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INFORMATION PROCESSING IN THE TASTE SYSTEM OF PRIMATES

BY EDMUND T. ROLLS

University of Oxford, Department of Experimental Psychology, South Parks Road, Oxford OX1 3UD, England

Summary

1. Analysis of the activity of single neurones in the gustatory pathways in primates (cynomolgus monkeys) shows that the tuning of neurones to the four prototypical stimuli 1·0 mol l^{-1} glucose, 1·0 mol l^{-1} NaCl, 0·001 mol l^{-1} quinine–HCl and 0·01 mol l^{-1} HCl becomes sharper as information progresses through the taste system from the first central relay in the brainstem, the nucleus of the solitary tract, *via* the thalamus to the primary taste cortex in the frontal operculum and insula to reach a secondary cortical taste area in the caudolateral orbitofrontal cortex.

2. Feeding monkeys to satiety with glucose has no effect on the gustatory responses of neurones in the nucleus of the solitary tract, the frontal opercular taste cortex or the insular taste cortex, but decreases the magnitude of the neuronal responses of orbitofrontal cortex taste neurones which respond to glucose to zero.

3. The responses of orbitofrontal cortex taste neurones decrease to foods on which the monkey is fed to satiety, but continue to foods which have not just been eaten, that is, they reflect sensory-specific satiety, the phenomenon in which the pleasantness of the taste of a food and its acceptability, but not those of other foods, is decreased by eating that food to satiety.

4. It has been found that the orbitofrontal cortex taste area or areas receives inputs from different modalities: single neurones with unimodal responses to taste (47 %), olfactory (12 %) and visual (10 %) stimuli are found in close proximity to each other. Moreover, some single neurones show multimodal convergence, responding, for example, to taste and visual inputs (17 %), taste and olfactory inputs (10 %), and olfactory and visual inputs (4 %). Some of these multimodal single neurones have corresponding sensitivities in the two modalities: they respond best to sweet tastes (e.g. 1 mol l^{-1} glucose), and respond more in a visual discrimination task to the visual stimulus which signifies sweet fruit juice than to that which signifies saline; or they respond to sweet taste and, in an olfactory discrimination task, to fruit juice odour. These results suggest that multimodal representations are formed in the orbitofrontal cortex secondary and related taste areas.

5. It is proposed that tuning becomes sharper in the taste system through unimodal processing stages so that, after this processing, associations can be made

Key words: taste, primate, hunger, olfaction, learning, neural network.

to other modalities with minimal interference and maximum capacity in an association memory; and so that satiety can operate with some specificity, allowing responses to foods eaten to decrease without producing a decrease in responsiveness to other gustatory stimuli.

6. It is suggested that, nevertheless, ensemble encoding is used because this allows the emergent properties of completion, generalization and graceful degradation to be generated in pattern association matrix memory neuronal networks used to build multimodal representations.

7. It is suggested that, in the cerebral cortex, competitive learning is part of what occurs in neuronal networks in order to build the finely tuned ensemble-encoded representations required for association memories in multimodal cortical areas and the amygdala, and autoassociation memories in brain areas such as the hippocampus, to operate. It is also suggested that the backprojections to the cerebral cortex from the hippocampus and amygdala, and between adjacent areas of the cerebral cortex, are used to influence the storage of information in the cerebral cortex, as well as for recall, attention and dynamic top-down processing.

8. Analysis of neuronal activity in the taste system thus leads to hypotheses about the principles of sensory analysis, and the taste system may be a useful model system for studying these principles.

Introduction

The aims of this paper are to describe information processing in the taste system of primates, paying particular attention to the general principles which emerge about information representation and processing as the multiple layers of a sensory analysis system are traversed. First, the taste pathways are described. Then analyses of how information is processed from stage to stage of the taste system of primates, made partly to advance our understanding of the control of food intake and its disorders such as obesity, based on the activity of single taste neurones are described. Key issues include how taste information is represented, how this representation changes from stage to stage of the taste system, where convergence from other modalities occurs to form multimodal representations, and where taste processing is interfaced to motivational processing.

The taste pathways in primates

A diagram of the taste pathways in primates is shown in Fig. 1. The three taste nerves, the facial (seventh) (chorda tympani and greater superficial petrosal branches), glossopharyngeal (ninth) (lingual branch) and vagus (tenth) (superior laryngeal branch) terminate in the rostral part of the nucleus of the solitary tract (NTS) in the rostrolateral medulla (Norgren, 1984; Beckstead & Norgren, 1979). Second-order taste neurones in this first central relay in the taste system project monosynaptically to the thalamic taste nucleus, the parvicellular division of the ventroposteromedial thalamic nucleus (VPMpc) (Norgren, 1984; Beckstead *et al.* 1980; T. C. Pritchard, R. B. Hamilton & R. Norgren, in preparation). This direct projection from the NTS to the taste thalamus is a remarkable difference from the

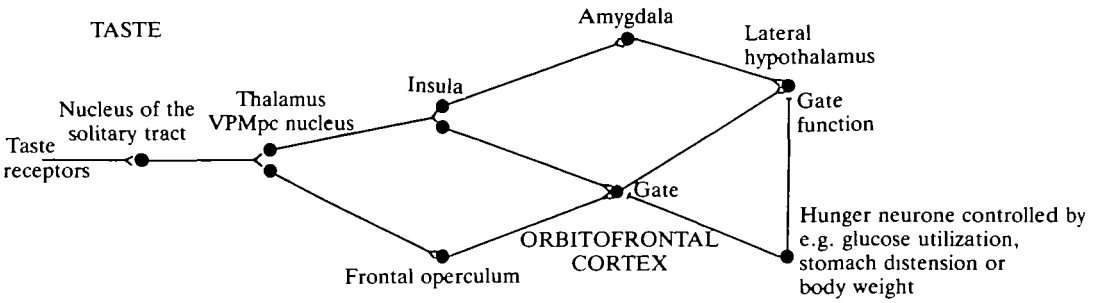

Fig. 1. Schematic diagram of the taste pathways in primates. The gate functions shown refer to the finding that the responses of taste neurones in the orbitofrontal cortex and the lateral hypothalamus are modulated by hunger.

taste system of rodents. In rodents, there is an obligatory relay from the NTS to the pontine parabrachial taste nuclei (the 'pontine taste area'), which in turn project to the thalamus (Norgren, 1984; Norgren & Leonard, 1973). The pontine taste nuclei also project to the hypothalamus and amygdala in rodents (Norgren, 1976), providing direct subcortical access to these subcortical structures important in motivational behaviour (e.g. feeding) and learning (Rolls, 1986*a*,*b*). In contrast, in primates there may well be no such direct pathway from the brainstem taste areas to the hypothalamus and amygdala (Norgren, 1984). This remarkable difference in the anatomy of the taste pathways between rodents and primates shows that, even in such an apparently phylogenetically old system as the taste system, the way in which the system functions and processes information may be very different in primates. This difference may be due to the great development of the cerebral cortex in primates, and the advantage of using extensive and similar cortical analysis of inputs from every sensory modality before the analysed representations from each modality are brought together in multimodal regions, as is documented below.

The thalamic taste area, VPMpc, then projects to the cortex, which, in primates, forms the rostral part of the frontal operculum and adjoining insula (Fig. 2), so that this is, by definition, the primary taste cortex (Pritchard *et al.* 1986). This region of cortex was implicated in gustatory function by Bornstein (1940*a*,*b*), who observed ageusias in a dozen patients with bullet wounds in this area. Patton (1960), Ruch & Patton (1946) and Bagshaw & Pribram (1953) made lesions in the same region in monkeys and noted a reliable, if temporary, elevation of taste thresholds. Benjamin & Emmers (1968) and Benjamin & Burton (1960) stimulated the peripheral taste nerves and recorded evoked potentials both on the lateral convexity of the postcentral gyrus and, with slightly longer latency, in the frontal operculum and insula. Burton & Benjamin (1971) interpreted this latter region as the pure taste area. The frontal opercular and insular cortices have been shown to be cytoarchitectonically distinct by Jones & Burton (1976), Mesulam & Mufson (1982*a*,*b*), Mufson & Mesulam (1982), Roberts & Akert (1963) and Sanides (1968, 1970).

