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Masking and Adaptation of Sugar Sweetness Intensity

JAN H. A. KROEZE

Psychological Laboratory, Utrecht University, Utrecht, The Netherlands

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KROEZE, J. H. A. *Masking and adaptation of sugar sweetness intensity*. PHYSIOL. BEHAV. 22(2) 347–351, 1979.—Subjects indicated the sweetness of solutions of sucrose and a mixture of sucrose and sodium chloride by means of magnitude scaling. The adapting effects of sucrose, sodium chloride and a mixture of both substances were investigated. The stimuli were delivered by a flow system to pre-defined tongue areas. Following adaptation to sucrose and to the mixture the subjective intensity of sugar sweetness decreased 54.2% and 54.6% respectively: these differences are statistically significant. Also a significant masking effect of sodium chloride was observed (87.9% reduction). No indications of cross-adaptation were found. The results were interpreted in favour of the independency of adaptation and masking.

Across fibern pattern in taste   NaCl taste   Neural coding in taste   Sugar taste   Sweetness intensity   Taste adaptation   Taste masking   Taste mixtures

IN A MIXTURE of sodium chloride and sucrose a weakening of the subjective intensity of one or both components has been reported [2, 30, 34]. This weakening is called suppression or masking. Beidler [3] has proposed a general formula predicting the response of taste cells to a stimulus A in the presence of a stimulus B. This formula is based upon the notion of competition for receptor sites. When two different stimuli do not compete for the same receptor sites, the formula reduces to one predicting the response to a single compound.

The effectiveness of a taste stimulus may also be reduced by a second stimulus in a non-competitive way: Terayama *et al.* [38] showed that several sugars, as for instance sucrose and glucose, change the state of the taste cell membrane (of the true slime mold Physarum polycephalum) in such a way that the effectiveness of salts (as NaCl and LiCl) is reduced. If the cell membrane of the slime mold can be considered a model system of the human taste cell membrane this noncompetitive interaction may also occur in humans.

Instead of simultaneous presentation, as in a mixture, one may present different components successively to the subjects. In this case it is possible to study the effect of a stimulus as influenced by a preceding stimulus. Usually a long-lasting stimulus shows a decrement of subjective intensity: this is known as sensory adaptation. In self-adaptation adapting stimulus and test stimulus are the same, whereas in cross-adaptation they are different.

Adaptation may be complete which means that the taste system has completely lost its sensitivity to a particular stimulus. However, in about fifty percent of human subjects complete adaptation cannot be attained. Amongst others completeness of adaptation seems to depend on the type of stimulus material, the intensity of the adapting solution [9], and the adaptability of the sensory system [22,24]. In a recent paper Gent and McBurney [8] suggest that temporal constancy of the adapting stimulus may be required for complete adaptation. The sip and spit method to some degree approximates a pulsatile stimulus to which the taste system does not adapt [25].

It is generally assumed that compounds which show cross-adaptation affect at least in part some common mechanism [8, 15, 17, 19, 20]. The exact nature of this mechanism is unknown, but there is evidence that adaptation is peripheral in nature [4,39].

Until now, adaptation and mixture effects have not been studied in relation to each other. In order to get a better understanding of this relationship a design was chosen in which the same subjects participated in both adaptation and mixture conditions.

METHOD

Subjects

Six non-smoking undergraduate psychology students, 3 males and 3 females, participated in the experiment. Their ages ranged from 18 to 20 years.

Stimuli

The two compounds used in the experiment were sucrose ($C_{12}H_{22}O_{11}$) and sodium chloride (NaCl), both of analytical grade purity ("ANALAR" from B.D.H.-chemicals Ltd.). The compounds were dissolved in distilled water. Stimulus concentration was 0.3 M for both stimulus types. A mixture of sugar and salt was made by mixing 0.6 M-solutions of each compound in equal volumes. The resultant concentration of both substances in the mixture then is 0.3 M. At the intensity chosen all subjects could clearly recognize the stimuli. Bartoshuk [1] showed that this concentration has about the same subjective intensity for sucrose and sodium chloride.

