J. Physiol. (1967), **192**, *pp.* 13–20
With 7 text-figures
Printed in Great Britain

THE RELATION BETWEEN NEURAL AND PERCEPTUAL INTENSITY: A COMPARATIVE STUDY ON THE NEURAL AND PSYCHOPHYSICAL RESPONSE TO TASTE STIMULI

BY G. BORG, H. DIAMANT, L. STRÖM AND Y. ZOTTERMAN

From the Department of Otorhinolaryngology, Umeå University and the Department of Physiology, Veterinärhögskolan, Stockholm, Sweden

(*Received* 10 *January* 1967)

SUMMARY

1. Recording the summated electrical response from the human chorda tympani in the middle ear provides data for a quantitative study of the relation between the neural activity and the strength of the stimulus applied to the tongue which can be compared with the relation between the subjective estimation and the stimulus strength.

2. Full comparative data obtained from two patients showed a very high correlation between the functions describing the subjective and the neural response in relation to the strength of citric acid and sucrose solutions applied to the tongue. In a third patient the same high correlation was obtained for NaCl and citric acid.

3. The good agreement between the individual neurophysiological experiments and the psychophysical group experiment favours the view that a fundamental congruity is found between neural activity and perceptual intensity.

INTRODUCTION

By a freak of nature the gustatory nerve fibres from the anterior part of the tongue run through the middle ear in the chorda tympani nerve. During middle ear surgery this nerve is often exposed which makes it possible to record the electrical responses of the nerve to the application of different sapid solutions on the tongue. Thus it has been possible to obtain valuable information about the relation between the strength of the gustatory stimulus and the summated electrical response from the nerve (Diamant, Funakoshi, Ström & Zotterman, 1963; Diamant, Oakley, Ström, Wells & Zotterman, 1965)

Recording from a human taste nerve offers, however, the further opportunity of comparing the relation between the stimulus strength and the

electrical response with the corresponding relation between molar concentration and the perceptual (subjective) intensity as estimated by the patient in psychophysical experiment.

This report complements previous studies of these relations (Borg, Diamant, Ström & Zotterman, 1967*a*, *b*) as both psychophysical and neural data were obtained from additional patients in response to citric acid and sucrose solutions of different molarities, thus enabling us to compare the neurophysical and the psychophysical functions in the same individual.

METHODS

Subjects. These experiments were carried out in the Department of Otorhinolaryngology at the University of Umeå in November 1965, February 1966 and August 1966. The data in this study are collected from experiments on five otosclerotic patients on whom stapes mobilization was performed.

Neural recording. The special precautions to be taken in an unscreened operation room in a big hospital and a description of the summator circuit used have previously been described (Diamant *et al.* 1965).

Psychophysical experiments. Two days before the operation psychophysical taste experiments with citric acid, NaCl and sucrose were carried out on the patients. The method of magnitude estimation was used. This method, which was introduced by Stevens (1957), requires that the subjects can handle numbers and make quantitative estimations on the ratio level. In a trial experiment all patients had to make estimations of surfaces of different sizes so that we could screen out those who obviously could not make magnitude estimations. The same stimuli and the same random order of presentation were used in the electrophysiological experiments. The stimuli were presented in pairs, the standard with one comparison stimulus. In addition psychophysical experiments with salt and citric acid were made on fourteen young students.

RESULTS

The results of psychophysical experiments with a group of fourteen young students are seen in Fig. 1. A straight line may be very nicely fitted to the psychophysical response to citric acid when plotted against molarity in log–log co-ordinates. A simple power function $R = cM^n$, with $n = 0{\cdot}67$, describes the relation. Although the fit of a straight line to the salt values is not so good, the relation may also be described with a power function of the form $R = \alpha + cM^n$, with a rather high α value and $n = 1{\cdot}0$. The result for salt is in accordance with previous results by Ekman, who introduced the additive constant α and found a power function of this form applicable to salt and sucrose (Ekman, 1961; Ekman & Åkesson, 1965) but with n slightly above 1·0.

In Fig. 2 both the relative psychophysical and neural response to citric acid are plotted in a log-log diagram (patient C.L.). Straight lines may be adjusted to the values, i.e. a power function may describe the relations. A Fechnerian log-function gives a better fit to the variation in neural activity.