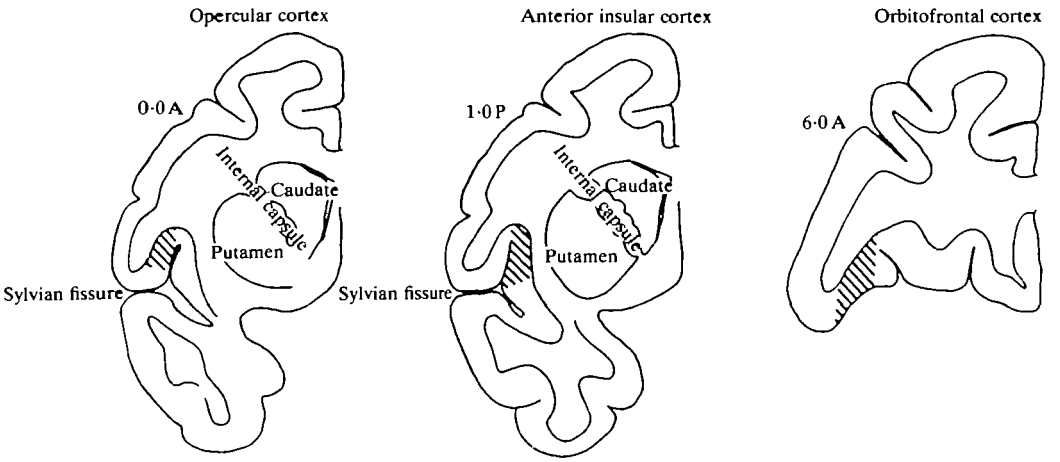

Fig. 2. Coronal sections to show the locations of the primary taste cortices in the macaque in the frontal operculum and rostral insula, and of the secondary taste cortex in the caudolateral orbitofrontal cortex. The coordinates are in millimetres anterior (A) or posterior (P) to sphenoid (see Aggleton & Passingham, 1981).

A secondary cortical taste area has recently been discovered by Rolls *et al.* (1989) in the caudolateral orbitofrontal cortex, extending several millimetres in front of the primary taste cortex (see Fig. 2). Injections of wheat germ agglutinin/horseradish peroxidase (WGA–HRP) for retrograde neuronal tracing were made into this region in three monkeys in which the exact location of this cortical taste region had been identified by recordings of the activity of single taste neurones. Labelled cell bodies were found in the frontal opercular taste cortex and in the insular taste cortex (Wiggins *et al.* 1987). Further, the caudolateral orbitofrontal cortex taste area did not receive inputs from VPMpc, but instead received projections from the mediodorsal nucleus of the thalamus, the thalamic nucleus which projects to the prefrontal cortex. These results show that the caudolateral orbitofrontal taste cortex is a secondary taste cortical area, and that it receives gustatory inputs from the primary frontal opercular and insular taste cortices. Afferents were also shown to reach the caudolateral orbitofrontal taste cortex from the more ventral part of the rostral insular cortex, the amygdala, the substantia innominata, the rhinal sulcus, and from the surrounding orbitofrontal cortex. Through some of these pathways visceral information may reach the caudolateral orbitofrontal taste cortex.

The anatomy of taste pathways beyond these is not known in detail, but in primates taste neurones are found in a more medial part of the orbitofrontal cortex (Thorpe *et al.* 1983), in the hypothalamus (Burton *et al.* 1976; Rolls *et al.* 1986) (which receives afferents from the orbitofrontal cortex) and in the amygdala (Sanghera *et al.* 1979), which receives inputs from the insular cortex (Mesulam & Mufson, 1982*a*,*b*) and from the orbitofrontal cortex (Porter & Nauta, 1979).

Gustatory responses in the nucleus of the solitary tract

Taste neurones have been found and their responses analysed in the rostral part of the nucleus of the solitary tract of macaque monkeys (Scott *et al.* 1986*a*). Different neurones were found which responded best to glucose, NaCl, HCl (sour) and quinine–HCl (bitter), but the tuning of the neurones was in most cases broad, in that, for example, 84 % of the neurones had at least some response to three or four of these four prototypical taste stimuli. To quantify the breadth of neuronal sensitivity, the breadth of tuning metric developed by Smith & Travers (1979) was applied. The proportion of a neurone's total response that is devoted to each of the four basic stimuli can be used to calculate its coefficient of entropy (H). The measure of entropy is derived from information theory, and is calculated as

$$H = -k \sum_{i=1}^{n} p_i \log p_i ,$$

where H is the breadth of responsiveness, k is a scaling constant (set so that $H = 1{\cdot}0$ when the neurone responds equally well to all stimuli in the set of size n), and p_i is the response to stimulus i expressed as a proportion of the total response to all the n stimuli in the set. The coefficient ranges from 0·0, representing total specificity to one of the stimuli, to 1·0, which indicates an equal response to all the stimuli. The values calculated from the responses to the four prototypical stimuli for the population of 52 neurones analysed in the nucleus of the solitary tract (NTS) are shown in Fig. 5. The mean coefficient was 0·87. Thus, neurones in this part of the taste system of primates have relatively broad tuning to different stimuli. It is suggested that the reason for this is that distributed encoding provides an efficient mechanism for information transmission in a relatively small number of neurones (Hinton *et al.* 1986; Erickson, 1985). A comparison across an ensemble of broadly tuned neurones, each with different but overlapping sensitivity to the different stimuli which activate the system, enables fine differences in the relative proportions of the stimuli to be detected at later processing stages.

Gustatory responses in the taste thalamus

T. C. Pritchard, R. B. Hamilton & R. Norgren (in preparation) were able to confirm that the parvicellular division of the ventroposteromedial (VPMpc) nucleus of the thalamus is the thalamic taste relay nucleus in primates by showing that single neurones in it responded to taste stimuli in macaque monkeys. The neurones were relatively broadly tuned, with a mean breadth of tuning of 0·73 (measured across responses to sucrose, NaCl, HCl and quinine–HCl). Responses to sweet and salt were most common, with 56 % responding best to sucrose, and 24 % responding best to NaCl. Relatively few neurones had best responses to HCl or quinine–HCl (14 %), and most of the responses to HCl and quinine–HCl were

described as side-band responses in NaCl-best neurones. In addition to gustatory neurones, some neurones in the nucleus responded to tactile stimuli.

Gustatory responses in the primary taste cortex

To investigate this region in the primate physiologically, Sudakov *et al.* (1971) recorded single-neurone activity in the frontal operculum and insula of the monkey in response to chemical stimulation of the tongue. Of 946 cells tested for gustatory sensitivity, only 33 (3·5%) gave responses, 30 of them excitatory. Every neurone responded to more than one of the three stimuli (NaCl, sucrose, milk) employed.

In a more recent and extensive series of investigations of the neurophysiology of the taste system of the primate, Rolls and his colleagues have analysed the responses of single neurones in several cortical areas concerned with taste in the cynomolgus macaque monkey, *Macaca fascicularis*. In a first area studied, the responses of 165 single neurones in the frontal operculum with gustatory responses to stimuli which included NaCl, glucose, HCl, quinine (QHCl), water and a complex taste stimulus, blackcurrant juice, were analysed (Scott *et al.* 1986*b*). The taste region was found to be located in the dorsal part of the frontal operculum (see Fig. 2). The neurones were found to be more specifically tuned to the prototypical stimuli glucose, NaCl, HCl and QHCl than were neurones recorded in the same monkeys in the nucleus of the solitary tract, with a mean breadth of tuning for the opercular neurones of 0·67 (Scott *et al.* 1986*a*,*b*). Neurones with gustatory responses were also found localized in a rostral and dorsal part of the insula (see Fig. 2) (Yaxley *et al.* 1989). These neurones were also found to be a little more specifically tuned to the gustatory stimuli than were neurones recorded in the same monkeys in the nucleus of the solitary tract, with a mean breadth of tuning of the insular neurones of 0·56.

