawn, NJ). Each flavor was given a distinct color by the addition of food coloring to allow for visual identification of the cube flavor (Durkee Specialty Brands, San Francisco, CA). All the flavored stimuli could easily be perceived at the tip of the tongue.

Test procedure

Stimulus delivery and response scoring were conducted in the same manner as the previous experiment. Four cubes were used in all stimulus sets. As before, if no cubes had been expectorated after 10 s (which happened in only six trials throughout the 1440 experimental trials in Experiment 2), the participant was instructed to expectorate all the cubes and any cube selected was considered incorrect. A 60 s interval passed between trials, and the participant followed a rinsing regime dependent upon the stimulus set during this interval. For sets that included bitter gelatin cubes, to suppress the build up of bitterness, the participants rinsed at least three times with a 100 mM saline solution and twice with distilled water, in that order, as they had in Experiment 1. For sets that did not include bitter gelatin cubes, the participants simply rinsed four times with distilled water.

In a given session, each individual completed 30 experimental trials in ~45 min. Each participated in one training session (which consisted of five trials of each stimulus set) and four experimental sessions, resulting in 120 experimental trials each. With the exception of the training session, participants assessed only one stimulus set in a given session and individuals warmed up with at least three unrecorded trials (occasionally, one or two additional practice trials were requested) before data collection began. The order of the stimulus sets was counter-balanced across individuals. Of the 12 participants tested, three began their first experimental session with one sweet and three blanks, three with one bitter and three sweet cubes, three with one salty and three bitter cubes, and three with one blank and three sweet cubes.

Data analysis

For all four stimulus sets, the criterion for an individual to be regarded as capable of discriminating the target cube was set at 12 correct rejections out of 30 (one-tailed binomial test, $P < 0.05$). The group mean % correct (± SE) for each stimulus set was calculated. The response time geometric mean was computed for each individual, as was the group mean (±SE) of this measure. The % correct value for each subject in each condition was converted to d' values, a measure of stimulus distinguishability, by using the table in Hacker and Ratcliff (Hacker and Ratcliff, 1979). Comparisons of group performance across conditions were made

using ANCOVA. When ANCOVA detected differences between conditions, Scheffe's test was used to evaluate which conditions were responsible. All data are reported as means ± SE.

Results

General findings

All performed significantly above chance (one-tailed binomial test, $P < 0.05$) when the target was sweet and the three distractors were blanks, as well as when the target was salty and the three distractors were bitter (see Figure 3, inset). In contrast, only ten of the 12 participants were significantly above chance performance when the target was bitter and the three distractors were sweet, and only eight of the 12 participants were significantly above chance when the target was the blank and the three distractors were sweet (one-tailed binomial test, $P < 0.05$).

Individuals varied greatly in their performance across conditions. For example, one made over 80% correct responses in three of the four conditions, but fell to chance performance in the 'three sweet, one blank' condition. In contrast, another participant performed less well in three of the four conditions, but remained above chance level performance in the 'three sweet, one blank' condition. However, on average, performance was above chance level for all stimulus sets (see Figure 3, inset).

Across stimulus sets, distinguishability as measured by d' varied significantly (ANCOVA, $P < 0.001$). Scheffe's test revealed that there was no significant difference in distinguishability between the 'three blanks, one sweet' and the 'three bitter, one salty' stimulus sets, nor between the 'three sweet, one bitter' and the 'three sweet, one blank' stimulus sets, although significant differences were found between all other stimulus sets ($P < 0.05$; see open bars in Figure 3). Also shown in Figure 3, by the closed bars, the response times were found to vary significantly (ANCOVA, $P < 0.05$) across certain stimulus sets, with significant differences found between the 'three blank, one sweet' and both the 'three sweet, one bitter' and the 'three sweet, one blank' stimulus sets, and between the 'three bitter, one salty' and the 'three sweet, one blank' stimulus sets (Scheffe's test, $P < 0.05$). It can be seen from Figure 3 that, as performance declined, response time increased, in accordance with the findings of Experiment 1.

