Journal of Neuropsychology (2011), 5, 243–254
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The neural basis of illusory gustatory sensations: Two rare cases of lexical–gustatory synaesthesia

C. L. Jones[1,2*], M. A. Gray[1], L. Minati[1,3], J. Simner[4], H. D. Critchley[1,5,6] and J. Ward[2,6]

[1]Psychiatry, Brighton and Sussex Medical School, UK
[2]School of Psychology, University of Sussex, UK
[3]Scientific department Istituto Neurologico "Carlo Besta", Milano, Italy
[4]Department of Psychology, University of Edinburgh, UK
[5]Sussex Partnership NHS Foundation Trust, UK
[6]Sackler Centre for Consciousness Science, University of Sussex, UK

Lexical–gustatory synaesthesia is a rare phenomenon in which the individual experiences flavour sensations when they read, hear, or imagine words. In this study, we provide insight into the neural basis of this form of synaesthesia using functional neuroimaging. Words known to evoke pleasant, neutral, and unpleasant synaesthetic tastes and synaesthetically tasteless words were presented to two lexical–gustatory synaesthetes, during fMRI scanning. Ten non-synaesthetic participants were also scanned on the same list of words. The synaesthetic brain displayed a different pattern of activity to words when compared to the non-synaesthetes, with insula activation related to viewing words that elicited tastes that have an associated emotional valence (i.e., pleasant or unpleasant tastes). The subjective intensity of the synaesthesia was correlated with activity in the medial parietal lobes (precuneus/retrosplenial cortex), which are implicated in polymodal imagery and self-directed thought. This region has also previously been activated in studies of lexical–colour synaesthesia, suggesting its role may not be limited to the type of synaesthesia explored here.

For people with so-called lexical-gustatory synaesthesia, words often trigger vivid but subjective experiences of food that have texture and temperature as well as complex tastes (Gendle, 2007; Pierce, 1907; Ward & Simner, 2003; Ward, Simner, & Auyeung, 2005). These are typically located in the mouth (although some individuals describe simply knowing an association) and there are few, if any, examples of odours (e.g., smoke, perfume). As such we have referred to them as 'tastes', but acknowledge that the experiences are more complex than simple chemosensory information. The words that elicit these experiences can be spoken or written, but more common words in the

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Correspondence should be addressed to Catherine Jones, The Clinical Imaging Sciences Centre, Brighton and Sussex Medical School, Falmer BN1 9RR, UK (e-mail: c.l.jones@bsms.ac.uk).

DOI:10.1111/j.1748-6653.2011.02013.x

language are more likely to elicit an experience and word frequency is also related to subjective intensity (Simner & Haywood, 2009; Ward *et al.*, 2005). Thinking of a word may even be sufficient to elicit a synaesthetic sensation, as in the tip-of-the-tongue state (Simner & Ward, 2006).

At present, very little is known about the neurological basis of this type of synaesthesia. The primary gustatory cortex lies in the insula (Small, 2010) and gustatory hallucinations have been linked to activity in this region (Henkin, Levy, & Lin, 2000). Interactions with smell, texture, and vision can occur in associative gustatory areas such as the orbitofrontal cortex/frontal operculum (e.g., Rolls, 1996; Rolls & Bayliss, 1994), although there is also evidence to suggest that olfactory stimuli may activate the anterior insula (although not the primary taste cortex) (Carmichael, Clugnet, & Price, 1994). Further, the anterior insula is involved in somatosensory processes related to stimulation of the oral cavity (e.g., De Araujo & Rolls, 2004; Small & Prescott, 2005). Given that the left insula is involved in language (Dronkers, 1996; Wise, Greene, Buchel, & Scott, 1999) as well as flavour, we have hypothesized that it may be a crucial region in lexical–gustatory synaesthesia. A previous structural imaging study of a synaesthete who experiences tastes when hearing musical intervals found differences in white matter connectivity and local grey matter volume in several regions including the auditory cortex (in Heschl's gyrus) and the nearby posterior insula (Hänggi, Beeli, Oechslin, & Jäncke, 2008). However, it is unclear whether the latter was taste related, auditory related or both.