The responsiveness of the neurones to different tastes was determined by measuring the responses of each neurone to the prototypical stimuli plus water and blackcurrant juice. The profiles of these sensitivities were then compared with each other using cluster analysis to determine the main types of neurone. The cluster analysis showed that there were a number of distinct groups of neurones (Yaxley *et al.* 1989). The mean profiles of each of the groups of neurones recorded in the insula are shown in Fig. 3. This analysis makes it clear that there were groups of neurones which responded primarily to each of the prototypical stimuli, to water, and to blackcurrant juice, as well as other groups of neurones which responded to combinations of these tastants.

The gustatory neurones in the areas of the frontal opercular and rostral insular cortex shown in Fig. 2 correspond well with the cortical area which receives projections from the thalamic taste nucleus VPMpc (Pritchard *et al.* 1986) and, together, these three studies define the primary taste cortex in primates. It is of interest that the small amount of evidence available for humans was interpreted as showing that the taste cortex was much more posterior, at the lower end of the postcentral gyrus (see Bornstein, 1940*a*,*b*; Norgren, 1988). The experimental work

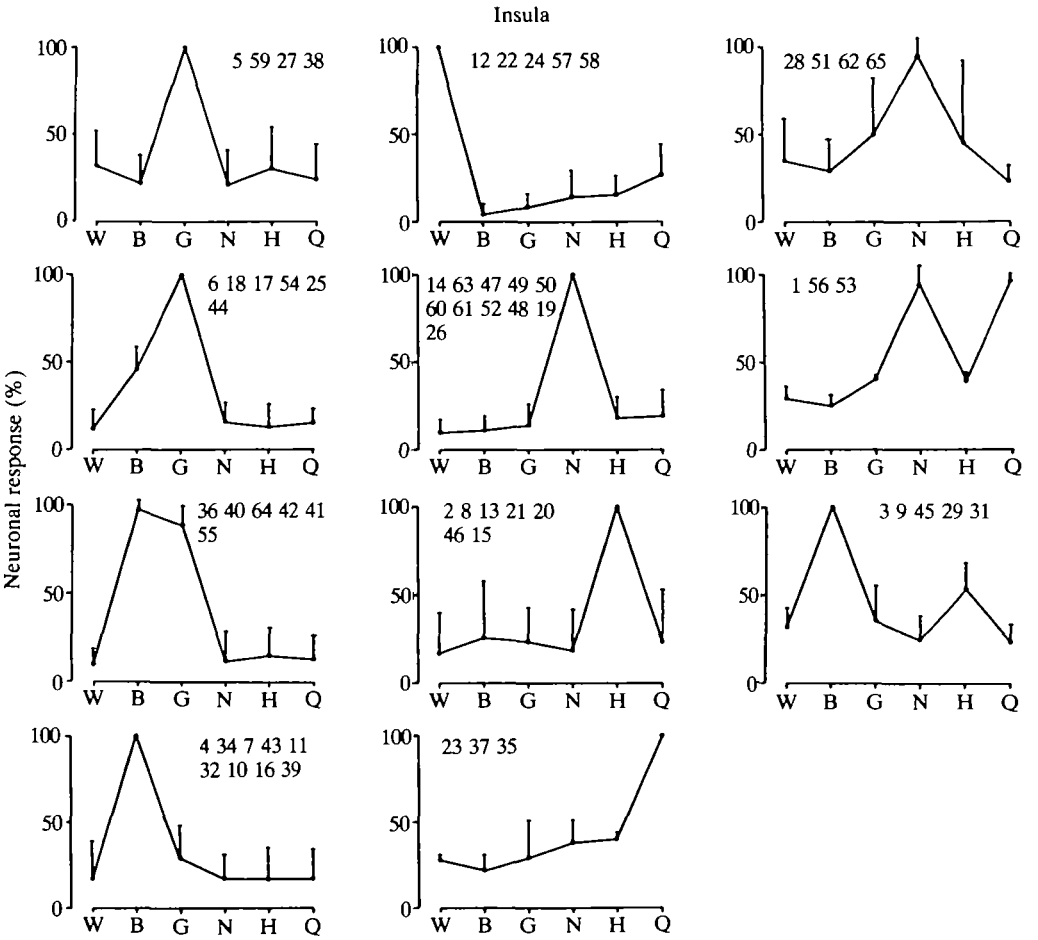

Fig. 3. The mean response profiles (+S.D.) of each of the main clusters of neurones found, using a cluster analysis, in the insular part of the primary taste cortex. The numbers of cells included in each cluster are annotated. W, water; B, blackcurrant juice; G, glucose; N, NaCl; H, HCl; Q, quinine–HCl.

just described in non-human primates suggests that the human primary taste cortex may be much more anterior, in the rostral insula and frontal operculum.

Gustatory responses in the caudolateral orbitofrontal secondary cortical taste area

In a study of the role of the orbitofrontal cortex in learning, Thorpe *et al.* (1983) found a small proportion of neurones (7·9 %) with gustatory responses in the main part of the orbitofrontal cortex. In some cases these neurones were very selective for particular gustatory stimuli. Therefore, when they set out to search for a secondary taste cortical area, Rolls *et al.* (1989) started recording at the anterior boundary of the opercular and insular cortical taste areas, and worked forward towards the orbitofrontal area investigated by Thorpe *et al.* (1983). In recordings

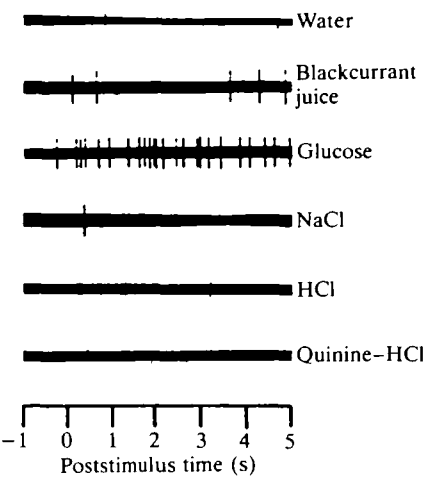

Fig. 4. Examples of the responses recorded from one caudolateral orbitofrontal taste cortex neurone to the six taste stimuli, water, 20% blackcurrant juice, 1 mol l^{-1} glucose, 1 mol l^{-1} NaCl, 0·01 mol l^{-1} HCl and 0·001 mol l^{-1} quinine–HCl.

made from 3120 single neurones, Rolls *et al.* (1989) found a secondary cortical taste area in the caudolateral part of the orbitofrontal cortex of the cynomolgus macaque monkey, *Macaca fascicularis*. The area is part of the dysgranular field of the orbitofrontal cortex, OFdg (see Fig. 2), and is situated anterior to the primary taste cortical areas in the frontal opercular and adjoining insular cortices. The responses of 49 single neurones with gustatory responses in the caudolateral orbitofrontal taste cortex were analysed using the taste stimuli glucose, NaCl, HCl, quinine–HCl, water and blackcurrant juice. Examples of the responses of one orbitofrontal cortex neurone to the stimuli are shown in Fig. 4, and quite sharp tuning is evident, in that the neurone responded primarily to the taste of glucose. The mean breadth of tuning coefficient (calculated over the responses to the four prototypical stimuli) for 49 cells in the caudolateral orbitofrontal cortex was 0·39. This tuning is much finer than that of neurones in the nucleus of the solitary tract of the monkey, and finer than that of neurones in the primary frontal opercular and the insular taste cortices. This increase in the sharpness of tuning across these different stages of processing in the taste system is indicated by the comparison shown in Fig. 5.

