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The representation of pleasant touch in the brain and its relationship with taste and olfactory areas

S. Francis, E. T. Rolls,[1,CA] R. Bowtell, F. McGlone,[2] J. O'Doherty,[1] A. Browning,[1]2 S. Clare and E. Smith[2]

Magnetic Resonance Centre, University of Nottingham, Nottingham NG7 2RD; [1]Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD; [2]Unilever Research, Port Sunlight Laboratory, Wirral L63 3JW, UK

[CA]Corresponding Author

ALTHOUGH there has been much investigation of brain pathways involved in pain, little is known about the brain mechanisms involved in processing somatosensory stimuli which feel pleasant. Employing fMRI it was shown that pleasant touch to the hand with velvet produced stronger activation of the orbitofrontal cortex than affectively neutral touch of the hand with wood. In contrast, the affectively neutral but more intense touch produced more activation of the primary somatosensory cortex than the pleasant stimulus. This indicates that part of the orbitofrontal cortex is concerned with representing the positively affective aspects of somatosensory stimuli, and in further experiments it was shown that this orbitofrontal area is different from that activated by taste and smell. The finding that three different primary or unlearned types of reinforcer (touch, taste, and smell) are represented in the orbitofrontal cortex helps to provide a firm foundation for understanding the neural basis of emotions, which can be understood in terms of states elicited by stimuli which are rewarding or punishing. *NeuroReport* 10:453–459 © 1999 Lippincott Williams & Wilkins.

Key words: Cingulate cortex; Emotion; Orbitofrontal cortex; Pleasure; Smell; Somatosensory cortex; Taste; Touch

Introduction

The aim of this study was to investigate in humans whether brain regions activated by the affective aspects of touch could be found. It is known that after the primary somatosensory cortical area (SI), the somatosensory pathways continue to the insula and orbitofrontal cortex, and via both these structures to the amygdala [1–4]. It is not known where in this pathway positively affective, that is pleasant, aspects of touch are represented. In the taste system of primates, it is known that there is segregation of function, with the primary taste cortex representing the identity and intensity of the taste, whilst the secondary taste cortex, in the orbitofrontal region, represents the reward-related or affective aspect of taste (in that neurons in it only respond to the taste of food when hunger is present) [5–8]. If there is such a segregation in the touch system, it is likely to be found in the outputs of the ventral somatosensory pathway to the orbitofrontal cortex and amygdala, for the ventral visual pathway provides a representation of objects in the inferior temporal visual cortex, and reward associations of visual stimuli are presented in the orbitofrontal cortex and amygdala [6]. A representation of the positively affective components of touch is more likely in the output of this ventral touch system than the somatosensory projections to the parietal cortex, for this dorsal somatosensory system is more likely to be involved in spatial aspects of somatosensory representation, such as the position of the limbs [9].

The design of the experiment was to compare the activations of different brain regions to a pleasant but soft touch to the hand (using velvet) with an affectively neutral hard tough to the hand produced by the end of a wood dowel. The rationale of this choice of stimulus was that the more intense but neutral stimulus would relatively strongly activate parts of the somatosensory system concerned with the intensity and identification of a somatosensory stimulus, whereas the soft pleasant tactile stimulus would relatively strongly activate parts of the brain concerned with representing the pleasantness of the touch. The level of activation in different brain areas was measured using functional magnetic resonance imaging (fMRI) [10,11].

In order to assess whether any activation related to the affectively pleasant aspects of the tactile stimuli were modality-specific or were related to a general change in affect, brain activation was also measured to positively affective stimuli in two other sensory modalities, taste and smell. The taste stimu-

lus used was sweet, produced by 1 M glucose, and the olfactory stimulus was vanilla.