In this study we investigate the brain activity using fMRI in, first, a single case study that we have previously documented in detail, namely JIW (Ward & Simner, 2003). In particular, we contrast the affective nature of synaesthetic experience (i.e., whether an association is pleasant or unpleasant) with the self-reported intensity of these associations. To pursue this aim, we generated four word lists (pleasant, neutral, unpleasant, no taste) with the first three sets being of equally high synaesthetic intensity and the fourth being of low intensity. For instance, for JIW the word 'family' is described as a ham sandwich (which he rates as pleasant), 'cure' is cucumber (which he rates a neutral) and 'six' is vomit (which he rates as unpleasant). We also took the opportunity to scan an additional lexical gustatory synaesthete, BW, who was presented with the same stimuli but – as is usual from case to case – had associated experiences that were unique to her and so our words were not matched for taste/intensity in the same way.

In non-synaesthetes, intensity and pleasantness of tastes have been linked to different neural substrates (e.g., Small *et al.*, 2003). Small *et al.* (2003) found that a region in the right orbitofrontal cortex and anterior cingulate cortex responded to pleasant relative to unpleasant tastes matched for intensity, and the left anterior insula was activated by the reverse contrast. The cerebellum, pons, mid-insula, and amygdala responded to intensity irrespective of valence (Small *et al.*, 2003). Additionally, sub-regions of the orbitofrontal cortex differentially respond to pleasant and unpleasant taste experience (O'Doherty, Rolls, Francis, Bowtell, & McGlone, 2001). When a pleasant food is eaten to satiety it loses its subjective pleasantness, and this correlates with activity in the orbitofrontal cortex (Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001).

Guided by these previous findings, we explored the neural activity associated with the affective component of synaesthetically induced taste sensations with specific interest in the involvement of gustatory and limbic regions including the anterior insula, anterior cingulate, and orbitofrontal cortex.

Methods

Participants

One male (JIW, age 43 years) and one female (BW, age 48 years) who have experienced lexical-gustatory synaesthesia for as long as they can remember took part. JIW and BW report no other types of synaesthesia. In addition, we recruited 10 non-synaesthete participants (mean age 34.4 years). All participants were right handed and none had a history of psychiatric disorder or was taking psychoactive medication. The study was approved by the University of Sussex, School of Life Sciences Research Ethics Governance Committee and all participants gave informed consent.

Stimuli

JIW was given an initial list of 117 words to rate for intensity (on a scale from 1 = *no taste* to 10 = *very intense taste*) and, for items >1, pleasantness was also rated (on a scale from 1 = *unpleasant*, 5 = *neutral*, 10 = *very pleasant*). From this initial list, four categories were selected: unpleasant (pleasantness ≤ 3), neutral (pleasantness between 4 and 7), pleasant (pleasantness > 8) and no taste. Each list contained 12 words (i.e., 48 different items in total). The first three lists (containing pleasant, unpleasant, and neutral words) were matched for intensity of taste (average intensity: pleasant = $9 \pm 0.60SD$, neutral = $8.17 \pm 1.11SD$, unpleasant = 8.67 ± 1.23). These were then presented visually and each word was repeated four times (i.e., total word presentation = 192). The words were interleaved with null events (fixation cross – at a level of 20% of presentations to facilitate the identification of haemodynamic responses to event stimuli). All four lists were matched for frequency (CELEX database: Max Plank Institute, http://celex.mpi.nl), age of acquisition (mean ratings from Bird, Franklin, & Howard, 2001; Gilhooly & Logie, 1980), and number of syllables. One-way ANOVAs for each psycholinguistic variable across the four lists were all non-significant.

BW was recruited to the study after the 10 non-synaesthetes had participated in the scanning session. Therefore, BW rated the same 48-item word list for pleasantness and intensity of taste. Using the cut-offs described above, 18 words were neutral, 7 were pleasant, and 4 were unpleasant. Nineteen words elicited no taste. Of those words with a taste, BW gave a mean intensity rating of 4.26. However, given that these words were not matched in the same *a priori* way as for JIW, BW's data were analysed parametrically rather than categorically.

