Ipsi- and bilateral interactions in taste

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In two experiments, the integration over spatial extent in taste was investigated for threshold sensitivity to NaCl and for suprathreshold intensity perception of saltiness. The area of stimulation was doubled by adding either an ipsilateral or a bilateral stimulus. The two stimuli could be of equal or unequal intensity. The data showed that at threshold level a probability summation model applied to all bilateral and most of the ipsilateral stimulus combinations. Probability summation failed to predict detection probability when two stimuli with different intensities were presented at the same tongue side. For suprathreshold stimuli, the magnitude of the saltiness sensation as estimated by a line-length method depended on the level of stimulation. The possible peripheral interaction mechanisms and central factors contributing to the taste response were discussed.

A common property of the senses is the capacity to integrate sensory information over area. The degree and form of integration vary both over and within sensory modalities, and may reflect the interactions that can occur at various stages in the transduction process, from the peripheral receptor mechanisms to the central response level.

In taste, spatial interactions have been investigated with anatomical, electrophysiological, and psychophysical methods. The innervation of a single papilla by multiple nerve fibers and the branching of a single chorda tympani fiber into multiple papillae make peripheral spatial interactions possible (Beidler, 1969). Miller suggested that this branching pattern forms the anatomical basis for the lateral interactions that he found between neighboring taste buds in rat fungiform papillae (Miller, 1971, 1974). In cats, antidromic stimulation between neighboring fibers has been proposed as an explanatory model for lateral inhibition as well as "crossadaptation" within units with overlapping receptive fields (Bernard, 1971; Wang, 1973).

In humans, spatial summation at threshold is partial, as Bujas and Ostojčić (1941) and Hara (1955) showed. Recently, we have found that doubling the stimulated area yields an increase in detection probability according to a simple probability summation hypothesis (Linschoten & Kroeze, 1991, 1992). The amount of summation is equally predictable for ipsilateral and bilateral stimulation.

Areal effects are found at suprathreshold level as well. Smith (1971) varied the area of stimulation at the tip of the tongue by means of an adjustable tongue-chamber, that enabled him to vary the exposed tongue area. When he stimulated bilateral adjacent sites, he found that taste intensity grew as a power function of area.

In the studies mentioned above, the effect of area on sensitivity and intensity was examined; the areas under

investigation were stimulated homogeneously. Little is known about spatial integration over areas that are simultaneously stimulated with unequal concentrations of the same taste compound. It is not evident a priori that simultaneous stimulation with two unequal concentrations leads to the same results as in our previous studies. Békésy (1964) showed that part of the stimulus information in such a case may code localization, which may occur at the cost of spatial summation. Bujas (1937) measured sensitivity for NaCl while simultaneously stimulating a contralateral part of the tongue with increasing concentrations of NaCl. Sensitivity decreased in a logarithmical way as the concentration applied on the contralateral side increased. This inducing effect was also found by Collings, Lindberg, and McBurney (1976). Recognition sensitivity to NaCl decreased when an adjacent ipsilateral site was stimulated with 3 M NaCl. In this study, the inducing stimulus was always presented 1 sec before the test stimulus.

The purpose of the present experiments was to get a more detailed picture of the spatial integration capacities in the human sense of taste. The effects of simultaneous stimulation with both equal and unequal concentrations of NaCl on threshold sensitivity and suprathreshold intensity perception were investigated, under ipsilateral as well as bilateral stimulus conditions.

EXPERIMENT 1

Method

Subjects. Eight male nonsmoking students (mean age, 22.38 ± 3.2) served as paid subjects. They were requested to refrain from eating, drinking, or chewing anything for at least 1 h prior to the beginning of each experimental session. Each subject was tested on 24 days in a 6-week period, at the same time on each day. A preliminary session served to familiarize subjects with the procedure and to get an approximate individual NaCl threshold.

