

Direct Tactile Stimulation of Dorsal Occipito-Temporal Cortex in a Visual Agnostic

Harriet A. Allen^{1,*} and Glyn W. Humphreys¹

¹Brain and Behavioural Sciences
School of Psychology
University of Birmingham
Edgbaston, Birmingham B15 2TT
UK

Summary

The human occipito-temporal cortex is preferentially activated by images of objects as opposed to scrambled images [1]. Touching objects (versus textures) also activates this region [2–10]. We used neuropsychological fMRI to probe whether dorsal regions of the lateral occipital cortex (LO) are activated in tactile recognition without mediation through visual recognition. We tested a patient (HJA) with visual agnosia due to bilateral lesions of the ventral occipito-temporal cortex but spared dorsal LO. HJA's recognition of visual objects was impaired [11, 12]. Nevertheless, his tactile recognition was preserved. We measured brain activity while participants viewed and touched objects and textures. There was overlapping activity in regions including LO and cerebellum for both stimuli for control participants, including new regions not before considered bimodal. For HJA, there were overlapping regions in the intact dorsal LO. Within a subset of the regions found in control participants, HJA showed activity only for tactile objects, suggesting that these regions are specifically involved in successful multimodal recognition. Activation of dorsal LO by tactile input is not secondary to visual recognition but can operate directly through tactile input.

Results

HJA Displayed Tactile but Not Visual Object Recognition

HJA was not able to name any objects from vision when the objects were presented either in or out of the scanner, even if these objects were subsequently recognized by touch. This fits with his lesion and confirms the diagnosis of visual agnosia [11, 13]. Despite this, HJA was able to perform perfectly on the one-back repetition task with visual images and reported that it was slightly easier to detect repeated scrambled than intact images. This is unsurprising because he should be able to discriminate differences between consecutive images by using his intact low-level visual mechanisms. HJA's lesion spares early visual areas but disrupts access to higher-level identification processes. Crucially, this will not disrupt other pathways to tactile object perception [8, 10]. Accordingly, HJA was able to recognize objects by touch (see also [11]). He named all the items he touched and displayed recognition latencies similar to those of our nonlesioned control participants (i.e., 1–3 s, depending on the complexity of the shape).

When performing the visual repetition task in the scanner, several brain regions associated with visual processing were

more active for objects than for scrambled images (see Table 1 and Figure 1A), including areas such as the dorsal LO, which are adjacent to his lesion. Areas in the parietal, caudate, and frontal regions were also more active. The recruitment of these areas might reflect the difficulty of the task for HJA because he could not use object identity to discriminate between these items.

For HJA, tactile object perception involved several regions, such as the medial frontal gyrus, that are normally ascribed to attention and decision-making processes. It also involved regions such as the superior LO and medial temporal gyrus, normally associated with visual processing. A conjunction analysis revealed that the left post-central gyrus and superior parietal lobule were significantly active in both the tactile and visual conditions (see Figure 1 and Table 1). Furthermore, there was overlap between the two conditions in the dorsal occipito-temporal regions and LO. These regions included the bimodal regions that previous studies termed LOTv [3, 10]. Extraction of the mean percent BOLD signal change (see Figure 2A) shows that in these regions there was no difference in the strength of activation from visual and tactile stimuli.

Given the difficulty in localizing brain areas specific to visual object identification in a participant incapable of visually identifying objects, we attempted to better understand the location of the dorsal occipital activity found for HJA by localizing his motion-selective regions. The dorsal region of the object-selective LO is adjacent to hMT (human homolog of motion-sensitive medial temporal regions) [1, 14]. The motion localizer produced clear bilateral activation in the cuneus, close to the occipital pole (see Table 1; also Supplemental Experimental Procedures and Figure S1). This activity was adjacent to the dorsal object-selective activity found with visual stimuli and allowed us to be confident regarding our judgments of dorsal visual regions.