Procedure

Prior to scanning, all non-synaesthetes underwent a training phase. Half the non-synaesthete group was presented with lists of words that, for JIW, were unpleasant, pleasant, or neutral paired with faces depicting disgusted, happy, and neutral expressions, respectively. The remaining non-synaesthetes were presented with the same list of words although pleasant and unpleasant words were swapped to create a mismatch with respect to JIW's experiences. Participants were asked to try to form associations between the words and the emotional facial expression in an attempt to control for the affective nature of the words and isolate the gustatory aspect of the stimuli. In a subsequent test phase (prior to scanning), each word was presented once and participants were instructed to indicate whether the word had been paired with a happy, neutral, or disgusted expression. All participants responded with over 90% accuracy.

Synaesthetes and non-synaesthetes performed the same task during scanning. Words were presented in white over a black background, and each word appeared on screen for 2,000 ms, during which time a button response was recorded. Participants were instructed to indicate whether the word did or did not contain the letter ‘e’ in a forced choice two button press task (yes or no). This was chosen to ensure attention to the stimuli and to discourage deliberate retrieval of synaesthetic/emotional association. An event-related design was used, with an inter-stimulus interval of 2,000 ms. The stimuli were separated by presentation of a fixation cross. Null events, represented by a fixation cross (but no word), were presented for 20% trials to reduce response habituation. Word presentation was split into two sessions each lasting 15 min, with a short break in between. Functional MRI scanning lasted approximately 40 min, after which a T1-weighted structural scan was acquired.

Data acquisition and image pre-processing

Imaging was performed on a Siemens Sonata 1.5 T system (Siemens AG, Erlangen, Germany). Echo-planar images were acquired with the following parameters: TE = 50 ms, TR = 3,800 ms, slice thickness 3 mm, 36 slices, in-plane resolution 3×3 mm^2, matrix size 64×64. There was one experimental session and the number of volumes acquired was 191. The slice packet was inclined by 30° with respect to the bicommissural plane in order to reduce susceptibility artefacts in orbitofrontal and temporal regions (Deichmann, Gottfried, Hutton, & Turner, 2003). Structural images were acquired by means of a magnetization-prepared rapid-acquisition gradient-echo sequence, with TE (echo time) = 4.44 ms, TR (repetition time) = 1,160 ms.

Data analysis was performed using SPM8 Statistical parametric mapping (Wellcome Department of Imaging Neuroscience, University College London, London, UK). Functional images were initially realigned (rigid body transformation) to correct for head movement, slice timing corrected, and then co-registered with T1-weighted structural scan. Normalization into standardized Montreal Neurological Institute space (Collins, Neelin, Peters, & Evans, 1994) was achieved via the segmentation of the T1-weighted image (Ashburner & Friston, 2005). Functional images were then smoothed with an 8-mm FWHM Full width half maximum Gaussian kernel.

First level analyses were performed modelling, with four separate and independent regressors, the responses evoked by words eliciting pleasant, neutral, unpleasant, or tasteless; movement parameters were also included in the design matrix as regressors of no interest. In this design, the baseline was modelled implicitly. The contrasts of interest (e.g., tasty minus tasteless words) were performed at the first level. The resulting summary statistics were entered into the second-level analyses, in which we tested whether there was significantly greater activity in primary or associative regions encoding taste/flavour information in synaesthetes, and whether there was a differential activation of such regions according to the valence of the taste (pleasant, neutral, or unpleasant). Such analyses were conducted by means of one-sample *t*-tests (implemented in SPM as a two-sample *t*-test, which, when one of the groups consists of a single subject, will test whether that subject falls within the ‘normal’ control range), testing whether each synaesthete was significantly different from the controls. As our synaesthete ‘group’ was comprised of a single subject, equal variance between groups was assumed in statistical comparisons.

Notably, it was not possible to maintain this design for BW, due to the unequal number of words in each group and because the intensity of taste was not matched. Therefore, a different analysis was performed, in which we examined how intensity and pleasantness modulated evoked activity by introducing parametric modulations. For consistency, we performed this analysis also on JIW.

In the 'Results' section (and Tables 1 and 2), we report only those activations that survive family-wise error (FWE) correction ($p < .05$) at the cluster level, using an additional extent threshold of 10 voxels. Additionally, where activations within regions of interest did not exceed this stringent threshold, we also report small volume correction (SVC) statistics. In this case, we report activations, FWE corrected for cluster extent, based on the restricted statistical space defined by regional masks of areas hypothesized *a priori* and based upon previous findings, to be engaged in lexical-gustatory synaesthesia, that is, the anterior insula, orbitofrontal cortex, and anterior cingulate.