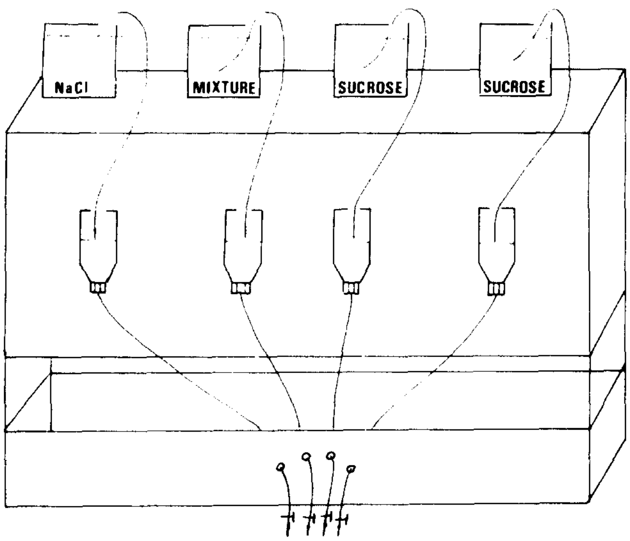

FIG. 1. Schematic diagram of the gravitational flow system used.

Such an inference of equal subjective intensity is only acceptable if both substances are estimated during the same experiment with subjects serving in both conditions. The temperature of the stimuli was 22°C (±0.4) and they were delivered by a gravitational flow system (Fig. 1).

The bottles were connected by silicone tubes to glass capillaries with an outflow of 0.8 ml/sec. As compared to the literature this quantity is rather low, but in combination with the restricted stimulation area the resultant density of stimulus material is sufficiently high. Before doing the experiment the method was extensively tried out on another group of subjects. It turned out that subjects recognized the stimuli in 100% of cases. Furthermore it was possible to produce well-differentiated psychophysical functions with this intensity in the middle of the range. In order to maintain a constant pressure at the lower end of the flow system, the liquid levels in the bottles were kept constant by siphoning from the upper vessels in the system at a rate which was the same as the loss of stimulus materials from the lower bottles.

During stimulus delivery the subject's tongue was put in a tongue box to ensure that a well-defined portion of the tongue was stimulated. Each subject had his own box especially fitted to his tongue. A schematic drawing of the tongue box is shown in Fig. 2. Only the left side of the tongue was stimulated. The part of the tongue exposed in the left hole of the tongue box has a surface of about 1.3 cm². During stimulation the capillary's outflow point was located at about 0.75 cm above the tongue.

Conditions

In each condition the subject's task was to judge the sweetness of a 2-sec stimulus. There were five conditions:

S_2 The sucrose solution was delivered for 2 seconds. The subject indicated the sweetness intensity of the stimulus immediately. This condition is called the control condition.

SN_2 The mixture was delivered for 2 seconds. The subject indicated the sweetness intensity of the mixture. This is the masking condition.

$S_{30}\rightarrow S_2$ The sucrose was delivered for 30 seconds. When this sucrose flow was terminated a 2-sec sucrose test stimulus was delivered from another capillary. The subject indicated the sweetness intensity. This is the adaptation condition.

$SN_{30}\rightarrow S_2$ Like the adaptation condition, but instead of sucrose the mixture is the adapting stimulus. This condition is the mixture adaptation condition.

$N_{30}\rightarrow S_2$ Like the adaptation condition, but NaCl is the adapting stimulus. This condition is called the cross-adaptation condition.

The choice of 30 seconds duration of the adapting stimuli was based upon two considerations. First it was felt that trials had to be as short as possible in order to prevent unnecessary fatiguing of subjects and to keep sessions as short as possible. On the other hand the adapting stimulus had to be long enough to ensure adaptation. From the literature (e.g. [9,17]) it can be seen that a 30-sec stimulus is long enough to induce at least partial adaptation. The part of the instruction in which the subjects were told to estimate sweetness only was very much stressed. The subjects were asked to repeat the instruction in their own words to ensure that they had understood it. Before each session the instruction was repeated.