Visual and Tactile Activation in Nonlesioned Control Participants

Before drawing conclusions from HJA, we needed to replicate the previous results for visual and tactile object perception in an older control group. Figure 1 (and Table S1) shows regions where viewing or touching intact objects produced greater activation than viewing scrambled images or touching textures. For viewed objects, there was activity in the expected bilateral ventral regions (e.g., lateral occipital and fusiform gyri), areas frequently implicated in object or shape perception. There was also bilateral activity in a dorsal region of the LO and in the left superior parietal lobule and medial frontal gyrus. This frontal and parietal activity may relate not so much to object perception itself but to the attentional demands of the one-back repetition task and focused attention [15–18].

For touched objects we found activation in the occipito-temporal regions (Figure 1 and Table S1). We did not, however, find activity in post-central gyrus, somatosensory, or parietal regions that have been shown to display activity in previous studies [3, 6]. There are two key possible reasons for this. First, motor activity and, to an extent, somatosensory activity was matched between the visual and tactile conditions so that

*Correspondence: h.a.allen@bham.ac.uk

Table 1. Areas Where Activation for Viewed and Touched Objects Was Greater Than that for Textures in HJA, and Areas Where Activation Is Greater for Moving than Static Patterns

Area Name	Z Max Location	Z Max	Size
Visual: Occipito-Temporal			
L occipital pole	-38, -92, 6	5.98	9163
L supramarginal gyrus	-64, -32, 24	5.55	1278
L precentral gyrus	-58, 0, 40	5.58	1126
R angular gyrus *	60, -52, 14	4.19	211
L precuneus	8, -64, 22	5.09	193
R middle temporal gyrus	66, -10, -14	4.68	186
R parahippocampal gyrus	30, -24, -14	4.42	177
L middle temporal gyrus	-58, 0, -28	4.59	110
Visual: Parietal, Central, Somatosensory			
L precentral gyrus	-34, -18, 54	4.9	243
R precentral gyrus	26, -12, 76	3.96	161
R parietal operculum	44, -22, 14	4.04	137
L insular	-36, 4, 0	5.42	360
R caudate	22, 0, 30	4.84	346
R precentral gyrus	40, -18, 48	3.84	123
R superior parietal lobule	20, -52, 74	4.31	119
Visual: Frontal			
R middle frontal gyrus	48, 10, 46	6.3	925
L frontal pole	-8, 68, 18	5.72	745
R frontal pole	46, 58, -16	4.7	448
L frontal orbital cortex	-32, 20, -20	4.9	274
R frontal pole	16, 58, 32	4.53	113
Tactile: Occipito-Temporal			
R lateral occipital cortex	28, -68, 40	5.43	1119
L precuneus	-6, -78, 42	4.64	214
R middle temporal gyrus	60, -48, 4	4.08	202
Tactile: Parietal, Central, Somatosensory			
L superior parietal lobule	-44, -40, 58	5.36	1516
L precentral gyrus	-28, -12, 78	4.09	337
R post central gyrus	16, -30, 74	4.25	322
R caudate	12, 10, 0	5.17	302
L precentral gyrus	-52, 2, 34	4.59	283
R precentral gyrus	52, 6, 36	4.57	196
R cerebellum	24, -68, -26	4.26	186
R precentral gyrus	30, -4, 30	3.67	165
Tactile: Frontal			
R middle frontal gyrus	44, 36, 18	3.93	96
Motion			
Left, extending to right cuneus	-6, -96, 20	6.23	1043
R cerebellum	16,-50,-16	4.89	269
L lateral occipital cortex	-46,-82,-2	3.9	112
Conjunction of Visual and Tactile			
L post central gyrus	-30, -36, 44		
L superior parietal lobule	-42, -38, 56		
Conjunction of Visual and Tactile: Overlap			
L precentral gyrus	-58, 0, 38		
R superior temporal gyrus	68, -24, 0		
L supramarginal gyrus	-56, -50,32		
R dLO	28, 80, 40		
L angular gyrus	-56, -50, 18		