Materials and Methods

Touch experiments: Imaging was performed on four healthy subjects, with seven experimental runs in total. The within-subject replications provided useful evidence on the reliability of the results. Each subject consented to the protocol using a 3.0 T echo-planar imaging (EPI) scanner built at the University of Nottingham [12]. T2*-weighted coronal images were obtained with 128×64 matrix size in plane resolution of 3 mm, 12 mm slice thickness, 23 ms echo time, and gradient switching frequency of 1.9 kHz. Twelve multi-slice images were generated every 2 s (i.e. TR = 2 s). Anatomical localisation was achieved via multi-slice echo-planar data sets acquired with isotropic 3 mm resolution on each subject using an inversion recovery sequence with grey matter (TI = 1200 ms) nulled. One of the touch stimuli was applied for duration of 16 s, followed by a resting period of 16 s. This procedure was repeated for a total of 32 cycles, and comparison of the BOLD signals in the on and the off periods enabled the activation produced by that stimulus to be measured. Following this the other stimulus was then used in an identical time series.

For the analysis, the images were corrected for motion, using a two dimensional re-registration algorithm, and then the global intensity was normalised. Temporal smoothing using a kernel approximate to the haemodynamic response function, and spatial filtering by convolving with an isotropic 3D Gaussian kernel in space, whose full-width at half maximum height is twice the voxel size, was then performed. Areas of activation were evaluated using a *t*-test to compare the BOLD signals in the on and off periods, selecting the time within the onperiod based on the time course of the activation in that area. The resulting z-maps were thresholded at $p < 0.005$ using the method of Gaussian random fields [13] to correct for multiple comparisons. The measure of activation taken for each brain area was the number of significant voxels in an area multiplied by the percentage change of BOLD signal within that area, and in addition comparisons were made for the percentage change alone and the number of significant pixels alone. The functional z-maps were registered to the corresponding anatomical images, and the centre of mass of each continuous cluster of significantly ($p < 0.005$) activated voxels was obtained in Talairach coordinates (using a linear algorithm which uses key landmarks, the anterior and posterior commissures, and the left, right, anterior, posterior, superior and inferior borders of the brain) [24,25]. The time course of the changes in signal intensity in each of the activated regions was also analysed.

Pleasant touch was produced by velvet wrapped on a small (2 cm) wooden dowel, which was moved round the palm of the hand with an average force of 13 g at 1 Hz. The neutral touch was produced by the cut end of a 4.5 cm wooden dowel with exposed grain moved on the palm of the hand with an average force of 300 g. The pleasantness of each stimulus was rated on a scale from +2 indicating very pleasant, through 0 for neutral, to −2 representing very unpleasant. The mean affective rating of the pleasant touch stimulus was 1.4 ± 0.1, and that of the neutral touch by the wooden dowel was 0.3 ± 0.1.

Taste and olfactory experiments: Taste stimuli were delivered intra-orally by two polythene tubes held between the lips. The volume of the taste stimulus delivered was 0.5 ml. The taste stimuli consisted of 1 M glucose. The procedure was that 0.5 ml of a taste stimulus was delivered at the start of an 8 s on period, and 0.5 ml of almost tasteless artificial saliva (25 mM KCl, 2 mM $NaHCO_3$) was then delivered at the start of the immediately following 8 s off period. This protocol was repeated 32 times. In one such block of trials only one tastant was used, so that the mean response to that tastant (relative to artificial saliva) could be calculated over that block of 32 trials. The subjects reported tasting the stimuli well in the first 6 s delivery, using a minor tongue motion to wash the tastant around the mouth. The subjects were also able to swallow the small quantity of liquid delivered in the period 6–8 s after a stimulus was delivered, so that they were then ready for the next liquid delivery when it occurred at the end of each 8 s time period. Six subjects were scanned up to three times. Head motion required some data sets to be discarded, leaving seven datasets to be analysed. The pleasantness rating of the glucose stimulus was assessed on a scale of +2, indicating very pleasant, through 0 for neutral, to −2 representing very unpleasant. The mean rating was +1, indicating that the glucose tasted pleasant to the subjects. In control experiments not described in detail here, 0.1 M NaCl was also used as the taste stimulus. It also produced activation in the taste areas described in this paper, and shows that the areas described were responding to taste and not to some non-taste quality of the glucose such as that is hypertonic. (The 0.1 M NaCl is mildly hypotonic.)