A cluster analysis showed that at least seven different groups of neurones were present. The mean profiles of these groups are shown in Fig. 6. For each of the taste stimuli glucose, blackcurrant juice, NaCl and water there was one group of neurones which responded much more to that tastant than to the other tastants. The other groups of neurones responded to two or more of these tastants, such as glucose and blackcurrant juice. In this particular region, neurones were not found with large responses to HCl or quinine–HCl (Rolls *et al.* 1989). In more recent studies by E. T. Rolls & L. L. Wiggins, the area of orbitofrontal cortex from which

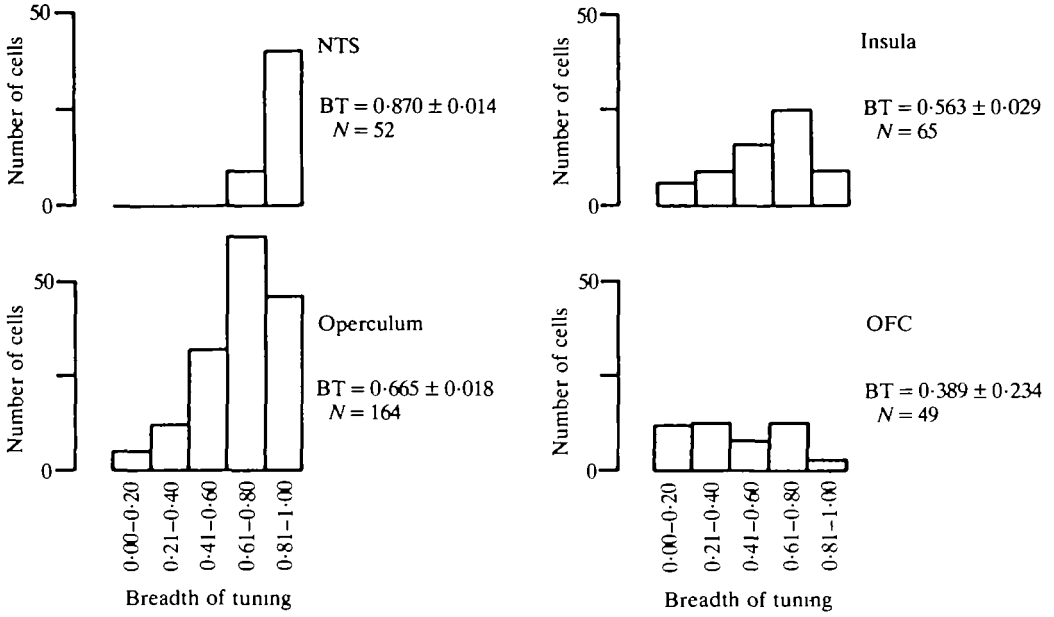

Fig. 5. The breadth of tuning index (see text) for neurones recorded in the nucleus of the solitary tract (NTS), the primary taste cortical areas in the frontal operculum and insula, and the secondary taste cortical area in the caudolateral orbitofrontal cortex (OFC) is shown. The means (±S.E.M.) and the number of neurones in the sample for each area are shown.

recordings have been made has been extended, and neurones with large responses to other stimuli, such as HCl, quinine and monosodium glutamate, have been found. In this study of further regions of the orbitofrontal cortex, Rolls & Wiggins are finding further areas with taste-responsive neurones, some of which are broadly tuned, but, as in the earlier studies (Thorpe *et al.* 1983; E. T. Rolls, Z. J. Sienkiewicz & S. Yaxley, in preparation), some of the neurones are very finely tuned. Moreover, as described below, some of these neurones are multimodal.

Effects of satiety on taste processing at different stages of the taste pathway

To analyse the neural control of feeding, the activity of single neurones has been recorded during feeding in brain regions implicated in feeding in the monkey (Rolls, 1981, 1986*a*,*b*, 1987; Rolls & Rolls, 1982). It has been found that a population of neurones in the lateral hypothalamus and adjoining substantia innominata of the monkey respond to the sight and/or taste of food (Burton *et al.* 1976). Part of the evidence that these neurones are involved in the control of the responses which are made to food when hungry is that they only respond to food when the monkey is hungry (Burton *et al.* 1976; Rolls *et al.* 1986). Indeed, it has been suggested that the modulation of the sensory response to a motivationally relevant sensory stimulus such as the taste of food by motivational state, for

example hunger, is one important way in which motivational behaviour is controlled (Rolls, 1975, 1982).

These findings raise the question of the stage in sensory processing at which satiety modulates responsiveness. It could be that the effects of satiety are manifest far peripherally in the taste pathways, for example in the nucleus of the solitary tract. Or it could be that peripheral processing is concerned primarily with stimulus analysis and representation, and to optimize this it is independent of

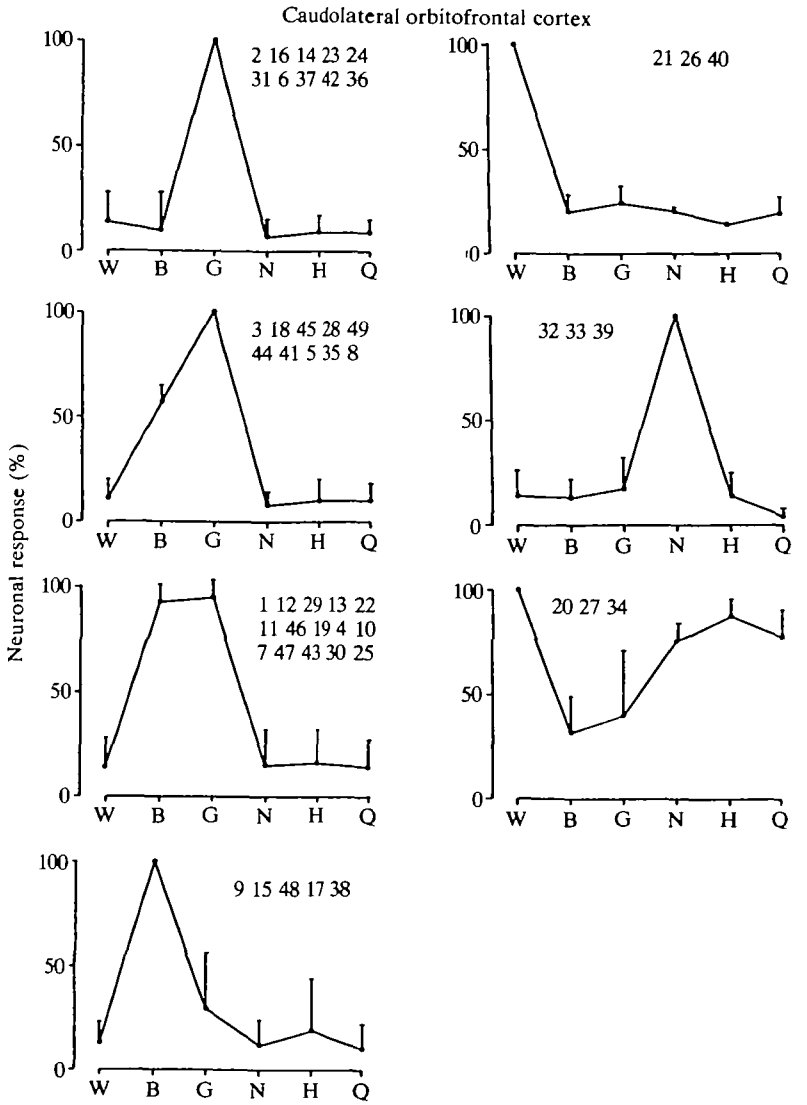

Fig. 6. The mean response profiles (+S.D.) of each of the main clusters of neurones in the secondary taste cortex (from the study by E. T. Rolls, Z. J. Sienkiewicz & S. Yaxley, in preparation). The numbers of cells included in each cluster are annotated. W, water; B, blackcurrant juice; N, NaCl; H, HCl; Q, quinine–HCl.

hunger. To provide evidence on where hunger controls taste processing in primates, the responses of single neurones at different stages of the taste system have been analysed while cynomolgus monkeys are fed to satiety, usually with 20% glucose solution. To ensure that the results were relevant to the normal control of feeding (and were not due, for example, to abnormally high levels of artificially administered putative satiety signals such as gastric distension or plasma glucose), we allowed the monkeys to feed until they were satiated, and determined whether this normal and physiological induction of satiety influenced the responsiveness of neurones in the taste system, which were recorded throughout the feeding until satiety was reached. The recordings were made in the monkey to make the results as relevant as possible to our understanding of sensory processing and the control of feeding, and its disorders, in humans.