Asterisks indicate regions similar to LOtv. R = right, L = left.

activity relating to this would be (in part) subtracted because of this comparison. Second, it should be noted that these areas have not shown significant activation in all studies of tactile object recognition [3]. Furthermore, both tactile perception

[19–21] and brain activation as measured by fMRI [22, 23] are known to decline with age. Reducing the activation threshold did show activation in the pre- and post-central gyri, but these results did not survive correction for multiple comparisons.

Finally, there was a large region of bilateral cerebellar activation for tactile objects. This region is similar to that implicated previously in tactile shape and object perception [24].

We tested for areas of conjunction between the results of the visual-object-versus-visual-texture contrast and the tactile-object-versus-tactile-texture contrast (Table S1). Several areas survived this comparison, including an area in the left dorsal LO similar to that previously named LOtv [3], as well as some slightly more anterior regions (left superior and middle temporal gyri). We also found bimodal activation in the cerebellum and in the right parahippocampal gyrus, from which it extended to the fusiform gyrus. To investigate the responses of the LO regions in more detail, we extracted the percent signal change from those areas significantly active specifically for objects in both tactile and visual conditions. Figure 2B shows that, although these regions were significantly active for both modalities, there was a stronger activation for visual stimuli in all but the left dorsal LO [$F(1,4) = 10$ $p = 0.04$].

Comparison of HJA and Nonlesioned, Age-Matched Control Participants

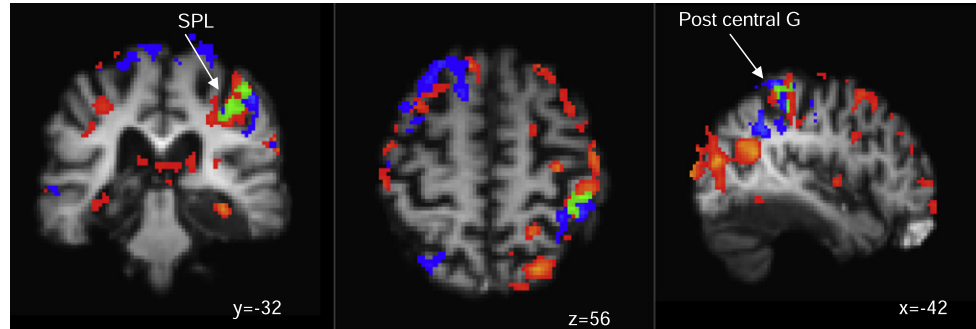
Comparison of activations in HJA and controls for touched objects showed shared activation in the left angular gyrus, bilateral LO, and calacarine sulcus (see Table S2). The frontal, central, and parietal regions did not overlap between HJA and controls. When HJA's BOLD activity was compared to the controls' activity for viewed objects [25], no regions were found to be significantly active in both cases.

We investigated whether regions that are not lesioned in HJA and that were activated by object stimuli in control participants irrespective of input modality were also active when HJA viewed or touched objects. We extracted values for percent signal change from HJA in the regions from the conjunction analysis of control participants (see Figure 2C). In two of the subregions of the right superior LO, activity from viewed objects was higher than for touched objects. In the remaining, more anterior regions, responses to viewed objects were reduced, and responses to touched objects were increased.

Discussion

We tested the neural basis for the ability of a visual agnostic to identify objects by touch. HJA was not able to name the presented objects from vision, but tactile recognition remained intact. When HJA felt objects, a network of brain regions was more active than when he felt textures. A subset of these overlapped both with those that were more active when he viewed objects than when he viewed scrambled pictures and with those areas activated in controls. The region of overlap between stimulation in response to viewed and touched objects included dorsal LO areas close to the region termed LOtv, which has been found to be activated by visual and tactile object perception [2, 3, 8, 9]. Furthermore, we found additional dorsal LO regions that were activated irrespective of modality in control participants. In HJA, two of these areas were more active for the touched objects than the viewed objects, suggesting that they could be associated with recognition itself. Two further regions were more active for the viewed objects in HJA, suggesting that, in this case, they might be involved in visual processing or imagery.