The olfactory stimuli (vanilla) were delivered birhinally by two Teflon tubes (to which odourants did not stick), which were less than the diameter of the nostrils, so that the subject could inhale nor-

mally through the nostrils. The olfactory stimulus was produced by delivering 50 ml of air at room temperature through a solution of standard vanilla essence in a 50 ml wash bottle. This olfactometer produced concentrations of vanilla equivalent to 1 p.p.m. [16]. The olfactory stimulus was delivered over the first 6 s of each 8 s on period. Each on period was followed by an 8 s off period. This protocol was repeated 32 times. Four healthy non-smoking subjects participated in the experiment with informed consent, each subject being scanned with the fMRI techniques described above up to twice yielding eight experimental runs. The ratings of the vanilla on the pleasantness scale (range +2 to −2) were on average +1.2 (i.e. pleasant), and on the intensity scale (range +2 to −2) were on average +0.4.

Results

Pleasant touch activates the orbitofrontal cortex: Coronal MRI sections of the brain of one of the subjects showing the areas activated by the pleasant touch are shown in Fig. 1. The activations in which pixels were significant at the $p < 0.005$ level (corrected in all cases for multiple comparisons using the method of Gaussian random fields) are shown. Activation was produced in the somatosensory cortex, in the medio-lateral orbitofrontal cortex, and in some other brain regions such as the thalamus on which we do not focus in this investigation. The Talairach coordinates of the regions activated by pleasant touch in the orbitofrontal cortex are shown in Table 1. The comparison condition in all experiments in this paper is the off period in this on–off paradigm. Seven experiments were run in four subjects. The coordinates for a subject with more than one experiment are averaged. The Talairach coordinates of the region of somatosensory cortex with significant activation averaged 43 (right), −30 (posterior) and 42 (superior).

To analyse quantitatively the activations produced by the different stimuli, regions of interest were defined to cover areas in which a group of voxels showed a significance of $p < 0.005$ (computed using Gaussian random field theory). The activations in the somatosensory cortex and orbitofrontal cortex, expressed as the number of significant voxels multiplied by the percentage change of BOLD signal, are shown for the seven experiments in Fig. 2. The mean