Stimuli. The tongue was stimulated with half-circular pieces of filter paper (Whatman no. 91), covering an area of 31.81 mm², soaked in solutions of NaCl (reagent grade) and/or water. Six concentrations were used (lowest, 0.007 M; highest, 0.053 M), with each concentration 1.5 times stronger than the preceding one. Thus

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the stimuli formed equal steps on a log concentration scale (0.17609 log unit). Each subject was stimulated with a set of four adjacent concentrations around his own threshold. Solutions were made once a week, with distilled water as diluent, and stored at 4°C. During testing, the solutions were kept at a constant temperature of 35.7°C in a thermostatically controlled water bath.

Conditions. The half circles were placed on the anterior dorsal surface of the tongue under the following stimulus conditions (Figure 1): *unpaired*, on three different locations of the anterior tongue (a medial and a lateral site on the left side of the tongue, L-med and L-lat, respectively, and a lateral site on the right side, R-lat), and *in pairs*, consisting of combinations of the three different locations (ipsilateral, two halves on the left side of the tongue, forming a full circle, Ipsi; bilateral complementary, a lateral half on the right side and a medial half on the left side, Bi-C; and bilateral mirrored, two lateral halves on the two tongue sides, Bi-M).

In the paired conditions, all possible combinations of the four concentrations with each other and with distilled water were used as stimuli.

Procedure. In a temporal two-alternative forced choice procedure, subjects were instructed to decide which of two successively presented stimuli had a taste different from water. Upon a tone signal, the subject rinsed his mouth thoroughly with distilled water, dried his tongue with a rectangular piece of filter paper to prevent dilution and spread of the stimulus solution, and kept the tongue extended about 2.5 cm between closed lips. Then, depending on the experimental condition, one or two half-circular pieces of filter paper were carefully placed on the extended tongue with teflon coated forceps. These papers were removed by the experimenter after ≈ 5 sec and replaced by the filter paper(s) for the second presentation within a trial. After an answer had been written down, the experimenter removed the filter paper(s). The subjects were instructed to guess when no taste difference between the two presentations within a trial could be detected. A trial ended with another rinse. The intertrial interval was 50 sec. The filter papers were removed with glass filters, which were connected to a vacuum pump (for details, see Linschoten & Kroeze, 1992).

In total, there were 74 different stimuli: 12 unpaired (4 concentrations $\times$ 3 locations), 12 equal pairs (11, 22, 33, and 44 in the

conditions Ipsi, Bi-C, and Bi-M), 20 unequal pairs in both the ipsilateral and the bilateral complementary conditions, and 10 unequal pairs in the bilateral mirrored condition. The difference in the number of unequal pairs originates from a possible unequal sensitivity between the medial and lateral positions (Linschoten & Kroeze, 1992) and from the consideration that interactions between the two sites might not be reciprocal. Therefore, a pair consisting of a medial concentration x and a lateral concentration y is regarded a priori as a different stimulus from the reverse pair, medial concentration y plus lateral concentration x . Since the lateral sites of the two tongue sides previously did not show any difference in sensitivity, pair xy and pair yx are considered as identical stimuli in the bilateral mirrored condition.

In each session, all stimuli were presented in random order. Each subject participated in 24 sessions of approximately 1 h.

Data analysis. For each subject, six psychometric functions were fit to the data, three functions for each of the unpaired halves and three for each of the paired conditions. To obtain these functions, the percentage of correct choices per stimulus concentration was first corrected for chance, so that they ranged from 0.0 to 1.0. These corrected scores were then converted into Z scores using the normal Gaussian distribution. A straight line was then fit to the Z scores using linear regression and plotted against the logarithm of the concentration. Thresholds were determined at the $Z = 0$ value, corresponding to halfway between chance and 100% correct.

To analyze the data in terms of detection probabilities, the estimated Z values for the four concentrations in each of the unpaired conditions were converted to estimated portions under the normal probability function, resulting in four observed detection probabilities per condition. For the paired conditions, Ipsi, Bi-C, and Bi-M, predicted detection probabilities were calculated according to the classical probability theorem, $P_{(x+y)} = P_x + P_y - (P_x \cdot P_y)$ (Eriksen, 1966; Green & Swets, 1966). These predictions were based on the observed probabilities for the corresponding half circles.