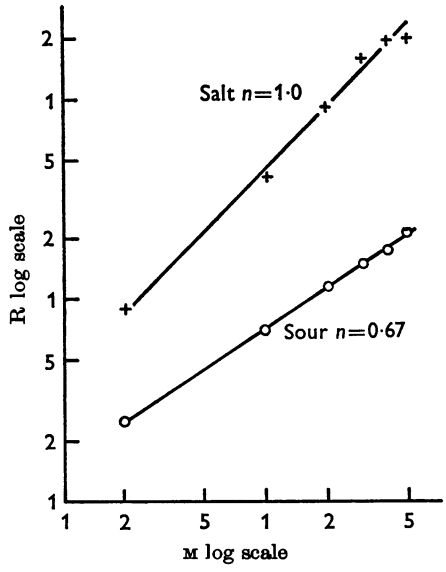

Fig. 1. Result of a psychophysical experiment on fourteen students. The perceptual intensity plotted against molarity of stimulus in a log–log scale.

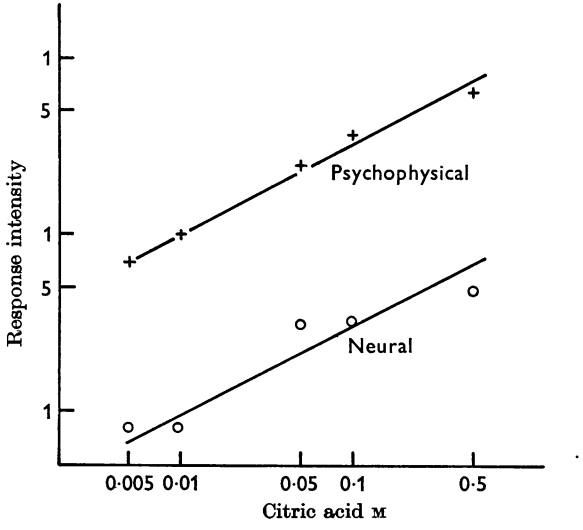

Fig. 2. Graphs from one patient (C.L.), showing subjective intensity and neural response plotted against molarity of citric acid in log–log scale.

If as a first rough estimation we describe both the neural and the psychophysical responses with power functions of the simple form $R = cM^n$, we find an astonishingly good agreement. The exponent of the psychophysical function $n_R = 0{\cdot}5$ is the same as that of the neurophysical function $n_N = 0{\cdot}5$.

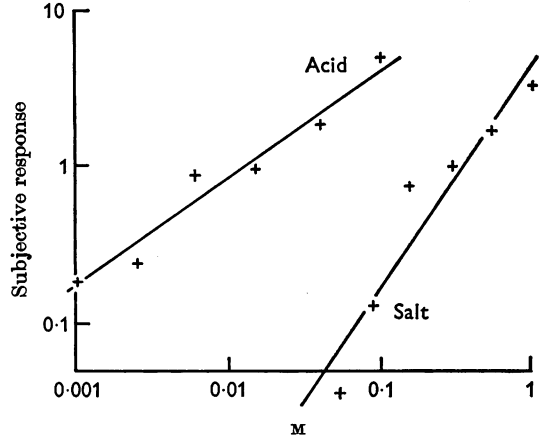

Fig. 3. Log–log diagram of relation between the subjective response and the molarity of salt and citric acid (patient V.R.).

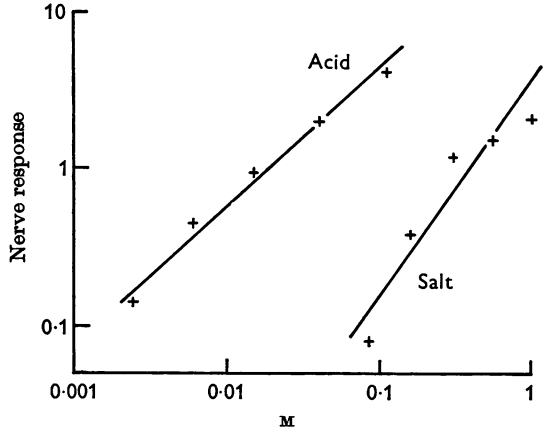

Fig. 4. Nerve response to salt and citric acid plotted against molarity. Patient H.N.

In November 1965 only one (V.R.) out of three patients was able to perform the psychophysical tests (Fig. 3). Unfortunately the chorda tympani response was very poor. We obtained, however, good responses to citric acid and NaCl solutions from another patient (H.N.,Fig. 4) although she failed in the subjective tests. When plotted in a log–log diagram her neural responses gave a good fit to straight lines of about the same slopes as that

of the subjective data from the patient V.R. It is apparent that in all these cases the slope of the salt line is definitely steeper than that of the acid line.