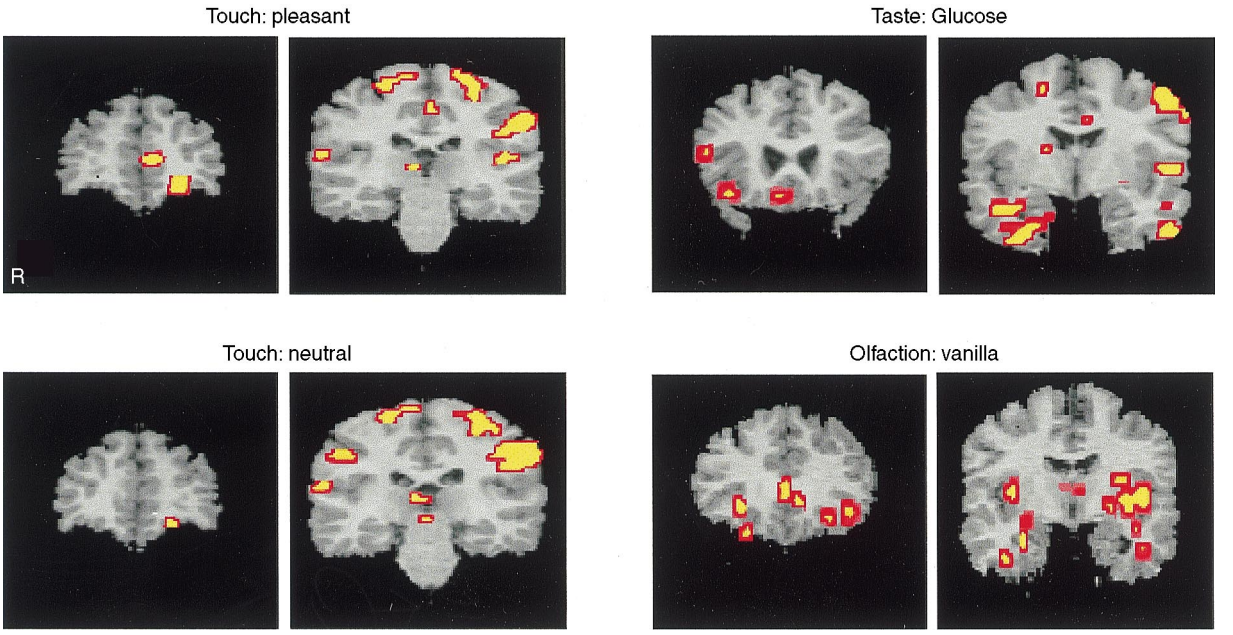

FIG. 1. Left. Coronal MRI sections of the brain of one of the subjects showing the areas activated by the pleasant and neutral touch stimuli, averaged over 32 repetitions of 16 s presentations of the somatosensory stimuli. The areas of significant activation are shown registered to a standard brain for all pixels with a probability of $p < 0.005$, corrected for multiple comparisons using the method of Gaussian random fields. The activations shown were calculated from the difference in pixel intensity over the 6 s period during which the activation for each brain region was maximal, from that measured during the control period with no somatosensory stimulation. Activation was produced in the somatosensory cortex, in the lateral orbitofrontal cortex, and in some other brain regions. The left pair of slices are through the orbitofrontal cortex (Talairach coordinates y = 32 above, 34 below). The other pair of slices are through the somatosensory cortex, with more activation in the left somatosensory cortex produced by the tactile stimulation which was delivered to the right hand for this particular experiment (y = 25 for both above and below). Right. Upper. Coronal MRI sections showing activation by taste of a region (left) which was in different subjects in the orbitofrontal cortex and/or anteroventral/subgenual cingulate cortex or adjoining medial orbitofrontal cortex (y = 22); the same section also shows activation in an insular area which is putative primary taste cortex; and (right) activation in a further part of the insula and also the anterior temporal cortex (y = −4; see Table 2). Lower. Coronal MRI sections showing activation produced (left) in part of the orbitofrontal cortex as well as in this subject in the anteroventral cingulate (y = 32), and (right) in part of the insula and also in the temporal lobe by an olfactory stimulus (y = −8). All data are from the same subject tested in the different conditions, and the right side of the brain (R) is on the left of each section.

Table 1. Talairach co-ordinates of the centres of the regions activated by pleasant touch in the orbitofrontal cortex

Subject	Left			Right		
	x (left)	y (anterior)	z (inferior)	x (left)	y (anterior)	z (inferior)
1	−19	31	−18	18	24	−21
2	−8	21	−19	12	21	−18
3	−9	22	−20	35	21	−17
4				42	28	−12

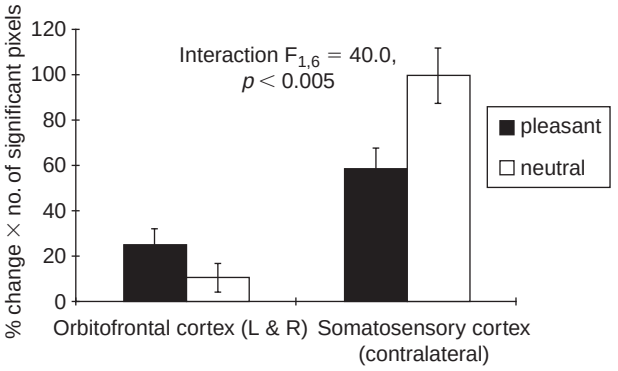

FIG. 2. Histograms showing the mean (± s.e.m., across seven experiments) of the change in activation of different brain regions during the pleasant and neutral somatosensory stimulation. The histograms show the average activation bilaterally in the orbitofrontal cortex, and contralateral to the stimulation for the somatosensory cortex. The measure of activation for each region is the average percentage change in activation in voxels with significant activation at $p < 0.005$, multiplied by the number of significant voxels.