Results and Discussion

Thresholds. The mean detection thresholds for the unpaired halves were 0.026M (L-med), 0.024M (L-lat), and 0.026M (R-lat). For the equal pairs, these values were 0.018M (Ipsi), 0.017M (Bi-C), and 0.015M (Bi-M). A multivariate analysis of variance (MANOVA) for repeated measures showed that neither the thresholds in the unpaired conditions nor those in the paired conditions were different from each other. This confirms our earlier findings that different sites on the anterior tongue are equally sensitive to NaCl, and that doubling the stimulated area yields the same increase in sensitivity, whether the information has to be integrated from one side of the tongue or is coming from the two tongue halves (Linschoten & Kroeze, 1992).

In Figure 2, the dotted lines represent (after carrying out linear regression analysis) the threshold functions for the averaged halves, and the dashed lines represent the threshold functions for the equal pairs. Since each subject was tested with his own set of concentrations, concentration *number* is plotted on the abscissa; Z-detection probability is on the ordinate. In each of the panels, these threshold functions are more or less parallel: mere area enlargement causes a constant increase in detection probability with growing concentration.

Figure 1. Filter paper conditions. The stimulus locations on the tongue, and the way in which the filter paper halves were paired.

Figure 2. Families of functions showing the detection probabilities (converted to Z values) of various combinations of concentrations of NaCl presented to two sites on the tongue. The parameters W, 1, 2, 3, and 4 refer to a fixed concentration level on one of the halves (water, Concentration 1-4), while the other half is soaked in various concentrations. The dotted line depicts detection probabilities for the unpaired halves, and the dashed line for the equal pairs (left, middle, and right panel for the Ipsi, Bi-C, and Bi-M conditions, respectively).

In the same figure, families of functions are shown for stimulation with unequal pairs. Each of the solid lines depicts how detection probability increases with growing concentration on one of the halves within a pair, while the other half is kept at a fixed concentration level. Since there was no difference between the observed values for xy and yx pairs in both the ipsilateral and the bilateral complementary conditions, the points in the figures are averaged over pairs containing the same concentrations. In the bilateral conditions, Bi-C and Bi-M (middle and right panel respectively), the lines connecting the points can be fitted with straight lines. The fits for the W through 4 regression lines are all significant with 3 df ($.915 < r < .995$). This means that the threshold concept and the sigmoid probability function hold for stimulation with unequal concentrations while stimulating peripherally independent sites on the tongue.

A horizontal line intersecting the families of functions at $Z = 0$ was used to produce the trading relationships depicted in Figure 3. Both panels show how concentration in one area can be traded with concentration in another area to keep equal detectability. The slopes (n) are shown in the figures. The point on the y-axis is the concentration needed to reach threshold when one of the halves is soaked in water. In both bilateral conditions, the exponent, being near to unity, suggests perfect summation of concentration.

In the ipsilateral condition (Figure 2, left panel) the family of functions for the unequal pairs do not follow a regular pattern; the water line and the Concentration 1 line can be described by linear regression functions ($r = .97$ for W and $r = .99$ for 1), but linearity is absent for both Concentration 2 ($r = .84$) and Concentration 3 ($r = .77$). The regression function for Concentration 4 has a low but

Figure 3. Trading relationship showing how concentration in one area can be traded with concentration in another area to keep equal detectability (left, bilateral complementary condition; right, bilateral mirrored condition).

significant fit ($r = .91$). The nonlinearity in Concentrations 2 and 3 comes from a dramatic drop in detectability of pair₂₃. Of the 8 subjects tested, 7 show this phenomenon, so that extraexperimental factors cannot easily be regarded as candidates for the sudden decline in detectability.

Detection probabilities. The estimated observed probabilities for each of the four concentrations in the three unpaired conditions were used to calculate predicted probabilities for all pairs in the paired conditions, with the exception of those pairs that contained water on one half. In Table 1 the predicted and observed values are shown.