In August 1966 we succeeded in obtaining from two patients (I.J. and S.P.) subjective estimations as well as electrical responses to sucrose and

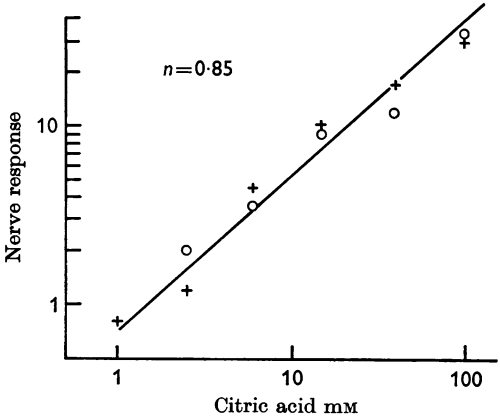

Fig. 5

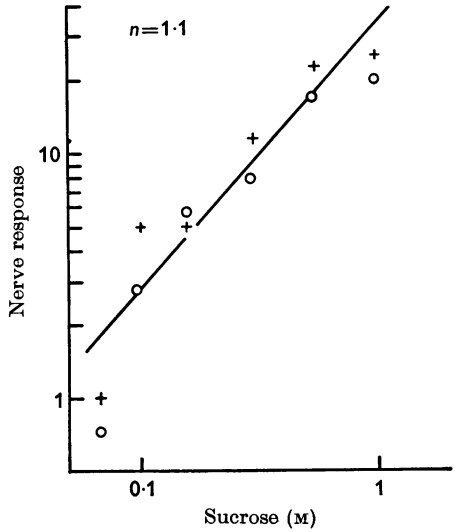

Fig. 6

Fig. 5. Nerve response to citric acid solutions (open circles) and psychophysical estimations (crosses) plotted against the molarity in log–log scale. Patient S.P.

Fig. 6. Nerve responses (open circles) and subjective estimation plotted against molarity of sucrose solution. Patient I.J.

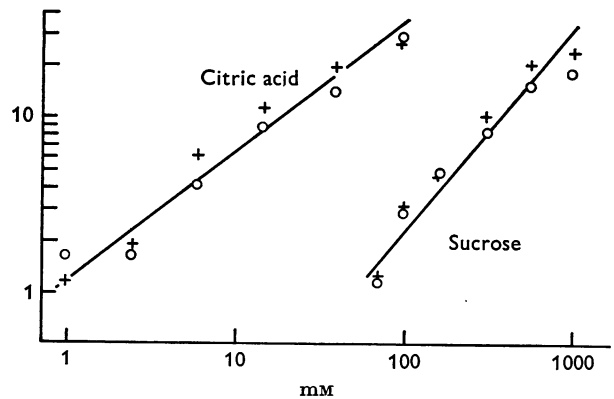

Fig. 7. Mean values of neural response (open circles) and of subjective response from two patients (I.J. and S.P.) plotted against molarity of citric acid and sucrose solution.

citric acid. In Fig. 5 both the relative psychophysical and the electrical responses to citric acid are plotted in a log-log diagram (patient S.P.). The diagram in Fig. 6 gives the relations for sucrose for patient I.J. Each point is the median of three observations in each series of tests on the same individual. How well the psychophysical functions follow the neural functions will be seen in Fig. 7 where the diagram gives the functions of the mean values obtained for these two last patients.

DISCUSSION

Quite aside from the question whether the function describing the relation between the strength of the sapid solution and the subjective estimation satisfies a Stevens' power function or a Fechnerian log function, it is apparent from the diagrams presented above that there is a remarkably close correlation between the subjective and neural data.

In a previous paper (Diamant *et al.* 1965) it was found that there are significant variations in the responses of the chorda tympani to different chemicals. It was also demonstrated that in spite of individual variations there was a good correspondence between the psychophysical and neural data on the sweetness of a series of biological sugars. This correlation between the subjective and neural functions in the same individual is still more clearly brought out in the present experiments where more complete data of both kinds was obtained for NaCl, sucrose and citric acid solutions.

When describing the relation as a power function it is clearly seen that for each of the three sapid substances, acid, sucrose and salt the exponent n of a simple power function, $R = cM^n$, will obtain a different value in such a way that the exponent for citric acid always is lower than 1, while that for sucrose and NaCl is equal to or higher than 1. The reason for this may be the fact that the range of discrimination is so much greater for citric acid than for salt and sucrose.