We have found that this modulation of taste-evoked signals by motivation is not a property found in early stages of the primate gustatory system. The responsiveness of taste neurones in the nucleus of the solitary tract is not attenuated by feeding to satiety (Yaxley *et al.* 1985). Thus, taste processing at this early stage of the taste system does not appear to be modulated by satiety, the signals for which include gastric distension (Gibbs *et al.* 1981) as well as other signals (Rolls & Rolls, 1977). We have also found that, in the primary taste cortex, both in the frontal opercular part (Rolls *et al.* 1988) and in the insular part (Yaxley *et al.* 1988), hunger does not modulate the responsiveness of single neurones to gustatory stimuli.

In contrast, in the secondary taste cortex, in the caudolateral part of the orbitofrontal cortex, it was found that the responses of the neurones to the taste of glucose decreased to zero while the monkey ate it to satiety, during the course of which his behaviour turned from avid acceptance to active rejection (Rolls *et al.* 1989). This modulation of responsiveness of the gustatory responses of the orbitofrontal cortex neurones by satiety could not have been due to peripheral adaptation in the gustatory system or to altered efficacy of gustatory stimulation after satiety was reached, because modulation of neuronal responsiveness by satiety was not seen at the earlier stages of the gustatory system, including the nucleus of the solitary tract, the frontal opercular taste cortex, and the insular taste cortex. Evidence was obtained that gustatory processing involved in thirst also becomes interfaced to motivation in the caudolateral orbitofrontal cortex taste projection area: neuronal responses here to water were decreased to zero while water was drunk until satiety was produced (Rolls *et al.* 1989).

In the secondary taste cortex, it was also found that the decreases in the responsiveness of the neurones were relatively specific to the food with which the monkey had been fed to satiety. For example, in seven experiments in which the monkey was fed glucose solution, neuronal responsiveness decreased to the taste of the glucose but not to the taste of blackcurrant juice (see example in Fig. 7). Conversely, in two experiments in which the monkey was fed to satiety with fruit juice, the responses of the neurones decreased to fruit juice but not to glucose (Rolls *et al.* 1989).

This evidence shows that the reduced acceptance of food which occurs when

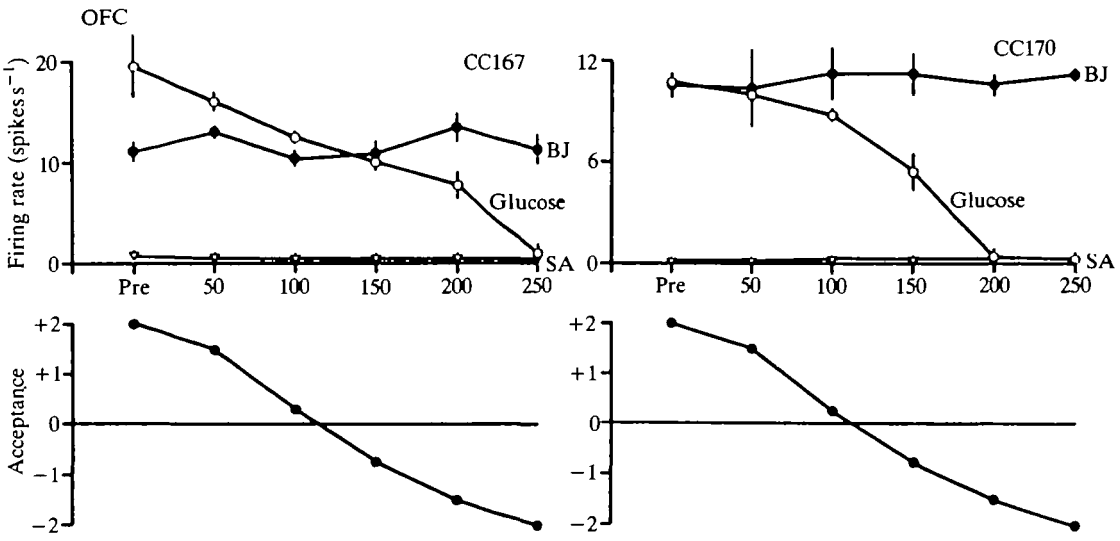

Fig. 7. The effect of feeding to satiety with glucose solution on the responses of two neurones in the secondary taste cortex to the taste of glucose and of blackcurrant juice (BJ). The spontaneous firing rate is also indicated (SA). Below the neuronal response data for each experiment, the behavioural measure of the acceptance or rejection of the solution on a scale from +2 to −2 (see text) is shown. The solution used to feed to satiety was 20 % glucose. The monkey was fed 50 ml of the solution at each stage of the experiment, as indicated along the abscissa, until he was satiated as shown by whether he accepted or rejected the solution. Pre, the firing rate of the neurone before the satiety experiment started. (From Rolls *et al.* 1989). Values are means ± S.D. ($N = 7$).

food is eaten to satiety, and the reduction in the pleasantness of its taste (Cabanac, 1971; Rolls, 1986*a*; Rolls *et al.* 1981*a*,*b*, 1982, 1983; Rolls & Rolls, 1977, 1982), are not produced by a reduction in the responses of neurones in the nucleus of the solitary tract or frontal opercular or insular gustatory cortices to gustatory stimuli. Indeed, after feeding to satiety, humans reported that the taste of the food on which they have been satiated was almost as intense as when they were hungry, though much less pleasant (Rolls *et al.* 1983). This comparison is consistent with the possibility that activity in the frontal opercular and insular taste cortices as well as the nucleus of the solitary tract does not reflect the pleasantness of the taste of a food, but rather its sensory qualities, regardless of motivational state. On the other hand, the responses of the neurones in the caudolateral orbitofrontal complex taste area and in the lateral hypothalamus (Rolls *et al.* 1986) are modulated by satiety, and it is presumably in areas such as these that neuronal activity may be related to whether a food tastes pleasant and to whether the food should be eaten.

The computation of sensory-specific satiety in the caudolateral orbitofrontal cortex taste area

The findings described above have implications for the nature of the mechan-

isms which underlie sensory-specific satiety. Sensory-specific satiety, as noted above, is the phenomenon in which the decrease in the palatability and acceptability of a food which has been eaten to satiety are partly specific to the particular food which has been eaten (Rolls, 1986*a*,*b*; Rolls *et al.* 1981*a*,*b*, 1982, 1983; Rolls & Rolls, 1977, 1982). The results just described suggest that such sensory-specific satiety cannot be largely accounted for by adaptation at the receptor level, in the nucleus of the solitary tract, or in the frontal opercular or insular gustatory cortices, to the food which has been eaten to satiety, otherwise modulation of neuronal responsiveness should have been apparent in the recordings made in these regions. Indeed, the findings suggest that sensory-specific satiety is not represented in the primary gustatory cortex. Instead, neuronal activity in the caudolateral orbitofrontal cortex is very closely related to sensory-specific satiety.