A MANOVA for repeated measures revealed no differences between the predicted and the obtained values for the equal pairs (upper part of Table 1). For the unequal pairs, the values are given in the lower part of Table 1. The observed values are averaged over the xy and yx pairs. The predicted values are calculated by $P_{X+Y} = (P_{X+Y} + P_{Y+X})/2$. A MANOVA indicated no differences between the observed and predicted values with bilateral stimulation [Bi-C, $F(1) = 1.43, p < .27$; Bi-M, $F(1) = 0.21, p < .659$], and no interactions with stimulus level were found.

In the ipsilateral case, however, there was a significant difference between the observed and predicted values ($F = 7.98, p < .026$). Post hoc paired t tests per stimulus showed that pair₂₃ and pair₃₄ were significantly less detected than could be predicted [pair₂₃, $t(7) = 6.81, p < .0001$; pair₃₄, $t(7) = 2.70, p < .03$]. Correction for multiple testing ($p' = p/6 = .0083$) would change this result, leaving only pair₂₃ as having significantly lower observed values. In the multivariate analysis, the averaged interaction effect with stimulus also was significant [$F(5,35) = 5.18, p < .001$]. Heterogeneous stimulation on one tongue side fails to produce straightforward predictability in terms of probability summation.

EXPERIMENT 2

Method

Subjects. Eight female and 7 male nonsmoking students (mean age, 21.4 ± 2.03) served as paid subjects. They were requested to refrain from eating, drinking, or chewing anything for at least 1 h prior to the beginning of each experimental session. The subjects were untrained and naive as to the purpose of the experiment.

Stimuli. Stimulation was performed with half-circular pieces of filter paper (Whatman no. 91), covering an area of 31.81 mm^2 , soaked in solutions of NaCl (reagent grade). Four concentrations were used: 0.125M, 0.25M, 0.5M, and 1.0M. Solutions were made once a week, with distilled water as diluent, and stored at 4°C . During testing, the solutions were kept at a constant temperature of 35.7°C in a thermostatically controlled water bath.

Conditions. The conditions were the same as in Experiment 1 (see Figure 1).

Procedure. The presentation method, rinsing procedures, and interstimulus interval were the same as in Experiment 1. The subjects were instructed to estimate the saltiness of each stimulus by using the line-length method (Kroeze, 1976). In this modified magnitude estimation method, judgments are made by positioning a needle along an ungraduated linear scale 300 mm long. On the back of the device, invisible to the subject, the experimenter could read

Table 1
Mean Predicted and Observed Detection Probabilities
for Equal Pairs and Unequal Pairs

Pair	Ipsi		Bi-C		Bi-M	
	Pred	Obs	Pred	Obs	Pred	Obs
Equal Pairs						
11	.20	.22	.24	.18	.24	.26
22	.40	.40	.42	.37	.43	.46
33	.64	.60	.64	.61	.65	.64
44	.84	.78	.83	.80	.83	.83
Unequal Pairs						
12	.30	.36	.33	.38	.35	.35
13	.47	.49	.48	.45	.49	.49
14	.65	.59	.64	.54	.64	.63
23	.54	.39	.55	.53	.55	.46
24	.70	.60	.69	.62	.69	.67
34	.77	.65	.75	.70	.76	.78

Note—Ipsi, ipsilateral, two halves on left side of tongue. Bi-C, bilateral complementary, lateral half on right side and medial half on left side. Bi-M, two lateral halves on the two tongue sides.

the estimated intensity, defined as millimeters of distance of the needle. After presentation of each stimulus, the needle was reset by the experimenter at the far left starting position (relative to the subject). The subjects were instructed to make ratio judgments; that is, when the perceived saltiness of a stimulus was twice as strong as that of another one, for example, the corresponding distance on the linear scale had to be twice as long.

In each session, all stimuli were presented in random order. Each subject participated in five sessions of approximately 1 h.

Results and Discussion

The geometric means of the five magnitude estimates for each stimulus were calculated. Since the subjects used the line scale differently, all geometric means were converted to the same scale. To do so, first the group mean, was determined by averaging over all geometric means ($N = 1,110$), and second, for each of the subjects, the arithmetic mean of the 74 geometric means was calculated. A weighting factor, defined as the ratio between the resulting group mean and each subject's grand mean, was used to multiply each of the individual geometric stimulus means. This way of rescaling converts the data of all subjects to a scale with a common mean, leaving the individual scale properties unaffected (Engen, 1971).