Results

Categorical effects of intensity and pleasantness

For each contrast we discuss within subject activations, considering JIW alone, the non-synaesthete group alone and then we also discuss any between group effects, that is, activations resulting from the comparison of JIW and the non-synaesthete group. Table 1 summarizes the results observed when comparing different conditions within JIW (left part of the table) and between JIW and the non-synaesthetes (right part of the table).

Average effect of word presentation

As anticipated, word presentation resulted in widespread activation in visual regions (specifically the lingual gyrus and the inferior occipital gyrus) but also in the cerebellum and bilateral insula for JIW (within subject). For the non-synaesthete group presentation of words also resulted in extensive activation including visual areas (again the lingual gyrus and the occipital gyrus), the cerebellum, superior parietal lobule, and left insula.

During word presentation, JIW showed additional activity in the middle occipital gyrus, precuneus, precentral gyrus, and thalamus when compared to the non-synaesthete group.

It is worth noting at this stage that for contrasts involving the comparison of synaesthetic taste conditions, we did not observe any above threshold activations (cut-off $p < .001$ uncorrected) in the non-synaesthetes.

Main effect of tasty words − tasteless words: [(pleasant + neutral + unpleasant) − tasteless]

Next, we compared words that evoke taste sensations versus words that have no taste associated with them (as previously rated by JIW). Tasty words elicited activation in visual regions, specifically the middle occipital gyrus and the lingual gyrus (see Table 1 left side). Second-level comparison of JIW versus the non-synaesthete group for tasty versus tasteless words elicited greater activation in the precuneus in JIW. This is shown in Figure 1 and Table 1 left side). The opposite contrast (tasteless > tasty) showed no activations.

Main effect of emotional tasting words − neutral tasting words [(pleasant + unpleasant) − neutral]

In JIW (within subject), words that evoked a valent/emotional synaesthetic sensation (i.e., which were pleasant or unpleasant), were associated with activation of the left anterior insula (−42, 18, 0), a region known to be involved in emotion processing. The activation maps are shown in Figure 2(A). To determine whether this left anterior insula activation is associated with a specific emotion (pleasant/unpleasant) we performed

Table 1. MNI coordinates for within synaesthete (JIW) activations and comparing mean scores of non-synaesthete group against JIW (one sample *t*-test)

	Within JIW						JIW versus non-synaesthetes				
Region	Brodmann area	MNI	Side	*t* score	Voxels	Region	Brodmann area	MNI	Side	*t* score	Voxels
Tasty words–non-tasty words (pleasant + neutral + unpleasant) – tasteless											
Middle occipital gyrus	18	30, −99, 6	Right	4.82	94	Precuneus	7	0, −51, 48	-	9.22	38
Lingual gyrus	17	−21, −102, −15	Left	4.54	124						
Emotional (pleasant + unpleasant) – neutral											
Anterior insula	13/14	−42, 18, 0	Left	3.81	11(SVC)	NSA					
Pleasant–unpleasant											
NSA						Lingual Gyrus	18	15, −87, −18	Right	6.55	23
Pleasant–neutral											
Cerebellum		3, −72, −12	Right	4.19	40						
Unpleasant–neutral											
Anterior insula	13	−42, 18, 0	Left	3.84	11(SVC)	Precentral Gyrus	18	0, −33, 75	Left	8.41	30
						Anterior insula	13	−42, 18, 0	Left	3.98	12(SVC)

Note. All activations are significant at cluster corrected level (FWE $p < .05$); SVC, small volume correction.