The findings lead to a proposed neuronal mechanism for sensory-specific satiety, which is as follows. The tuning of neurones becomes more specific for gustatory stimuli through the nucleus of the solitary tract, gustatory thalamus, frontal opercular taste cortex and insular taste cortex (see Rolls, 1987; Fig. 5). Satiety, habituation and adaptation are not features of the responses in these regions. The tuning of neurones becomes even more specific in the caudolateral orbitofrontal cortex, but here habituation with an onset time course of several minutes and lasting for 30 min to 2 h is a feature of the synapses which are activated and, in addition, there may be some effect on satiety of internal signals such as gastric distension and glucose utilization. Because of the relative specificity of the tuning of orbitofrontal taste neurones, this results in a decrease in the response to that food, but different foods continue to activate other neurones. One output of these neurones may be to the hypothalamic neurones with food-related responses, for their responses to the taste of food show a decrease which is also partly specific to a food which has just been eaten to satiety (Rolls *et al.* 1986).

It is suggested that the computational significance of this functional architecture is as follows. If satiety were to operate at an early level of sensory analysis then, because of the broadness of tuning of neurones, responses to both non-foods and foods would become attentuated (and this could well be dangerous if poisonous non-foods became undetectable). Further, by operating at a late stage of analysis, where tuning has become sharp, the satiety can be relatively sensory-specific, rather than generalizing to a wide range of foods. Moreover, when a food has been eaten to satiety, the intensity of its taste is decreased relatively little (Rolls *et al.* 1984), probably therefore reflecting neuronal activity in the primary taste cortex. The pleasantness of the taste of a food just eaten to satiety is what decreases, and it is therefore appropriate that this function be separated to a different area, the secondary taste cortex, in which the neuronal responses to the food eaten decrease to zero.

Multimodal representations in the taste system

At some stage in taste processing, it is likely that taste representations are

brought together with inputs from different modalities, for example with olfactory inputs, to form a representation of flavour. Takagi and his colleagues (Tanabe *et al.* 1975*a*,*b*) have found an olfactory area in the medial orbitofrontal cortex. In a mid-mediolateral part of the caudal orbitofrontal cortex is the area investigated by Thorpe *et al.* (1983) in which are found many neurones with visual and some with gustatory responses. During our recordings in the caudolateral orbitofrontal cortex taste area our impression was that it was different from the frontal opercular and insular primary taste cortices, in that there were neurones with responses in other modalities within or very close to the caudolateral orbitofrontal taste cortex (E. T. Rolls, Z. J. Sienkiewicz & S. Yaxley, in preparation). We have therefore investigated systematically whether there are neurones in the secondary taste cortex which respond to stimuli in other modalities, including the olfactory and visual modalities, and whether single neurones in this cortical region in some cases respond to stimuli from more than one modality.

In this investigation of the caudolateral orbitofrontal cortex taste area (Wiggins *et al.* 1988; Rolls & Wiggins, 1989) we found that, of the single neurones which responded to any of these modalities, many were unimodal (taste 47%, olfactory 12%, visual 10%), but were found in close proximity to each other. Some single neurones showed convergence, responding, for example, to taste and visual inputs (17%), taste and olfactory inputs (10%) and olfactory and visual inputs (4%). Some of these multimodal single neurones had corresponding sensitivities in the two modalities, in that they responded best to sweet tastes (e.g. 1 mol l^{-1} glucose), and responded more in a visual discrimination task to the visual stimulus which signified sweet fruit juice than to that which signified saline; or responded to sweet taste and, in an olfactory discrimination task, to fruit odour. An example of one such bimodal neurone is shown in Fig. 8. The neurone responded best among the tastants to NaCl (N), and best among the odours to onion odour (On) and also well

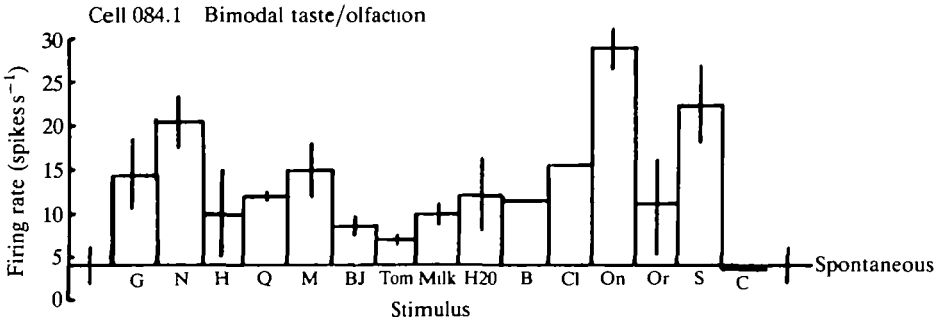

Fig. 8. The responses of a bimodal neurone recorded in the caudolateral orbitofrontal cortex. G, 1 mol l^{-1} glucose; N, 0·1 mol l^{-1} NaCl; H, 0·01 mol l^{-1} HCl; Q, 0·001 mol l^{-1} quinine–HCl; M, 0·1 mol l^{-1} monosodium glutamate; BJ, 20% blackcurrant juice; Tom, tomato juice; B, banana odour; Cl, clove oil odour; On, onion odour; Or, orange odour; S, salmon odour; C, control no-odour presentation. The mean responses ± S.E. ($N = 4$–8) are shown. The neurone responded best to the tastes of NaCl and monosodium glutamate and to the odours of onion and salmon.

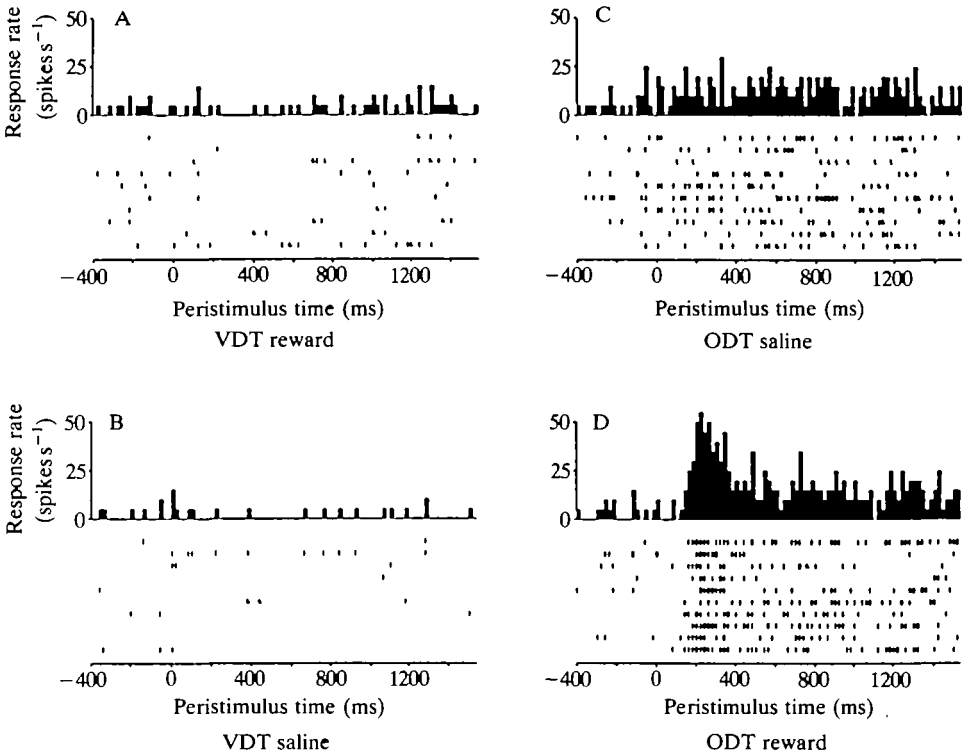

Fig. 9. The responses of a neurone recorded in the caudolateral orbitofrontal cortex to olfactory stimuli in an olfactory discrimination task (ODT) (right half of diagram). The neurone responded to the onion odour which indicated that the monkey should not lick a tube or he would obtain saline (lower), and did not respond to a fruit juice odour which indicated that the monkey could lick to obtain fruit juice (reward, upper). The responses were specific to olfactory stimuli, and did not occur when the monkey performed a visual discrimination task (left). The neuronal responses are shown as peristimulus rastergrams and time histograms. The olfactory or visual stimuli were switched on at time zero. The trials were run in random sequence controlled by computer.