The mean saltiness judgments for the unpaired half circles and the equal pairs are given in Table 2. A MANOVA for repeated measures revealed no differences between the estimates for the different stimulation locations, nor any interaction with concentration. Intensity increases as a function of concentration with the same rate, both at the medial and the lateral sites of the left tongue side and at a right lateral location. Doubling the stimulated area using equal concentrations on the two halves yields saltiness estimates that do not differ across the three paired stimulus conditions.

For the unequal pairs in the ipsilateral and the bilateral complementary conditions, the mean estimates for the corresponding medial lateral and lateral medial pairs were not different, which means that the total perceived salti-

Table 2
Mean Saltiness Estimates for Halves and Equal Pairs

Half	Unpaired		
	L-med	L-lat	R-lat
1	49.16	46.67	56.93
2	83.15	81.86	90.36
3	115.47	119.21	120.93
4	150.55	142.17	154.93
Pair	Paired		
	Ipsi	Bi-C	Bi-M
11	70.14	72.25	73.17
22	121.60	116.77	120.57
33	161.70	163.87	153.14
44	205.19	206.60	193.22

Note—L-med, left medial; L-lat, left lateral; R-lat, right lateral. Ipsi, ipsilateral, two halves on left side of tongue. Bi-C, bilateral complementary, lateral half on right side and medial half on left side. Bi-M, two lateral halves on the two tongue sides.

ness of a pair is not influenced by localization effects. In Table 3 the averaged means of corresponding pairs are given along with the mean estimates for the bilateral mirrored condition.

In Figure 4, families of functions are depicted that show how perceived saltiness increased with concentration applied to one location for various fixed concentrations applied to the additional location. The dotted line represents the function for the averaged unpaired half, and the dashed line connects the points for the equal pairs. In each of the figures, these lines are fairly parallel. This means that doubling the stimulated area caused a fixed amount of increase in perceived saltiness. This parallelism also implies that doubling the stimulated area causes the concentration necessary to evoke a certain perceived intensity to be a constant proportion of the concentration needed in the half-area condition. In the ipsilateral condition, the ratio $\text{conc}(\text{paired})/\text{conc}(\text{unpaired})$ is 0.5; in Bi-C, 0.55; and in Bi-M, 0.53.

Stimulation with unequal pairs did not produce parallel psychophysical functions; instead, these functions clearly show convergence. That is, the effect of a second stimulus

Table 3
Mean Saltiness Estimates for Unequal Pairs,
Averaged Over Localization

	Ipsi	Bi-C	Bi-M
1WW1	49.79	60.72	49.91
2WW2	71.00	81.67	80.60
3WW3	106.35	104.17	90.31
4WW4	125.81	131.70	120.11
1221	107.15	104.10	92.05
1331	129.03	126.66	120.62
1441	157.03	144.53	133.38
2332	154.45	145.21	148.50
2442	169.79	160.59	157.46
3443	186.45	179.34	169.79

Note—Ipsi, ipsilateral, two halves on left side of tongue. Bi-C, bilateral complementary, lateral half on right side and medial half on left side. Bi-M, two lateral halves on the two tongue sides.

is dependent on the level of the first; adding Concentration 4 to Concentration 1 has a greater effect in terms of increase of sensation than adding it to Concentration 3.

Isosensation lines will result when horizontal cuts are made through the psychophysical functions. Figure 5 shows these trading relations between the two stimulated sites—that is, combinations of concentrations that would maintain perceived saltiness constant at five different sensation levels. In all the paired conditions, it is obvious that the integration over concentration is level dependent; the slopes of the trading functions are steepest at the lowest sensation level, and they become progressively flatter with higher perceived intensity.

GENERAL DISCUSSION

When the tongue is stimulated in a homogeneous way, spatial summation is similar for threshold and supra-threshold stimuli. The increase in both sensitivity and perceived intensity as a function of area is independent of the level of stimulation. Furthermore, doubling the stimulated area yielded the same amount of summation with ipsilateral and with bilateral stimulation. The threshold results are in fact a replication of our previous findings (Linschoten & Kroeze, 1991, 1992). With respect to the suprathreshold data, Smith (1971) also reported that the exponent of the psychophysical function remained invariant for different areas of stimulation.