A: HJA



B: Controls

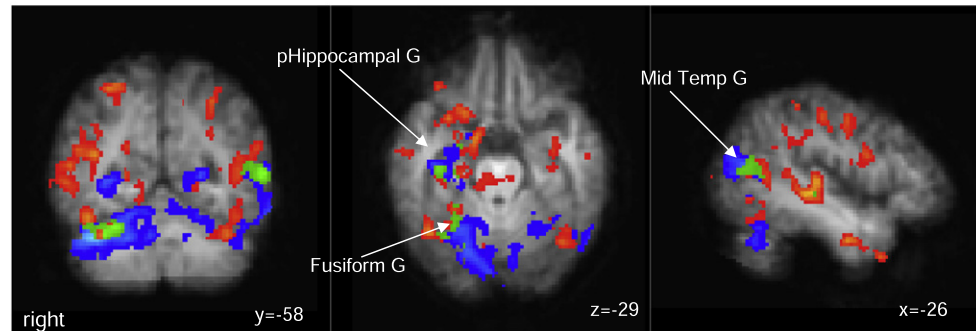


Figure 1. Areas Where BOLD Activation for Objects Is Higher Than Activation for Textures or Scrambled Objects

Activation in the visual condition is in red and shows areas where the BOLD signal was higher for pictures of intact objects than for scrambled versions of those pictures. Activation in the tactile condition is in blue and shows areas where activation was higher when participants made stereotyped grasping motions to objects presented to their right hand than when they made the same movements to textured surfaces. Areas that are significantly active (according to a strict conjunction method; see [Experimental Procedures](#)) for both conditions are shown in green. Images are in radiological format.

(A) HJA.

(B) Nonlesioned, age-matched controls.

Our data indicate, for the first time, that at least some regions in the LO can be activated normally from touch, even when input from ventral LO is lesioned and visual recognition is prevented. This is consistent with estimates of effective connectivity from fMRI; these estimates have implied that there are direct connections between somatosensory cortex and LO [10]. Similarly, early blind participants asked to recognize objects by touch or form representations of objects show activation in areas similar to those activated in sighted participants [4, 5], indicating that visual experience is unnecessary for occipito-temporal regions to be active in tactile object recognition. However, in early blind individuals, LO may be recruited as a result of deafferentiation from visual input, which may not reflect the position in sighted individuals [26]. Here we provide evidence that activation of dorsal LO is driven, in part, directly by touch in a normally developed brain.

Tactile Recognition in Dorsal LO

In our control group, we replicated and extended the previous findings that some areas of the visually defined LO are active for both tactile and visual object recognition [2, 3, 5]. We found bimodal activity extending from the dorsal LO ventrally into the parahippocampal gyrus. Some of these regions (those with peaks in dorsal LO or middle temporal gyri) are similar to those (e.g., LOTv [2, 6, 7, 10]) previously found to be multimodal in the occipito-temporal cortex. Processing of tactile inputs initially involves somatosensory cortex and neighboring areas, and indeed, trans-cranial magnetic stimulation (TMS) over primary somatosensory cortex reduces performance on simple tactile

discrimination tasks [27]. TMS over the occipital cortex, however, reduces performance in difficult tactile orientation-discrimination tasks [27]. Similarly, lesions that include the dorsal LO disrupt the processing of touched objects or shapes [9, 28].