The sweetness judgments were made by positioning a needle along a linear scale of 300 mm length. The experimenter could read the estimate at the back of this device. This way of scaling has shown to be as reliable as magnitude estimation and has the advantage of better response standardization [13]. The interstimulus time was defined as the time between the onset of a test stimulus and the onset of the next stimulus (whether adaptation or test). It was fixed at 50 sec throughout the experiment. Combined with a rinse this interval is long enough to restore normal sensitivity after stimulation [9]. In several recent psychophysical studies even shorter intervals are used [23, 26, 27]. Furthermore Meiselman [20] showed that there is no difference in magnitude estimates in adaptation experiments between procedures with 45-sec rest intervals and 5-min intervals when using NaCl and sucrose.

Immediately after each response the subject's tongue was rinsed with distilled water. The five conditions were repeated 48 times so that each subject received a total of 240 stimuli during the experiment. These stimuli were divided into 24 series of 10 presentations each. In each series all conditions occurred twice in a random order. There were 3 sessions for each subject, one session a day at the same hour

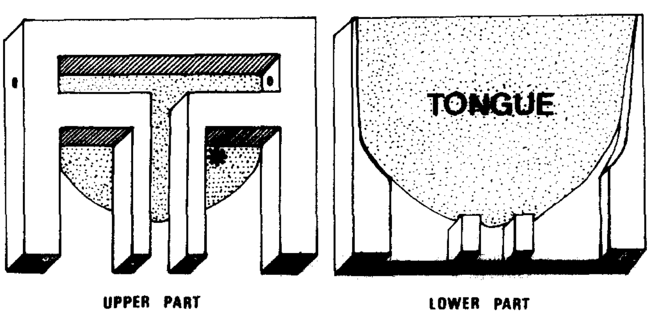

FIG. 2. The tongue box in which a part of the tongue could be exposed to the flow. The asterisk indicates the spot where the flow arrives at the tongue surface.

on consecutive days. A session lasted for about 2 hr and it was divided into 4 sub-sessions of 23 min. In one sub-session two series were delivered. Between sub-sessions there was a 5-min break.

RESULTS

From the 48 sweetness judgments of each condition for each subject geometric means were computed, which form the data on which further calculations were performed (Table 1). In fact the arithmetic mean would have been about as appropriate as the geometrical mean, since the distribution of the 48 replications can be viewed as an error-distribution. The individual distributions did not depart significantly from symmetry, although a small amount of positive skewedness was present in two individual results. The geometrical means were preferred because these are more compatible to Steven's law, which states that geometrical means of replications are linearly related to the logarithm of intensity.

TABLE 1

GEOMETRIC MEANS OF 48 REPLICATIONS OF EACH CONDITION PER SUBJECT

Subject	Conditions				
	S_2	SN_2	$S_{30}\rightarrow S_2$	$SN_{30}\rightarrow S_2$	$N_{30}\rightarrow S_2$
1	185.4	119	10.6	12.5	215.4
2	45.5	6	1.5	5.0	78.8
3	181.2	16	136.1	134.6	172.9
4	72.1	2	20.2	36.7	60.5
5	74.5	16.7	100.1	58.8	22.9
6	243.0	17.4	98.7	116.3	242.9

A two-way analysis of variance [11] showed a significant effect for both conditions and subjects (cond.: $df=4$, MS=13,225.49, F=5.11, $p<0.01$; subj.: $df=5$, MS=12,274.11, F=4.71, $p<0.01$; MS (residual)=2,603.21). In Fig. 3 the arithmetic means of the values in Table 1 are shown. Table 2 provides a summary of Student's t-tests for dependent means calculated on the paired conditions. As can be seen in Fig. 3 and Table 2 the results of this experiment may be stated as follows:

1. There is a significant adaptation effect. The mean estimate of sweetness intensity is reduced from 133.6 mm (S_2) to 61.2 mm ($S_{30}\rightarrow S_2$), a reduction of 54.2%.
2. No cross-adaptation from NaCl on sucrose could be observed: the scores in condition S_2 and $N_{30}\rightarrow S_2$ are essentially the same.
3. The mixture of salt and sugar significantly reduces the sweetness estimates of subsequently presented sugar. The mean sweetness estimate is reduced from 133.6 (S_2) to 60.7 ($SN_{30}\rightarrow S_2$), a reduction of 54.6%.
4. A strong masking effect is found: in the mixture sweetness is estimated at 29.5 mm as compared to 133.6 mm when NaCl is absent, a reduction of 87.9%.
5. The mixture adaptation condition ($SN_{30}\rightarrow S_2$) and the adaptation condition ($S_{30}\rightarrow S_2$) show essentially the same results which means that probably the adapting sugar component alone is responsible for the reduction of perceived sweetness.