The influence of intensity

The perceived intensities of all the stimuli used in the second experiment were assessed by all 12 participants. They were given 35 uncolored gelatin cubes: five unflavored cubes, ten cubes containing 5 mM quinine–HCl, ten cubes containing 75 mM sodium cyclamate and ten cubes containing 75 mM sodium chloride. As for the previous experiment, the cubes were presented in a unique restricted random order (no one flavor was presented more than three times in a row and blanks were not presented more than twice in a row). They
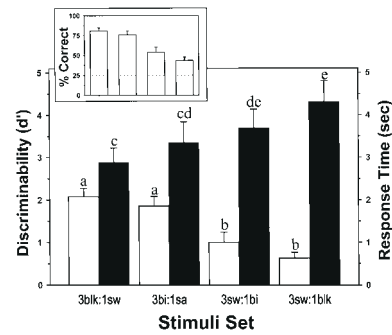

Figure 3 Main figure—average discriminability (d') and average response time (s), Experiment 2. The mean d' value ± SE (open bars) and the mean response time ± SE (grey bars) for each stimulus set was taken across all 12 participants. Values that are not significantly different from each other ($P > 0.05$, according to ANCOVA and Scheffe's test) are indicated by the same letter. Conditions are identified as follows. 3blk: 1sw = three blanks, 1 sweet; 3bi: 1sa = three bitter, one salty; 3sw: 1bi = three sweet, one bitter; 3sw: 1blk = three sweet, one blank). Inset—average % correct, Experiment 2. The mean % correct (±SE) for each stimulus set was taken across all 12 participants. The dotted lines indicate chance level performance. Conditions follow the same order as in the main figure.

were asked to rate the taste intensity of the cubes within the context of all the taste sensations they had experienced in their lives on the labeled magnitude scale (Green *et al.*, 1993, 1996). A 60 s interval passed between ratings and the rinsing regime was matched to that already described for the second experiment.

Ratings for the cubes indicated that the bitter cubes were moderately strong (on average 20.8, with a standard error of 4.5), sweet cubes were moderately weak (13.3 ± 2.4), salty cubes were fairly weak (7.5 ± 1.7) and the neutral cubes were barely detectable (1.0 ± 0.4). To control for any relative differences in scale usage or in scale anchoring due to personal experience or differences in sensitivity, the average perceived signal strength and the average signal-to-noise-ratio were calculated. Average perceived signal strength was determined for each individual by subtracting the average taste intensity of the distractor cubes from the average taste intensity of the target cubes for each stimulus set. The average perceived signal-to-noise ratio was determined for each individual by dividing the average taste intensity of the target cube by the average taste intensity of the distractor cubes for each stimulus set. No significant correlations were found between signal strength or signal-to-noise ratio and number correct, d', or reaction time for any of the stimulus sets. Thus, it seems unlikely that individual differences in perceived intensity had a major influence on the discriminative ability of each person.

Discussion

Experiment 1 demonstrated that humans are able to localize and selectively remove a bitter-tasting target from a field of tactile distractors using taste sensations alone. This finding has parallels in the gustatory and ingestive behavior of other

vertebrates (e.g. fish) (Lamb and Finger, 1995) and although humans feed very differently, it is likely that taste localization does aid in the oral manipulation involved in chewing, moistening and swallowing. Furthermore, taste localization may play a role in the recognition of foods as familiar and safe. For example, some people report anecdotally that they identify diet sodas as containing non-nutritive, high-potency sweeteners rather than sugars because of differences in spatial, as well as temporal, properties (in addition to occasional side-tastes).

Experiment 1 also indicated that individuals varied in their ability to discriminate the gustatory target from distractors, and this variation was not correlated with the bitterness intensity ratings given by the participants when the cubes were presented subsequently. Additionally, as the number of texturally identical stimuli increased, localization of taste targets became more difficult, with selective rejection of the taste stimulus taking longer and being less accurate. And while some of the increase in response times can be attributed to difficulty in manipulating an increasing number of cubes, this difficulty does not completely account for the observed increases in response times. This seems to imply that taste quality and tactile conjunctions are not processed preattentively and that searches for the flavored target cube that rely upon taste localization occur through a serial, rather than a parallel, process (Treisman, 1986, 1988; Wolfe, 1992).

Experiment 2 clearly demonstrated that humans can localize and remove an appetitive gustatory target from a field of tactile distractors via taste sensations alone. This indicates that the ability of individuals to identify and remove a target is not restricted to aversive stimuli as demonstrated in Experiment 1, but is a more general gustatory phenomenon.