activation (across all seven experiments) for the contralateral somatosensory cortex (central and postcentral sulcus) was 98.9 ± 12.2 (mean ± s.e.m.) for the neutral touch and 57.8 ± 8.7 for the pleasant touch (see Fig 2). In contrast, the mean activation of the orbitofrontal cortex was 11.3 ± 6.3 (mean ± s.e.m.) for the neutral touch and 24.8 ± 7.0 for the pleasant touch (see Fig. 2). A two-way analysis of variance across the subjects with one factor brain region (bilateral orbitofrontal cortex *vs* contralateral somatosensory cortex) and the other factor type of stimulation (pleasant vs neutral) showed a highly significant interaction ($F(1,6) = 47.8$, $p < 0.001$). This indicates that the orbitofrontal cortex was relatively much more activated by the pleasant than by the neutral touch, compared with the somatosensory cortex. The interaction effect was significant for the contralateral orbitofrontal cortex ($p < 0.005$, activation = 20.8) and significant ipsilateral activation was also produced (4.1, interaction $p < 0.005$). The measure of activation used was appropriate because it reflected the extent of the activation as well as the percentage change, but using just the average percentage change over significant voxels also revealed the significant interaction ($F(1,6) = 7.0$, $p < 0.037$).

The time courses of the elicited activations in different brain areas are shown in Fig. 3. The time to peak activation was slower (~18 s) in the orbitofrontal cortex than in the somatosensory cortex (~12 s), but there was no difference between pleasant and affectively neutral stimuli for either area. Although the orbitofrontal cortex is probably further on in the processing stream than the somatosensory cortex, the difference in timing is more likely to reflect differences in the intrinsic haemodynamics of each area, related, we suggest, to the lower peak firing rates and probably more spatially sparse representation likely to be present in the orbitofrontal cortex [6]

Some activation was also found in other brain areas in some subjects. For example, pleasant and neutral touch activated the subgenual cingulate region (area 25), which is adjacent to and connected to the medial orbitofrontal cortex in three experiments; the dorsal anterior part of the cingulate (area 24) in three experiments; the insula in two experiments; and the striatum in two experiments.

Areas activated by taste and olfactory stimuli: Figure 1 shows areas responsive to the taste of glucose thresholded at $p < 0.005$. It is shown in Fig. 4 and Table 2 that across the experiments the glucose stimulus gave significant activation bilaterally in the insula in a region which probably

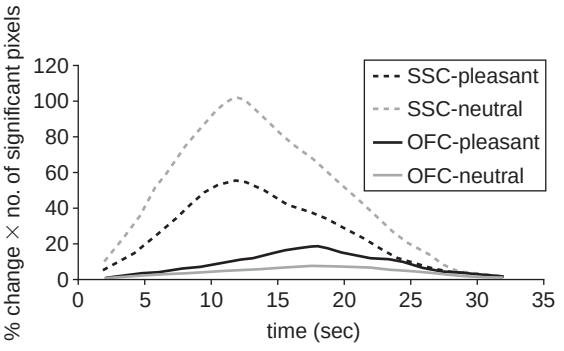

FIG. 3. Time course of the activation produced by pleasant and neutral stimuli in the right somatosensory cortex and in the left orbitofrontal cortex. The change of activation shown is the percentage change in the fMRI BOLD signal. The time course is the average over the seven experiments.

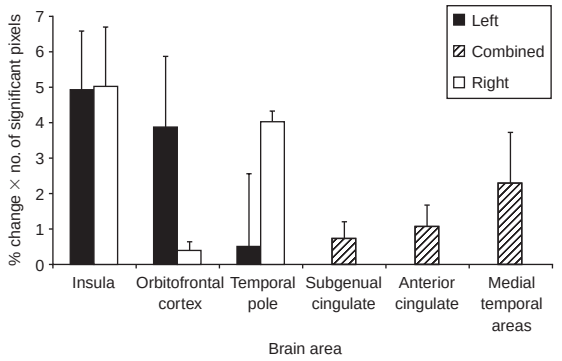

FIG. 4. Histograms showing the mean activation (±s.e.m., across seven experiments) of different cortical areas by the taste of glucose. The measure of activation for each region is the average percentage change in activation in voxels with significant activation at $p < 0.005$, multiplied by the number of significant voxels.