Under heterogeneous stimulation conditions, the concentrations applied to different sites on the tongue can be traded one for the other to keep detectability constant. Above threshold, the trading relations suggest generous summation at low sensation levels. The degree of summation decreases with increasing saltiness sensation. Along this line of reasoning, it could be argued that summation will cease to occur at an even higher sensation level, which would correspond with the point of convergence in Figure 4.

The amount of summation at threshold could be predicted on the basis of the detection probabilities of the unpaired halves. This was true for all equal pairs and for the unequal pairs with bilateral stimulation. A deviation from this overall regular pattern of predictability was found with heterogeneous ipsilateral stimulation around threshold. The interaction effect between stimulus pair and detection probability remained when pair₂₃ was left out of the analysis. There is a trend from greater than chance summation at low concentration levels toward hypoadditivity at higher levels. This could reflect an occlusion mechanism such as that which Lawless and Stevens (1989) proposed for mixtures of piperine and capsaicin. In our case, then, an assumption would be that overlapping receptive fields contain papillae that are differentially sensitive to increasing concentrations of sodium chloride. In the cat, chorda tympani fibers have been found that respond only to a specific concentration of a compound, and not to others (Wang, 1971).

Occlusion, however, cannot explain the drop in detectability of pair₂₃. This phenomenon seems real, in that all

Figure 4. Families of functions showing the perceived saltiness of various combinations of concentrations of NaCl presented to two sites on the tongue. The parameters W, 1, 2, 3, and 4 refer to a fixed concentration level on one of the halves (water, Concentration 1-4), while the other half is soaked in various concentrations. The dotted line depicts saltiness for the unpaired halves, and the dashed line for the equal pairs.

but one subject produced it, whereas other pairs containing Concentration 2 or 3 were not affected. It is striking, and probably not coincidental, that pair₂₃ normally would give rise to a detection probability that would lie in between those for pair₂₂ and pair₃₃—that is, near the 50% point.

It is well documented that the taste quality of NaCl changes with concentration (see, e.g., Cardello, 1979; McBurney and Bartoshuk, 1973; O'Mahony, 1973) and that water can have various tastes (e.g., Bartoshuk, 1974). In this case—that of having to choose between water and a taste—the taste of water may resemble that of the combination of Concentration 2 and 3. Alternatively, if the two concentrations do have a different taste, mixture suppression might occur. That the “tastes” are not physically mixed would not be a problem, since suppression has been found to occur between spatially contiguous sites that have been stimulated with different compounds (Gillan, 1982).

The question arises whether in the case of suprathreshold stimuli there exists a model that—analogueous to the probability summation model for threshold stimuli—could predict the perceived magnitude of the heterogeneous pairs. In olfaction several such models have been developed. Berglund, Berglund, and Lindvall (1976) and Berglund, Berglund, Lindvall, and Svensson (1973) used a “vector-sum” model to predict mixture intensity. In this model, the angle α between the perceived intensities of the individual components reflects the similarity of the odor qualities. A similar vector-sum model was proposed for bilateral interactions with unequal dichorhnic stimulation (Cain, 1977; Garcia Medina & Cain, 1982). Perceived intensity conformed to a Pythagorean combinatorial rule, based upon the respective masses of the substances entering each nostril. Neither of these models applies to the present suprathreshold results—that is, there is not a single, invariant α for the range of stimuli used here. In-

Figure 5. Isosensation functions, showing how concentration in one area should be combined with concentration in another area to keep perceived magnitude constant at five sensation levels.

stead, we found that another simple rule might describe the data. This rule states that the integrated sensation is a power function of the constituent sensations, or $S_{AB} = (S_A + S_B)^n$. The magnitude of the exponent proved to be invariant within and over all the conditions, and had a mean value of 0.94 ± 0.01 . However, additivity of sensations is more likely to be the outcome of a perceptual rather than a sensory process.

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