We also found two further bimodal regions. First, there was a relatively anterior bimodal region in the parahippocampal gyrus. Although the parahippocampal cortex is not typically reported to be selective for objects, it does show selectivity to some categories of visual stimuli. Together with the documented selectivity for places [29], the parahippocampal cortex has also been found to be selective for objects in multi-voxel pattern analysis [30] and PET studies [31]. It has also been shown to have higher activation for viewed objects with a strong (versus weak) contextual association, e.g., a treadmill or kettle [32]. The objects used in the present study were all selected to be grasped and coincidentally had high associations with particular contexts, such as the kitchen. Pietrini and colleagues [5] found that the same category-specific areas were active both when participants viewed images of graspable objects and when they touched exemplars of that category (without vision). Thus, it seems that when objects are commonly touched or grasped, the LO appears to be activated by both modalities, and this may extend to all regions selective to graspable objects.

We also found a large cerebellar region that was active for both modalities. Previous studies have found similar regions of the cerebellum to be active during tactile shape discrimination [6, 24, 33]. The left anterior lobe has been found to be activated when participants feel both objects and nonobjects [6], and both the left anterior and right posterior lobes can be

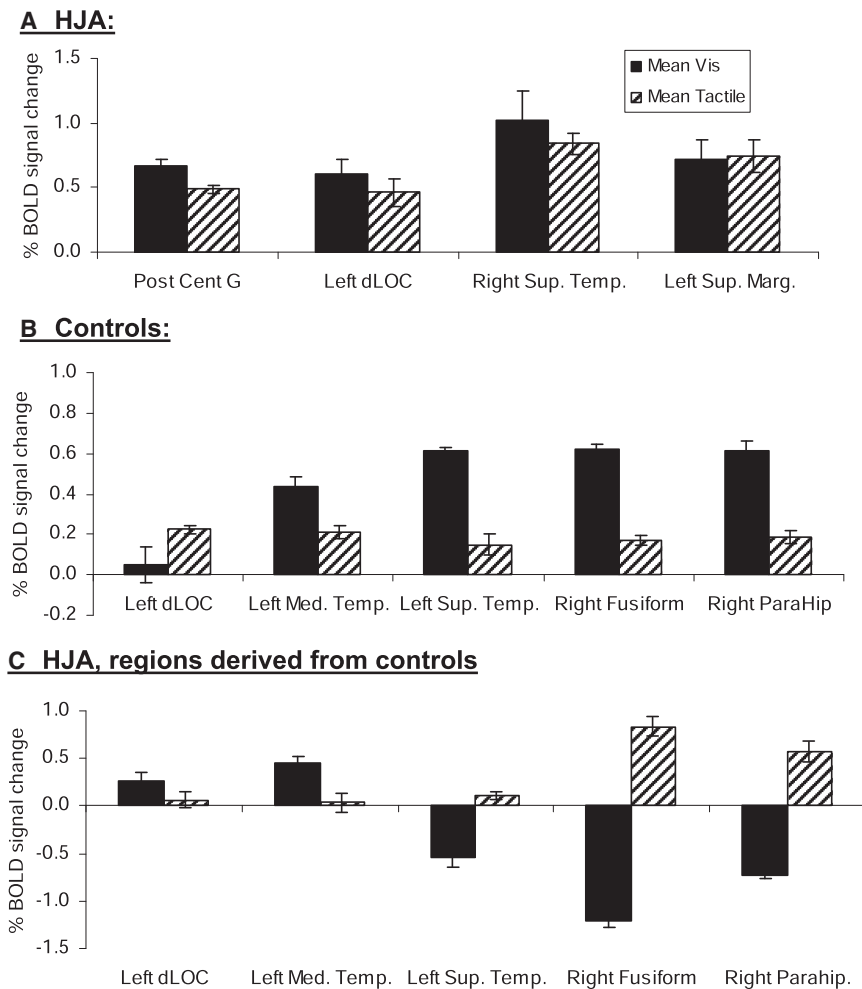


Figure 2. Percent Signal Change from Regions of Overlapping Significant Activation from Visual and Tactile Conditions

(A) Areas active for both viewed and touched objects (compared to textures or scrambled images) in HJA. Only the post-central gyrus survived the conservative minimum Z statistic method ([25]; see Experimental Procedures), but the other three are included to show that there is no difference in signal strength in any of the regions.