Table 2. Increasing bold activation (MNI coordinates) associated with increasing intensity of synaesthetic taste (parametric modulation) in JIW and BW

Region	Brodmann area	MNI coordinates	Side	*t* score	No. of voxels
Parametric increase in intensity of synaesthetic taste					
BW					
Precuneus/retrosplenial cortex	31	−12, −54, 30	Left	5.43	122
Middle temporal gyrus	21	−54, −27, −12	Left	4.4	58
Precentral gyrus	6	−39, −6, 33	Left	4.29	41
Supramarginal gyrus	40	−57, −48, 30	Left	4.25	126
Middle frontal gyrus	8	−24, 24, 42	Left	4.15	46
JIW					
Inferior occipital gyrus	17	30, −96, −9	Right	4.99	95
Precuneus	7	21, −57, 60	Right	4.46	69
Fusiform gyrus	18	−24, −99, −18	Left	4.41	89
Cerebellum	48	3, −63, −6	Right	4.4	48

Note. All activations are significant at cluster corrected level (FWE $p < .05$). The non-synaesthete group shows no supra-threshold activation.

planned contrasts between the three levels (pleasant, unpleasant, and neutral). Words eliciting unpleasant tastes compared with neutral tasting words revealed greater activation in the same left anterior insula region, for JIW, shown in Figure 2(B). Presentation of pleasant tasting words compared to neutral tasting words was associated with activation of the right cerebellum. For the reverse contrasts (neutral > unpleasant; neutral > pleasant) no supra-threshold activation is present.

When comparing JIW against the non-synaesthete group activation for tastes associated with an emotional valence versus neutral taste, we did not observe activation that superseded our threshold (i.e., FWE corrected at cluster level). However, when contrasting unpleasant versus neutral tasting words, JIW shows hyperactivation in the left anterior insula (−42, 18, 0) when compared to the non-synaesthetes, suggesting this

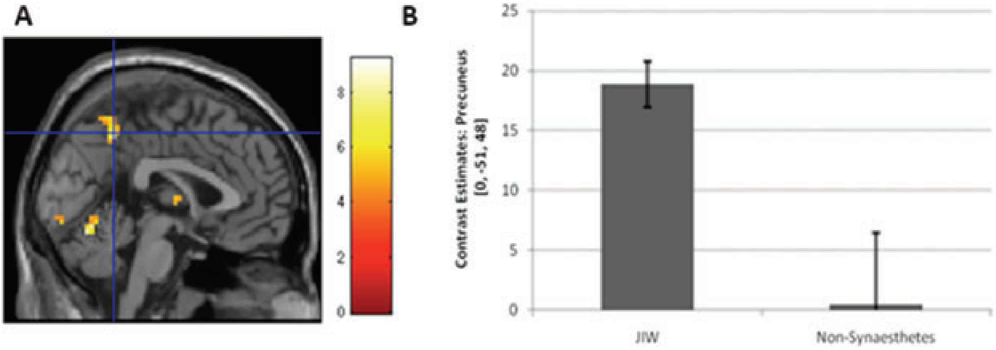

Figure 1. (A) Precuneus activation (cross-hairs at peak coordinate: 0, −51, 48), resulting from the comparison between JIW > non-synaesthetes for tasty words > tasteless words (threshold set at $p <$ .001 uncorrected for the purpose of illustration and superimposed on canonical brain, the precuneus only survives cluster correction). (B) Contrast estimates (betas) for synaesthete and non-synaesthetes in the precuneus (0,−51, 48 – peak activation). Error bars show *SD*.

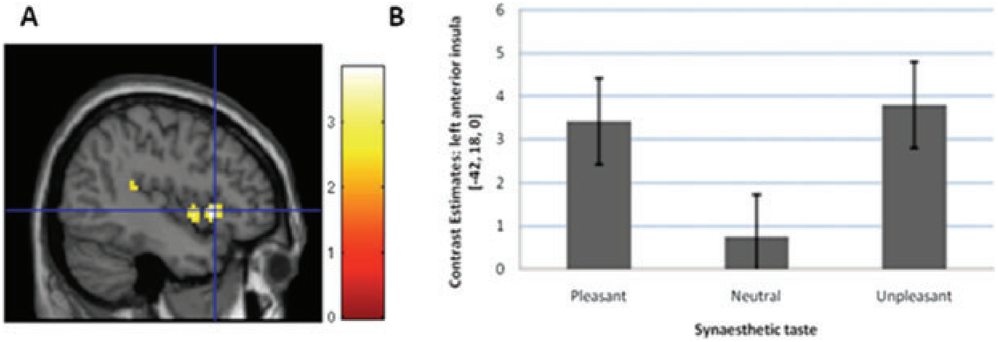

Figure 2. (A) Left anterior insula activation (−42, 18, 0 – crosshairs at peak voxel) in JIW for emotional tasting words (pleasant + unpleasant) > neutral tasting words (threshold set at $p < .001$ uncorrected for the purpose of illustration and superimposed on canonical brain). (B) Contrast estimates plotted for the region of peak activation in the left anterior insula for each taste valence. Error bars show *SD*.

insula region processes the negative affect associated with experiencing an unpleasant synaesthetic taste.