to salmon (S). The olfactory input to these neurones was further defined by measuring their responses while the monkey performed an olfactory discrimination task. In the task, if one odour was delivered through a tube close to the nose, then the monkey could lick to obtain fruit juice (reward trials). If a different odour was delivered, the monkey had to avoid licking, otherwise he obtained saline (saline trials). The neurone shown in Fig. 9 responded well to the smell of onion (the discriminative stimulus on saline trials), and much less to the odour of fruit juice (the stimulus on reward trials). It had a selective and specific response to odour, and did not respond non-specifically in the discrimination task, as shown by the absence of neuronal activity while the monkey performed a visual discrimination task (see Fig. 9A,B). The different types of neurones (unimodal in different

modalities, and multimodal) were frequently found close to one another in tracks made into this region (see Fig. 10), consistent with the hypothesis that the multimodal representations are actually being formed from unimodal inputs to this region. These results show that there are regions in the orbitofrontal cortex of primates where the sensory modalities of taste, vision and olfaction converge, and that in many cases the neurones have corresponding sensitivities across modalities.

Neurones with taste responses have also been found in the mid-mediolateral part of the orbitofrontal cortex (Thorpe *et al.* 1983). These taste neurones were intermingled with neurones with visual responses, and some bimodal visual and taste neurones, with corresponding sensitivities across the modalities, were also present. This cortical region is implicated in a certain type of learning, namely in extinction and in the reversal of visual discriminations. It is suggested that the taste

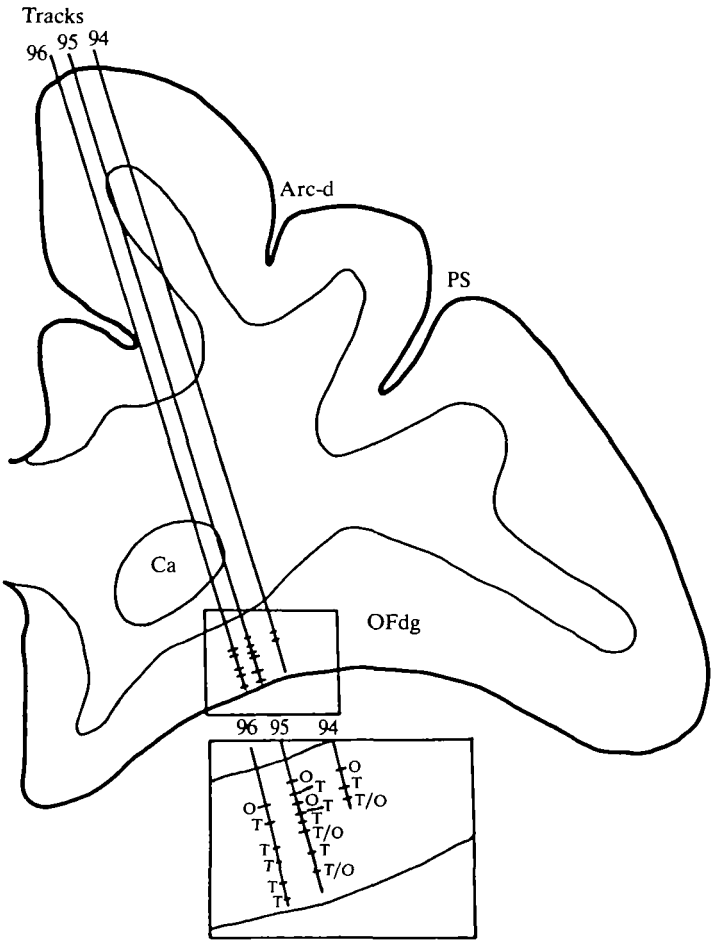

Fig. 10. Examples of tracks made into the orbitofrontal cortex in which taste (T) and olfactory (O) neurones were recorded close to each other in the same tracks. Some of the neurones were bimodal (T/O). Arc-d, arcuate sulcus; PS, principal sulcus; OFdg, orbitofrontal cortex, dysgranular part; Ca, caudate nucleus.

neurones in this region are important for these functions, for they provide information about whether a reward has been obtained (see Thorpe *et al.* 1983; Rolls, 1986*a*,*b*, 1987). Moreover, the bimodal and some of the visual neurones were useful in predicting the taste associated with a visual stimulus. Evidence that this was the case was obtained, for many of the visually responsive neurones responded only to a visual stimulus associated with a rewarding taste (e.g. glucose as compared with saline). If the experimenter altered the taste with which the visual stimulus was linked (i.e. reversal of the visual discrimination task), then these visual neurones typically altered the visual stimulus to which they responded, so that their visual responses remained associated with a given taste. This part of the orbitofrontal cortex thus seems to implement a mechanism which can flexibly alter the responses to visual stimuli, depending on the reinforcement (e.g. the taste) associated with the visual stimulus (see Thorpe *et al.* 1983).

To respond to inputs from different modalities, neurones must be able to form associations between unimodal inputs. In the following section, it is suggested that, to form such associations, the unimodal inputs must be relatively finely tuned, and that this accounts for the fact that multimodal representations, between, for example, taste and olfaction or taste and vision, are made only after a number of stages of sensory analysis, and when relatively fine tuning has been developed in each of the modalities.

The computational implications for taste processing of the formation of multimodal associations

The evidence just described on the taste system indicates that neurones become more finely tuned through the different stages of the taste system (see Fig. 5), and that multimodal representations are formed only when such finely tuned representations have been built, for example in the orbitofrontal secondary taste cortex and the amygdala (see Sanghera *et al.* 1979). It is suggested that the relatively sharp tuning is because the interface between the modalities utilizes a simple pattern association neuronal network following a Hebb rule, which requires sharp tuning of the inputs to it. The sharp tuning is required to maximize the storage capacity and minimize interference (see Rolls, 1987, 1989*a*,*b*). At the same time, the representation must remain ensemble-encoded (with each stimulus being represented by the activity of a group of neurones, not just by one very sharply tuned 'grandmother cell') to obtain the very biologically useful emergent properties of such networks. These points and the operation of simple networks for pattern association can be made using the model network shown in Fig. 11 (see also Kohonen *et al.* 1981; Kohonen, 1988; Willshaw, 1981).

Consider a population of n neurones with vertically oriented dendrites intersected by a set of n horizontally running axons (Fig. 11). The unconditioned (unlearned) stimulus (for example a taste) forces a pattern of firing (through unmodifiable synapses) onto the n vertically oriented neurones in Fig. 11. The conditioned stimulus (for example an odour paired in time with the taste) is represented by the pattern of firing of the n horizontal axons. At each intersection

of an axon with a dendrite, there is a modifiable synapse. When there is simultaneous activity in a horizontal (presynaptic) axon and a vertical (postsynaptic) neurone, then the synapse becomes modified. (The modification may consist of an increase in strength of the synapse, and the rule is often referred to as the Hebb rule.) In such a memory, information is stored in a correlation matrix formed by the outer product of a vector of n neurones representing the conditioned stimulus with a vector (perhaps also of n neurones) representing the unconditioned stimulus. Many associations can be stored in the same matrix by adding each such product to the previous summed contents of the synaptic weight matrix.