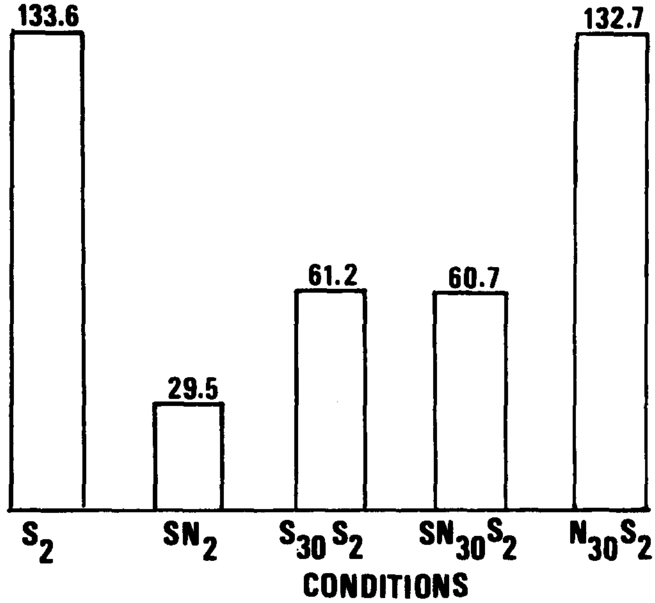

FIG. 3. Mean intensity expressed as line length (in mm) under the five conditions. These are the arithmetic means of the six subjects taken together.

DISCUSSION

The results confirm the well-known effect of adaptation. As can be seen from Table 1 there is large variability between subjects; thus Subject 3 adapted little and the intensity estimates of Subject 5 increased rather than decreased. The absence of cross-adaptation between sodium chloride and sucrose has also been found in earlier work [17,35]. Cross-adaptation is more likely to occur between compounds with the same quality [10, 18, 19, 36], although there seems to be an exception for the taste of bitter where probably two different mechanisms are involved [15].

If masking and cross-adaptation were both based on the binding mechanism, some systematic relation between them

TABLE 2

SUMMARY OF STUDENT'S T-TESTS CALCULATED ON THE PAIRED CONDITIONS

	SN_2	$S_{30}\rightarrow S_2$	$SN_{30}\rightarrow S_2$	$N_{30}\rightarrow S_2$
S_2	4.81 ($p<0.005$)	2.37 ($p<0.05$)	2.67 ($p<0.025$)	0.50
SN_2		−0.83	−1.25	−3.92 ($p<0.01$)
$S_{30}\rightarrow S_2$			−1.11	−1.62
$SN_{30}\rightarrow S_2$				−1.68

might be expected. However, the results indicate that such a relation between masking and cross-adaptation does not exist. Thus, in this case of masking, the decrement of sweetness probably cannot be ascribed to interference at the receptor level, unless one is willing to accept the view that adaptation and masking both occur at the receptor level, but have nothing to do with each other.

Another argument in favor of the independency of masking and adaptation found in this experiment may be the completely identical effect of conditions $S_{30}{\rightarrow}S_2$ and $SN_{30}{\rightarrow}S_2$. Thus, in a mixture with NaCl the judged intensity of sucrose sweetness is lower (SN_2 in Fig. 3), whereas the adapting effectiveness of sucrose in this mixture is not changed ($SN_{30}{\rightarrow}S_2$ in Fig. 3). Obviously masking and adaptation of sugar sweetness by NaCl are different processes.