Parametric modulations of intensity and pleasantness

The analyses above are only suitable for our first synaesthete, JIW. However, it is possible to analyse both BW and JIW using parametric analysis by entering individual intensity and pleasantness ratings as regressors of interest for each event. We created two first-level analyses modelling pleasantness and intensity as parametric modulations.

In BW, increasing intensity of synaesthetic taste was associated with widespread activity in the brain, with greatest activation in the precuneus (see Table 2 for full list of activations). For decreasing intensity, there was no activation above threshold. In JIW, increasing intensity of taste was also associated with widespread activation, with greatest activation in the inferior occipital gyrus and the precuneus (see Table 2). Decreasing intensity showed no activation above threshold.

Increasing pleasantness of synaesthetic taste revealed activity (cluster corrected FWE $p < .05$) in the medial frontal gyrus in BW (MNI: 0, 60, 21), but in JIW, activation did not exceed threshold level. Activation was not observed above threshold for decreasing pleasantness of synaesthetic taste in either BW or JIW.

Discussion

The results of this study clearly demonstrate that, when lexical–gustatory synaesthetes process words that induce synaesthetic sensations, they activate additional neural networks, relative to non-synaesthetes processing the same stimuli. Further, these findings suggest that the subjective experiences of synaesthesia and the accompanying neural correlates may be differentiated into intensity and affective processing components.

With regards to the affective properties of the synaesthesia, JIW was found to have greater activity in the left anterior insula to valent words. Specifically, this was for words eliciting unpleasant synaesthetic experiences relative to those eliciting neutral experiences matched for subjective intensity and relative to the non-synaesthete group. Although the insula responds to a wide variety of gustatory stimuli (Small, 2010), it is often noted to have a particular importance in disgust (e.g., Small *et al.*, 2003). In JIW, the contrast unpleasant–neutral activated the left antero-ventral insula significantly and this same region was hyperactive in JIW when compared to the non-synaesthetes. Evidence from lesion reports indicates this left antero-ventral insula region is important in the recognition and experience of disgust (Jones, Ward, & Critchley, 2010). Finally, unlike studies on the affective properties of 'real tastes', we were unable to find any significant activity in the orbitofrontal cortex or in the anterior cingulate cortex related to the affective properties of synaesthetic tastes. However, given the low statistical power of our study, it would be unwise to draw conclusions about an absence of activity here.

With regards to the subjective intensity of this type of synaesthesia, one region appears to be particularly important – namely the medial parietal cortex. This includes the precuneus (in JIW) extending into the retrosplenial cortex (in BW). This region is not generally implicated in studies of flavour perception, and we did not predict an involvement of this region. In both JIW and BW, this activity correlated positively with subjective intensity (when modelled parametrically). In JIW, precuneus activation was also observed when words eliciting synaesthesia (combined unpleasant + neutral + pleasant) were contrasted with words, matched psycholinguistically, to words that do not elicit synaesthesia (note that we did not perform this analysis on BW as the stimuli were not matched in the same way). Cavanna and Trimble (2006) present a review of the possible functions of this region. The precuneus is activated by polymodal imagery – visual, spatial, motoric, and auditory, particularly from an egocentric perspective (e.g., my movements vs. your movements). It would be interesting to know how this region is activated in non-synaesthetes by imagery associated with food, taste, or the act of eating. It is also implicated in self-directed thought as part of its wider role in the so-called 'default mode network' (e.g., Raichle *et al.*, 2001). That is, it tends to be active during rest relative to during task performance, but such that 'rest' may constitute a contemplative mode in which attention is directed towards one's own thoughts. For synaesthetes such as JIW and BW, this state of affairs appears to be reversed – it is activated by the presence of task, but only when the stimuli elicit synaesthesia. The precuneus is also implicated in altered states of consciousness – its activity is increased during meditative yoga but decreased in sleep or vegetative states (see Cavanna & Trimble, 2006) and may be central in the Integrated Information Theory of Consciousness (Tononi, 2004).