To recall an association from the memory, the conditioned stimulus is applied to the horizontal axons. Each axon activates each dendrite in proportion to how much the particular synapse was modified during learning. The firing of each vertical neurone then represents the sum of effects produced through all its synapses. This is the sum over all conditioned stimulus input axons of the firing on that axon multiplied by the synaptic strength at the synapse at each axon–dendrite intersection in the matrix.

There are many biologically desirable properties of this type of information store, including recall of a complete stimulus from the memory when only part of a stimulus is shown (i.e. completion), generalization to a similar stimulus if a stimulus which has never been seen before is shown, and considerable tolerance to partial destruction or absence during development of synapses or neurones in it (graceful degradation) (see e.g. Rolls, 1987). This type of information store also

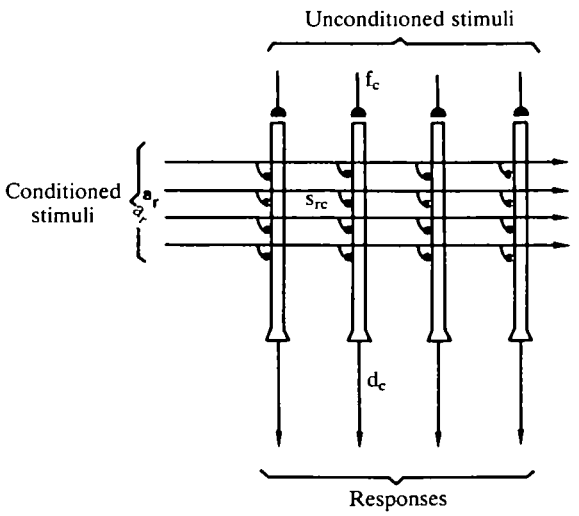

Fig. 11. Neurones connected to form a matrix memory. The vertical rectangles represent the dendrites of the neurones (d_c) which respond unconditionally to application of the unconditioned or forcing stimuli (f_c) to produce the responses. The conditioned stimuli are applied to the horizontally running axons (a_r), each one of which forms a modifiable synapse (s_{rc}) with each dendrite it passes.

shows some of the other features of biological memory, such as interference, which depends on how similar (correlated) the conditioned stimuli are. Anatomical and physiological evidence is also consistent with the idea that information storage in some parts of the brain uses such a distributed storage system (see e.g. Rolls, 1987, 1989*a*,*b*). In the orbitofrontal cortex there are, for example, NMDA receptors, which are part of a neuronal mechanism for implementation of the Hebb-like synaptic modification rule (Cotman *et al.* 1988). Another useful property of this type of memory is that it is fast, with only one synaptic delay being interposed between application of the input stimulus pattern and appearance of the output pattern.

To derive the benefits of information storage in a matrix memory, such as completion, generalization and graceful degradation, it is important that each individual stimulus (e.g. a taste or an odour) or object in the environment be represented by the firing pattern of an ensemble of neurones. This is because completion, generalization and graceful degradation rely on some of the neurones which represented the original object or event being activated by the incomplete event, by the similar event, or after some of the synapses or neurones in the network have been destroyed. However, each event must not be represented over a very large population of neurones which overlaps almost completely with the population activated by a different event for, if this were the case, then the matrix memory would display great interference and would be a very inefficient memory storage system. Given that neurones have positive firing rates which appear in many parts of the brain against a very low or zero level of spontaneous firing, the only way in which the relatively orthogonal representations required can be formed is by making the number of neurones active for any one input stimulus relatively low. (The correlation between a pair of vectors with elements which can take only positive values will only be low if only a few of the elements are non-zero, see Jordan, 1986). With sparse representations, a large number of different patterns can be stored in the memory. These two arguments lead to the suggestion that, in the brain, the representation of information is a compromise between the fine tuning required to maximize the capacity and minimize interference in association memories and the ensemble representation required for the emergent properties of such memories.

It is suggested that, in the secondary orbitofrontal cortex, associations are learned in this way, between, for example, a taste as an unconditioned stimulus and an odour or a visual stimulus as the conditioned stimulus. Presentation of the conditioned stimulus later, for example the odour, leads to recall of the taste associated originally with that odour. It is suggested that this requirement for multimodal representations to be formed by associations in this way accounts for some of the major changes in the representation of information as it progresses through a sensory system: by the stage at which the multimodal representation is formed, the representation should be ensemble-encoded, yet should involve quite sharply tuned neurones, so that different stimuli activate different, yet partially overlapping, ensembles of neurones. Moreover, to ensure that generalization

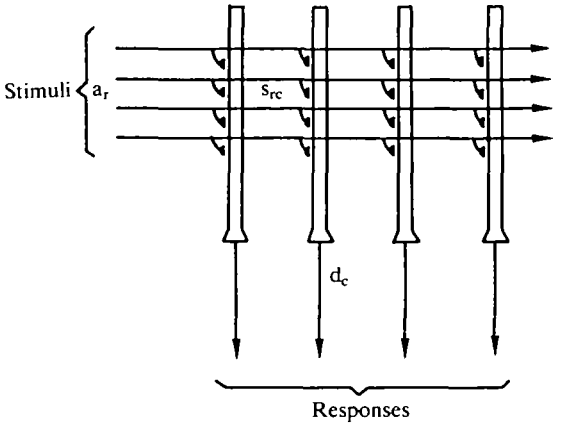

Fig. 12. A matrix for competitive learning in which the input stimuli are presented along the rows of input axons (a_r) which make modifiable synapses (s_{rc}) with the dendrites of the output neurones, which form the columns (d_c) of the matrix.

occurs usefully, it is desirable that the ensembles produced by different stimuli overlap (i.e. correlate with each other) to a degree which reflects the similarity of the stimuli.

It is interesting to consider what types of neuronal network might be useful in forming, in the unimodal processing stages, the desired representations for the multimodal areas. One type of network of interest is competitive (see Rumelhart & Zipser, 1985; Linsker, 1988; Rolls, 1989*a*,*b*). A competitive network has the architecture shown in Fig. 12. Application of an input to the horizontal axons results in an output through the synapses which initially have random values, so that different input vectors activate different output ensembles of neurones. The output neurones then compete with each other by mutual inhibition (through an inhibitory pool of neurones), so that only a few neurones are left responding highly. Synaptic modification then occurs between active inputs and the output neurones which are left firing. This process is repeated for each of the stimuli in a set a number of times (with normalization of the synaptic strength on each dendrite to prevent a winner-take-all outcome – see Rolls, 1989*a*,*b*). The network self-organizes so that the different inputs or groups of inputs are categorized onto different output neurones, which become feature analysers, in which a feature can be defined as being produced by a correlated set of inputs in the input information space (see Rolls, 1989*a*,*b*). Competitive networks effectively remove redundancy from the input information space, and produce outputs which reflect the different categories of stimulus pattern received by the network. The outputs can thus be finely tuned yet ensemble-encoded representations of the input stimuli, and would therefore be suitable as inputs to pattern association networks for cross-modal association.

It is suggested elsewhere (Rolls, 1989*a*,*b*) that competitive networks may reflect one aspect of the way in which the cerebral cortex, for example the primary taste

cortex, categorizes the inputs it receives. The structure of the cerebral cortex is more complex than that of a simple competitive net, in that there are, for example, backprojections from the succeeding cortical area which terminate in the superficial layers of the preceding cortical area, probably on the apical dendrites of cortical pyramidal cells. It is suggested that these backprojections provide some supervision to what would otherwise be an unsupervised (competitive) learning system, to assist the net to form categories which not only reflect correlations in the input information space but also reflect the utility of the categories being formed for later processing stages, including multimodal stages in which the utility of a category can be assessed by whether it is correlated with an input from another modality (Rolls, 1989*a*,*b*). The taste system may provide a useful model system for understanding sensory categorization, for categorization can be studied independently of the computation of invariance (with respect to, for example, size and rotation), which must complicate greatly the processing performed in some sensory systems, such as the visual system.

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