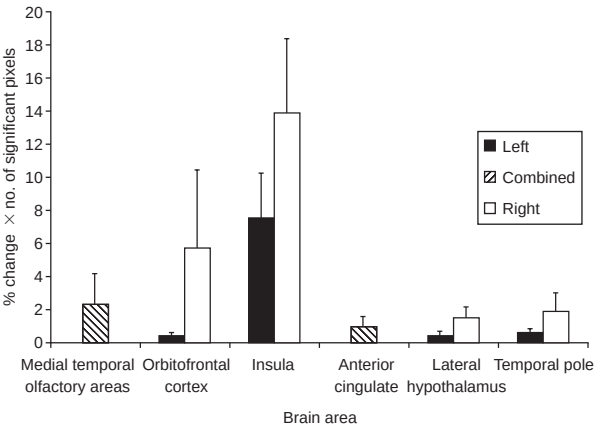

FIG. 5. Histograms showing the mean activation (±s.e.m., across seven experiments) of different cortical areas by the small of vanilla. The measure of activation for each region is the average percentage change in activation in voxels with significant activation at $p < 0.005$ level, multiplied by the number of significant voxels.

corresponds to the primary taste cortex, and in a region of the medial orbitofrontal cortex which may correspond to the secondary taste cortex by comparison with areas in non-human primates [6,7]. In some experiments, taste activation was also found in other areas (see Fig. 4 and Table 2), viz: the subgenual cingulate cortex close to the medial orbitofrontal cortex; the right temporal pole cortex; areas close to the medial wall of the temporal lobe close to areas often thought to be olfactory, sometimes including medial parts of the amygdala; and the anterior part of the cingulate cortex, area 24/32, sometimes at the anterior pole of the cingulate, and sometimes more dorsal.

Taste experiments with 0.1 M NaCl solution as the tastant produced comparable activation in the insula and orbitofrontal cortical areas described, confirming that the activation produced by glucose is taste-related, and not due to tonicity (isotonicity for glucose is ~0.3 M and for NaCl 0.15 M).

As shown in Fig. 1 for one subject, and in Fig. 5 in histogram form across the experiments, the vanilla odour produced activation in medial temporal olfactory areas (corresponding to primary olfactory areas such as the pyriform cortex, medial nucleus of the predominantly right orbitofrontal cortex (see Table 3 for coordinates). In addition, there was consistent activation in the insula, and in some subjects in cingulate areas, the lateral hypothalamus, and the temporal pole (see Table 3).

Table 2. Talairach co-ordinates (average centres of mass) of activations produced by the taste of glucose

Area	Side	Tx (L/R)	Ty (A/P)	Tz (S/I)	No. experiments
Orbitofrontal cortex	Right	6	18	−12	2
	Left	−9	24	−16	6
Insula	Right	45	3	4	5
	Left	−44	1	−3	7
Temporal pole cortex	Right	43	5	−20	4
Medial temporal lobe	Right	18	−8	−20	4
Subgenal cingulate	Left	−4	20	−6	2
Anterior cingulate	Left/Right	−1	21	23	4

Table 3. Talairach co-ordinates (average centres of mass) of activations produced by the odour of vanillin

Area	Side	Tx (L/R)	Ty (A/P)	Tz (S/I)	No. experiments
Orbitofrontal cortex	Right	21	29	−14	5
Medial temporal olfactory area	Right	17	−8	−20	4
Insula	Right	42	0	4	8
	Left	−45	−6	5	5
Anterior cingulate	Left/Right	2	13	33	4
Lateral hypothalamus	Right	6	−4	−5	3
Temporal pole	Right	40	−2	−29	3

Discussion

This study shows that different aspects of touch are represented in different brain areas. Activation of the primary somatosensory cortex was found to be related to the physical aspects of the stimulation. In particular, the primary somatosensory cortex responded more to the neutral intense stimulus (a textured piece of wood) than to a pleasant but soft tactile stimulus (velvet). In contrast, the orbitofrontal cortex responded to a greater degree to the pleasant touch stimulus than to the neutral touch. This result provides evidence for the first time that affectively positive (i.e. pleasant) aspects of touch are represented in the orbitofrontal cortex. Evidence that it is the pleasantness and not the intensity that accounts for these differences is that in an experiment in which the same neutral stimulus was used by with a lighter force, there was not significant activation of the orbitofrontal cortex. Further evidence for this is that in another study now in progress, it is being found that activation of the orbitofrontal cortex is more related to the affective aspects of the tactile stimuli than to their physical intensity. It is of course likely that the somatosensory information represented in the orbitofrontal cortex reaches it through the primary somatosensory cortex [4,9]. Nevertheless, the new findings described here indicate that the pleasantness of the touch is made manifest in the representation in the orbitofrontal cortex.