What is the role of the precuneus in this form of synaesthesia? It could be that this region is responsible for generating the content of the synaesthesia *per se*. In this account, the synaesthetic experience may be a vivid and spontaneous 'image' (but in a non-visual sense) that is phenomenologically similar to (or mistaken for) a perceptual experience. An alternative is that it reflects attention directed inwards to reflect upon a personal experience (i.e., the synaesthesia) but it is not generating the content of the synaesthesia *per se*. The idea that the precuneus is involved in the integration of multimodal information, underpinning conscious experience, indicates it may function to bind information related to the synaesthetic elements e.g. the inducer (in this case language) and concurrent (in this case taste/flavour). The intraparietal sulcus lies adjacent to the precuneus and there is evidence to suggest hyperactivity in this region can be associated with the grapheme–colour synaesthesia (Weiss, Zilles, & Fink, 2005) and also has a higher density of grey matter in grapheme–colour synaesthetes (Weiss & Fink, 2009). The activation in the precuneus associated with increasing intensity of synaesthetic taste in JIW is likely to extend into this region of the intraparietal sulcus

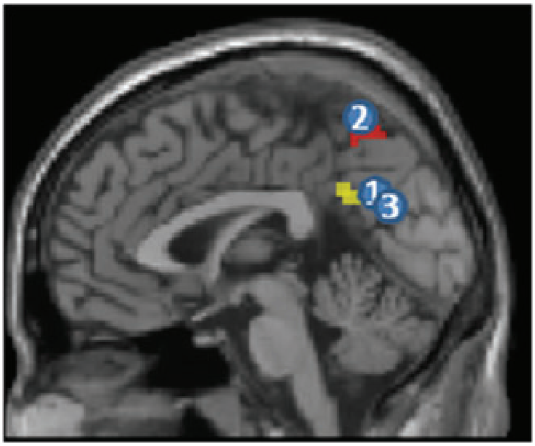

Figure 3. Activation maxima from three previous studies of synaesthesia overlayed on regions of activation from the synaesthetes in our study (MNI template). The regions are displayed projected on to a midline section ($x = 0$). Red and yellow regions represent precuneus/retrosplenial activation associated with increasing intensity of synaesthetic taste in JIW and BW, respectively. Region 1 = ventral precuneus activation with synaesthetic colour when viewing familiar names (Weiss *et al.*, 2001); region 2 = dorsal precuneus/retrosplenial activation with synaesthetic colour when viewing time words relative to other words (Steven *et al.*, 2006); region 3 = dorsal precuneus/retrosplenial activation for synaesthetic colour when listening to spoken words relative to tones.

(determined using the SPM anatomy toolbox by Eickhoff *et al.*, 2005). At present, we cannot distinguish these possibilities. However, activity in the precuneal region is present in other forms of synaesthesia. To our knowledge, it has been reported in at least three previous fMRI studies of synaesthesia all involving linguistic stimuli and in which colours are evoked (Nunn *et al.*, 2002; Steven, Hansen, & Blakemore, 2006; Weiss, Shah, Toni, Zilles, & Fink, 2001). All coordinates fall within the regions of activity associated with the experience of synaesthetic tastes, identified for either JIW or BW as shown in Figure 3. In addition, structural imaging studies of grapheme–colour synaesthetes have shown increases in cortical surface area in the precuneus relative to a control group (Jäncke, Beeli, Eulig, & Hänggi, 2009) and differences in grey matter density in the precuneus between different sub-groups of grapheme–colour synaesthetes (Rouw & Scholte, 2010). In both studies, the coordinates lie within the same clusters reported here. Thus, the precuneus may have a wider importance in synaesthesia than has hitherto been recognized.

In summary, the results show that there are functional differences in the brains of lexical–gustatory synaesthetes when processing words that elicit synaesthesia. These differences occur in a network of regions including those involved in taste and emotion processing (including the insula) and the medial parietal cortex that appears to be linked to the intensity (rather than quality) of the synaesthetic experience.

Acknowledgement

Funding: CLJ is supported by the Medical Research Council and the Brighton and Sussex Medical School.

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Received 9 August 2010; revised version received 04 March 2011