(B) Signal change in left superior/dorsal LO and in subregions active for both visual and tactile objects in the occipito-temporal cortex in control participants for viewed or touched objects versus viewed or touched textures.

(C) Signal change from HJA in the same areas as in (B). Error bars show standard error of the group mean in (B) and of the mean of the four runs in (A) and (C). Abbreviations are as follows: dLO, dorsal lateral occipital; sup, superior; temp, temporal; marg, marginal gyrus; med, medial; parahip, parahippocampal gyrus; post cent, post-central sulcus. dLO is roughly equivalent to LOTv of Amedi et al. [3]. Left medial temporal and superior temporal regions are slightly anterior, and the fusiform and parahippocampal regions are farther anterior and ventral.

reflect input from a visual recognition system. The data suggest an effect that stems directly from cross-modal tactile input.

Experimental Procedures

Participants

HJA suffered a posterior cerebral artery stroke peri-operatively in 1981 (aged 61). Structural MRI showed bilateral lesions of the inferior temporal gyrus, lateral occipital gyrus, the fusiform gyrus, and the lingual gyrus (see Supplemental Data). The present investigations were performed when he was 86 years old. Neurological and psychological findings have been published extensively elsewhere [11, 12, 34–37]. In brief, HJA was described as suffering from “integrative agnosia,” suggesting that his object-recognition deficit was due to an impaired ability to group local and global information to generate a coherent object percept.

Seven older control participants aged >74 years were recruited from the local community and screened for safety in the MRI environment. All had good vision or wore MRI-compatible goggles to match their regular optical prescription. Participants gave informed consent and were paid a small fee for participation. Control participants were slightly younger than HJA, reflecting a difficulty in recruiting participants who were age-matched and also matched on level of activity and intellect. The procedures were in accordance with the Birmingham University Imaging Centres ethical guidelines.

Visual Stimuli

Stimuli were photographs and line drawings of everyday objects and scrambled versions of these, presented using the Psychophysics Toolbox extensions to Matlab (<http://www.mathworks.com/> [38, 39]). Color photographs were used in an attempt to optimize recognition. The images included photos of the items used in the tactile experiment as well as a set of unfamiliar objects (see Figure S3). We hoped to investigate activation differences relating to differences in recognition rate between the different stimulus types, but HJA was unable to consistently name any of the visual items as they were presented in the scanner. After the visual scan, HJA was asked to name any objects that he recalled; he reported that he saw no identifiable objects. He was then shown the visual object images again but was unable to consistently name any object.

active when participants feel both reference and test shapes [33]. Here, we compared tactile object recognition with touching textures; although the motor component was the same in our two conditions, only in the object-recognition condition did participants explore shape. From this we conclude that cerebellar activity in haptic object recognition is due to the exploration of shape. Cerebellar activity has also been found for visual object recognition (e.g., [31]). Previous studies of multimodal object recognition have not explicitly investigated the role of the cerebellum, and the present study was also not designed for this end. Comparison of our results with previous findings, however, does suggest that the anterior lobe of the cerebellum could be involved in shape processing irrespective of input modality.