It was notable that the area of the orbitofrontal cortex activated by pleasant touch was different from the areas activated by pleasant taste (glucose) and by pleasant smell (vanillin). The touch area is 3–10 mm lateral (see Fig. 1 and Table 1), and is especially strong in the right hemisphere; the taste area is 6–9 mm lateral, and is especially strong in the left hemisphere (Table 2); and the olfactory area is moderately far lateral, centred at 21 mm lateral, with strong activation (at least with the odour of vanillin) especially in the right orbitofrontal cortex. The olfactory area in which we found activation is similar to that reported in PET studies [17], and the findings help to validate both methods. The value of using olfactory stimuli in this experiment is that it shows with the same methods and some of the same subjects that the areas activated by touch, taste and olfactory rewards in the orbitofrontal cortex are at least partly separable. The taste area activated in the left hemisphere is similar to that found to be activated by an aversive taste (salt) in a recent PET study [18], and shows that the interpretation of that study that this taste region is especially concerned with aversive taste is not correct (the pleasant taste used in that study, chocolate, has a strong olfactory component).

Some of the other brain areas activated by the pleasant stimuli used in this study were of interest. The fact that activation of parts of the cingulate cortex, including the subgenual cingulate, was found in at least some subjects by the pleasant touch, taste, and olfactory stimuli suggests that this region is not involved only in the processing of affectively negative stimuli such as pain [19] and aversive taste [18]. The bilateral activation of the insula, which probably corresponds to the primary taste cortex, was expected [15], but it was interesting that taste also activated a temporal pole area, and more on the right than the left. A cortical region in the right temporal pole was also activated by olfactory stimuli (see Table 3). The function of this area is currently unknown.

It is known from work in non-human primates (macaques) that orbitofrontal cortex neurons are activated by the taste of food only when hunger is present [5,7]. This is an indication that it is the reward value of the taste that is represented in the orbitofrontal cortex. Evidence that strongly supports this is the fact that macaques will work to obtain electrical stimulation of this part of the orbitofrontal cortex, if they are hungry [21–23]. It has also been shown that the reward value of olfactory stimuli is represented in theli is represented in the orbitofrontal cortex [24]. The discoveries that three different primary or unlearned types of reinforcer (touch, taste, and smell) are represented in the orbitofrontal cortex is helping to provide a firm foundation for understanding the neural basis of emotions, which can be understood in terms of states elicited by stimuli which are rewarding or punishing [5,6,24]. The evidence indicates that not only is the orbitofrontal cortex involved in learning about rewards [5,6,25,26], but it is also an important brain region for the representation of rewards, including stimuli such as pleasant touch. This is the first evidence we know on where positive affective aspects of touch are represented in the brain. There is considerable research on the brain regions activated by pain [19]. It will be of interest in future studies to investigate whether the positively and negatively affective aspects of touch are represented in the same brain regions, which would then be concerned generally with affect; or whether different brain areas, or subregions within areas, are concerned differentially with the pleasure, as compared to the pain, produced by tactile stimulation. At the neuronal level, there must be different populations of neurons concerned with reward and punishment, and indeed this has been shown to be the case in for example the primate orbitofrontal cortex for visual, taste, and olfactory stimuli [5–7].

Conclusion

This investigation provides evidence that an area of the human orbitofrontal cortex is activated by pleasant touch. The investigation also shows that nearby regions of the orbitofrontal cortex are activated by taste (glucose), and by odour (vanilla). The discoveries that three different primary or unlearned types of reinforcer (touch, taste, and smell) are represented in the orbitofrontal cortex is helping to provide a firm foundation for understanding the neural basis of emotions, which can be understood in terms of states elicited by stimuli which are rewarding or punishing [5].

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