If the masking effect is essentially different from adaptation what then could be the mechanism causing it? Although available data do not permit a statement about the exact localization and nature of the masking process, some reasonable possibilities may be indicated. The first that has to be mentioned uses a central concept in current taste theory: the across fiber pattern (AFP). The AFP is the spike frequency profile which can be obtained by monitoring single fibers of the afferent nerve while applying a taste stimulus to the tongue. The intensity of the stimulus is proportional to the total numer of spikes in the entire AFP, while taste quality is coded by the differences among single-fiber spike frequencies. These differences constitute a profile which is specific for a certain quality [5, 6, 32]. A significant relation has been found between behavioral measures of taste quality and the AFP [14,37]. The AFP-theory is based upon the fact that a certain fiber responds to a variety of compounds [31,32]. Responding of the same unit to NaCl as well as to sucrose does not contradict the independency of their binding mechanisms, since independent sites for sucrose and NaCl can be located at the same receptor cell. This means that the independent sites contribute to the same spike train in the afferent fiber. The essential feature of a masking hypothesis which takes into account the AFP-theory is summation of spike frequencies originating from independent receptor sites. Thus the degree of non-peripheral masking is dependent upon the AFP's of the components in the mixture. This means that two substances that have profiles which are negatively correlated in the way shown in Fig. 4 will strongly mask each other's quality. If one of them were sweet then the subject might be expected to give low estimates of sweetness intensity. Apparently this way of masking by summation does not affect the number of spikes, which is the code for intensity. This would mean that mixture experiments in which the overall stimulus intensity is judged will not show masking as easily as experiments in which the intensity of a specified quality is judged.

This explanation accepts the idea of fusion in taste, which means that components in a mixed state may give rise to percepts qualitatively different from the percepts belonging to the separate components. This does not necessarily mean that subjects cannot recognize the components in a mixture, since masking will seldomly be complete.

The second possibility starts with the concept of a highly specific taste system. If the taste system has a high specificity through all levels, then interaction of patterns cannot occur. In this case it is more convenient to accept the idea of spatial inhibition: activity in one fiber type suppresses the simultaneous activity in another fiber type and vica versa.

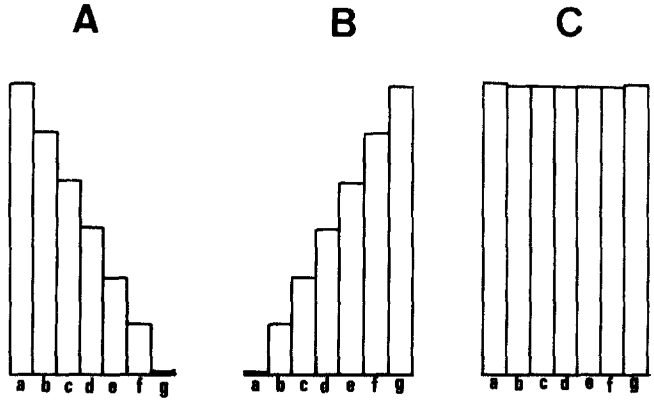

FIG. 4. Two hypothetical profiles and their mixtures expressed as the sum of the two components. Profile A shows the hypothetical pattern across fibers a, b, . . . g, and profile B shows another pattern across the same fibers. If the components A and B are mixed, without weakening their molarity, pattern C results. The spike frequency of the combined patterns is the sum of the separate spike frequencies.

Under the summation hypothesis the total number of spikes is not affected, but the identity of the stimulus is obscured, while masking by inhibition reduces the number of spikes. It is possible to test these two alternatives in an electrophysiological experiment.

Evidently it cannot be said that there is no specificity at all in the taste system. The receptor sites seem to be rather specific to certain substances. Furthermore the discovery of highly specific fibers [7, 12, 28, 29] would contradict such a statement. Specificity and patterning do not necessarily exclude each other. If all fibers were equally sensitive to all substances then patterning would be the only means of signaling taste quality. It is likely that the patterning is invented by the biological system in order to overcome the disadvantages of multiple sensitivity.

Since psychophysical experiments have the disadvantage that the gap between stimulus and response is maximal, it cannot be excluded on the basis of this experiment that the masking is brought about by higher, e.g. attentive mechanisms. However, it may be expected that in such a case the phenomenon is vulnerable to instruction variables or variables related to simultaneous stimulation in other sense modalities.

The results obtained in this study should not be generalized too easily to other stimulus intensities, especially not to mixtures of near threshold concentration. At the threshold other processes may confound the results. For instance NaCl in near threshold concentrations has been reported to have a sweet taste.

To test some of the possibilities mentioned here, it would be interesting to study across fiber patterns of mixtures.

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