Conclusions

Despite a large bilateral lesion in the ventral occipito-temporal cortex, HJA was able to recognize graspable tactile objects. As with our control participants, some regions in the visually activated object-selective cortex (LO) were selective for both viewed and touched objects. We also found additional areas in the parahippocampal gyrus and cerebellum that were sensitive to both viewed and touched objects. A subset of multimodal object-selective regions in the dorsal LO is specifically responsive to objects recognized by touch alone. For HJA, this dorsal LO activation for tactile object recognition is unlikely to

Tactile Stimuli

The objects used in the tactile scan were a set of 20 nonmetallic, hand-sized, everyday objects (e.g., tennis ball, mug, plastic fork, banana; see top row, Figure S3). In a pilot experiment, we established that these objects could be named within 4 s after palpation in one hand. HJA named all objects he touched when he was tested after the scanning session. The texture stimuli were 18 flat-textured stimuli (e.g., cotton, paper, raffia) glued to flat pieces of wood (approximately 25 cm by 30 cm). All items were checked for magnet safety and compatibility, and none created an artifact on the images.

Scan Procedure for Viewed Objects

Images were presented in blocks. The scan started with 16 s of fixation, followed by four blocks of stimuli interleaved with 16 s blocks of fixation. There were two blocks of intact images and two blocks of scrambled images in each scan. Each image was presented for 800 ms, and there were four sets of 20 images in each block. This entire scan was repeated twice for each control participant and twice on two scan sessions (i.e., there was a total of four scans) for HJA. We had participants perform a one-back matching task on the images (intact and scrambled) to ensure that they maintained attention. Responses were made via an optical key pad that participants held in their right hand.

Scan Procedure for Touched Objects and Textures

Participants' right hands were rested on a platform (adjusted for each participant) just above their mid-thigh in the scanner. In each scan there were six blocks (12 s) in which the experimenter presented objects (4 s) and six blocks in which the experimenter presented textures. The timing of presentation was controlled by tones presented to the experimenter's headphones with Presentation software (www.neurobs.com). Block order was different and counterbalanced over the scans. There was a 12 s gap between each block. The participants' task was to briefly palpate the object by using a set of practiced, stereotyped movements. These grasping-type movements were the same for the textures and objects and were practiced outside the scanner. The objects were placed into the palm of the hand so that the hand would close over it. The texture boards were presented so that the finger tips could move over the surface. If the same object was presented twice in a row, participants had to raise one finger of their left hand (this happened about once per scan). There was a possibility that the movements of the experimenter would lead to artifactual activations in the BOLD signal. For two control participants, the movements of the experimenter were tracked with a Qualsys movement-tracking system. Analyzing the data from these participants with, and without, including the movement data as a regressor made little difference to the results. Nevertheless, the experimenter was instructed to make no unnecessary movements. Control participants underwent the scan for the tactile task twice, and HJA underwent the scan four times.

MRI Acquisition and Analysis

For full details of scanning parameters and analysis, please see [Supplemental Experimental Procedures](#). High-resolution (1 × 1 × 1 mm) T1-weighted scans were carried out for all participants. Functional scans were carried out with an echo planar (EPI) sequence with 100 (tactile scan) or 120 (visual scan) volumes.

All scans were analyzed with FEAT (fMRI Expert Analysis Tool) version 5.4, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Standard preprocessing steps (removing slice-timing and head motion corrections with MCFLIRT [40], spatial smoothing and temporal filtering) were applied. Non-brain matter was removed with BET [41]. All functional scans registered to the higher-resolution structural image, which was registered, in turn, to the MNI brain [42].

We identified regions of significant activation for HJA by averaging results for each type of scan. Data for control participants were averaged over the group. In both cases, a fixed-effects model was used, forcing the random-effects variance to zero in FLAME (FMRIB's Local Analysis of Mixed Effects [43, 44]). We used a fixed-effects analysis on the control group because we only wished to confirm the previous findings in our subpopulation and did not intend to generalize our results to the population. In all cases, Z (Gaussianised T/F) statistic images were thresholded through the use of clusters determined by $Z > 2.6$ and a (corrected) cluster significance threshold of $p = 0.05$ [45]. For the conjunction analysis, we used the method of Nichols et al. [25]. This conservative method requires activation to be significant in both comparisons separately but does not require both comparisons to be independent of each other.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and two tables and can be found with this article online at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01056-2](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01056-2).

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