As shown in Figure 3, subject performance varied across the different stimulus sets. These differences are best accounted for by interactions that occurred between the taste and touch sensations of the target cubes and the taste and touch sensations of the distractor cubes in each set. Considering first the stimulus sets with a single taste present, participants performed best in the 'three blanks, one sweet' condition. Performance with a sweet target was comparable to performance with a bitter target stimulus in Experiment 1. In contrast, participants performed the worst in the 'three sweet, one blank' condition, where the unflavored target cube is presented against a background of the more intense distractor cubes. Thus, while people are capable of removing a nearly tasteless cube from a field of flavored distractors, this was a more difficult task. 'Tactile capture' of taste may occur for the tasteless target cube which then competes with the localization of taste. In other words, it is possible that the blank target presented with the three sweet distractors may have been perceived as eliciting some sweet taste itself. The phenomenon of 'tactile capture', in which taste sensations appear to be localized by touch, was described by Todrank and Bartoshuk (Todrank and Bartoshuk, 1991) and seems to account for cases in which damage to large portions of the taste receptor field does not always affect subjective taste experience.

When considering stimulus sets with two tastes, the results are less clear-cut. In the 'three bitter, one salty' condition, people performed slightly less well than they had in the 'three blanks, one sweet' condition, but there was no significant difference between the two conditions. However, they performed significantly worse in the 'three sweet, one bitter' condition, at a level comparable to that of the 'three sweet, one blank' condition. The stimuli which composed the two-taste stimulus sets were chosen to represent an asymmetrical suppression (salt suppresses bitterness more than vice versa) and a symmetrical suppression (sweetness and bitterness suppress one another to similar extents) and might account for the difference in performance, but such conclusions would be premature at this time.

Thus, Experiment 2 indicated that humans can localize and selectively remove a target taste in the presence of distractors of another distinct taste quality; however, having a second taste present in the distractor cubes clearly did not enhance people's ability to remove the target cube. This indicates that flavored distractors did not provide taste-enhancing contrast through some sort of perceptual 'pop-out' effect (Treisman, 1986, 1988). This observation, that humans can localize and selectively remove a target taste in the presence of distractors of another distinct taste quality, suggests there is an oral–lingual gusto-topic map in the brain that allows for the simultaneous spatial localization of multiple segregated taste qualities in the oral cavity. Alternative explanations, such as taste-induced tactile perception, or polymodal taste fibers that are also sensitive to touch (Shikata *et al.*, 2000), cannot account for this ability.

In both Experiments 1 and 2, perceived stimulus intensity did not seem to be related to the ability to localize and remove a target stimulus via taste sensations. Furthermore, longer decision intervals to determine which cube was the target were not associated with improved performance. To the contrary, more accurate decisions were made more quickly. This suggests that subjects were not using a search strategy that involves manipulation of the cubes in the mouth. Rather, they appear to have decided quickly when they were more certain and taken longer when they were less certain, as has been found in olfactory identification studies (Desor and Beauchamp, 1974).

As stated earlier, there are examples for taste localization in other vertebrates. In goldfish, taste localization subserves sophisticated food sorting behaviors (Lamb and Finger, 1995). In brief, these fish typically feed by sucking up a mouthful of bottom debris and substrate. Then, using a highly developed muscular palatal organ (which forms the roof of the oral cavity), they sort the contents of the mouth by taste. Local contraction of the palatal organ musculature,

which is entirely dependent upon the local characteristics of the gustatory stimulation, traps the 'desirable' food particles between the palatal organ and the floor of the oral cavity. Once the food particles have been trapped, the waste is flushed out from the oral cavity; subsequently, the food particles are swallowed. Thus, particles with an appetitive quality are actively retained while neutral, aversive and non-food particles are expelled (Finger, 1988, 1997).

Unlike goldfish, humans are not dependent on the ability to localize taste in order to feed, so the reason for this capability remains unclear. What possible functions could this ability have in human feeding, which is very different from that of goldfish? Localization may: (i) aid in identification of what is in the mouth and where it is within a heterogeneous bolus and (ii) help manipulate specific sub-components of a heterogeneous bolus in the mouth. These functions are important because: (i) identification of the oral bolus is necessary for determining familiarity and safety and (ii) manipulation aids in mastication, hydration, swallowing and digestion. And while these functions could be performed without the ability to localize taste, they would be more difficult. Although there remains the possibility that localization of taste is vestigial and serves no important function in humans, everyday experience speaks to the role of localization of taste in food recognition.

Acknowledgements

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