In recent psychophysical experiments with salt and sugar, Ekman & Åkesson (1965) have shown that the exponent of the power function varies considerably between individuals from 1·11 to 1·97 for salt and from 1·39 to 1·98 for sucrose. The authors point out that two alternative interpretations are possible: (*a*) The differences are 'perceptually real', i.e. they reflect some kind of variation with regard to sensitivity defined in a rather wide sense. (*b*) The differences reflect the different ways in which the subjects handle numbers, i.e. basically an inability of some or all objects to give adequate quantitative reports of their subjective experiences. The close correspondence between the neurophysiological and psychophysical results of the present and our previous study (Diamant *et al.* 1965), together with the fact that we have found a rather great individual cross variation

of the electrical response to salt and sugar from the chorda tympani of man, appear to support to some extent the first interpretation that there are some real perceptual differences.

Katz (1950) found that there is a linear relation between the height of the receptor potential of the muscle spindle and the peak frequency of the nerve fibre discharge, and Döving (1964) found such a relation in the frog between the peak amplitude of the electro-olfactogram, Ottoson's EOG in the frog, and the discharge of impulses from secondary neurone of the olfactory bulb. Such a linear relation between receptor potential and impulse frequency in the labellar sugar receptor of the blowfly was recently reported by Morita & Yamashita (1966).

The very close agreement between the subjective and neural function is not surprising considering that our subjective estimation, carried out by the neural analyser in our central nervous system, must work on the information it receives from the peripheral receptors. The receptor potential evoked by the sapid solution is transformed into a volley of spikes propagated to the next neurone where this volley sets up a post-synaptic potential which is transmitted to the next relay station in the same characteristic way of impulse frequency modulation. Thus it should not be surprising that the summated electrical response which we obtain from the chorda tympani varied linearly with the amplitude of the receptor potential (Kimura & Beidler 1961) as well as with the amplitude of the post-synaptic potential evoked in the cerebral cortex.

Although complete electrical data from the chorda tympani with corresponding psychophysical data were obtained in three cases only, the good agreement between these experiments and the group experiment favours the view that we have found a fundamental congruity between neural and perceptual intensity.

This investigation has been supported by grants from Svenska Maltdrycksforskningsinstitutet and from Statens Medicinska Forskningsråd.

REFERENCES

BORG, G., DIAMANT, H., STRÖM, L. & ZOTTERMAN, Y. (1967*a*). A comparative study of neural and psychophysical responses to gustatory stimuli. 'Second Symposium on Olfaction and Taste', *Wenner-Gren Center Series*, no. 8. Held in Tokyo September 1965. Oxford: Pergamon Press.

BORG, G., DIAMANT, H., STRÖM, L. & ZOTTERMAN, Y. (1967*b*). Neural and psychophysical responses to gustatory stimuli. '*Skin Senses*', Symposium held in Tallahassee 16–19 March 1966. (In the Press.)

DIAMANT, H., FUNAKOSHI, M., STRÖM, L. & ZOTTERMAN, Y. (1963). Electro-physiological studies on human taste nerves. In *Olfaction and Taste*, ed. ZOTTERMAN, Y., pp. 193–203. Oxford: Pergamon Press.

DIAMANT, H., OAKLEY, B., STRÖM, L., WELLS, C. & ZOTTERMAN, Y. (1965). A comparison of neural and psychophysical responses to taste stimuli in man. *Acta physiol. scand.* **64**, 67–74.

DÖVING, K. (1964). Studies of the relation between the frog's electro-olfactogram (EOG) and single unit activity in the olfactory bulb. *Acta physiol. scand.* **60**, 150–163.

EKMAN, G. (1961). Methodological note on scales of gustatory intensity. *Scand. J. Psychol.* **2**, 185–190.

EKMAN, G. & ÅKESSON, C. (1965) Saltness, sweetness and preferences; a study of quantitative relations in individual subjects. *Scand. J. Psychol.* **6**, 241–253.

KATZ, B. (1950). Depolarization of sensory terminals and the initiation of impulses in the muscle spindle. *J. Physiol.* **111**, 261–282.

KIMURA, K. & BEIDLER, L. M. (1961). Microelectrode study of taste receptors of rat and hamster. *J. cell. comp. Physiol.* **58**, 131–140.

MORITA, H. & YAMASHITA, S. (1966). Further studies on the receptor potential of chemoreceptors of the blowfly. *Mem. Fac. Sci. Kyushu Univ.* E, **4**, 83–93.

STEVENS, S. S. (1957). On the psychophysical law. *Psychol. Rev.* **64**, 153–181.