

Visual Cortex Extrastriate Body-Selective Area Activation in Congenitally Blind People “Seeing” by Using Sounds

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Summary

Vision is by far the most prevalent sense for experiencing others' body shapes, postures, actions, and intentions, and its congenital absence may dramatically hamper body-shape representation in the brain. We investigated whether the absence of visual experience and limited exposure to others' body shapes could still lead to body-shape selectivity. We taught congenitally fully-blind adults to perceive full-body shapes conveyed through a sensory-substitution algorithm topographically translating images into soundscapes [1]. Despite the limited experience of the congenitally blind with external body shapes (via touch of close-by bodies and for ~10 hr via soundscapes), once the blind could retrieve body shapes via soundscapes, they robustly activated the visual cortex, specifically the extrastriate body area (EBA; [2]). Furthermore, body selectivity versus textures, objects, and faces in both the blind and sighted control groups was not found in the temporal (auditory) or parietal (somatosensory) cortex but only in the visual EBA. Finally, resting-state data showed that the blind EBA is functionally connected to the temporal cortex temporal-parietal junction/superior temporal sulcus Theory-of-Mind areas [3]. Thus, the EBA preference is present without visual experience and with little exposure to external body-shape information, supporting the view that the brain has a sensory-independent, task-selective supramodal organization rather than a sensory-specific organization.

Results

To investigate whether visual experience in the perception of body shapes [4] is necessary for the emergence of the body-perception network and specifically that of the visual extrastriate body area (EBA; [2, 5]), we trained and tested a group of fully and congenitally blind individuals (without any visual experience; see [Table S1](#) available online) who learned to categorize various images including body shapes on a visual-to-auditory sensory substitution device (SSD) termed “The vOICe” [1]. This SSD topographically converts visual images into auditory “soundscapes” by using a predetermined algorithm. Behaviorally, following ~70 hr of specialized training (over several months), our subjects were able to perceive high-resolution visual information of various object categories [6, 7]. Specifically, ~10 hr of training were devoted to learning

to identify SSD-soundscapes that contained body-shape silhouettes and outlines, an input that is normally not available to them, via an atypical sensory modality. Subjects could also identify the exact body posture depicted in the external body image and mimic it ([Movie S1](#)).

To investigate the role of visual experience in body-shape processing, we first inspected the activation generated in the congenitally blind who perceived body-shape information via sounds at the group level, and we compared it to that of a group of normally sighted subjects who perceived the same images of body silhouettes visually (see [Supplemental Experimental Procedures](#)). As expected from previous literature and in accordance with the modality of input, the activation of the sighted peaked in the visual cortex ([Figures S1A](#) and [S1B](#); middle panel) and specifically showed significant bilateral extrastriate visual-cortex activation (more significant in the right hemisphere, see [Figure S1](#) and [Table S2](#) detailing the additional peaks in multisensory parietal and frontal cortices [5]). In the blind, although we found a strong peak in the auditory cortex fitting the input modality ([Figure S1A](#); left panel; [Table S2](#)), the strongest activation for the entire cortex ([Figure S1B](#)) was found in the right extrastriate visual cortex, specifically at the location of the EBA (in the posterior inferior temporal sulcus [ITS]/middle temporal gyrus). Accordingly, the peak overlap of the activations between the two groups ([Figures S1A](#) and [S1B](#); right panel) included a full overlap in the right extrastriate visual cortex.

We further examined the visual cortex activation consistency across the various blind participants. We computed the statistical parametric map of body-shape activations in each of the subjects and plotted the cross-subject overlap probability map over all the individual subjects in each of the two groups ([Figure 1A](#)). As expected, the highest overlap between the sighted subjects' activations for body images was found in the visual cortex, including the extrastriate visual cortex ([Figure 1A](#); middle panel). In the blind, because we used an auditory input we found maximal overlap in the auditory cortex. However, surprisingly, the largest cross-subject overlap outside the auditory cortex for body-shape soundscapes was found in the extrastriate visual cortex ([Figure 1A](#); left panel; overlap probability of 100%). Moreover, activation was fully anatomically consistent between all (100%) individual subjects across both groups solely at the location of the EBA. We also plotted the visual cortex peaks of all individuals from both groups ([Figure 1B](#)). The panels represent all of the subjects' peaks with (bottom panel) and without (top panel) a group tag, thus showing that the groups cannot be distinguished by simple examination of the peak distributions. We also compared the distribution of the single subjects' peaks across the groups by using clustering analysis to independently divide the peaks according to their spatial locations. A k-means clustering analysis ([8, 9] see details in [Supplemental Experimental Procedures](#)) generated two clusters, each showing a mixture of peaks of both blind and sighted individuals rather than a distinct anatomical cluster for each population ([Figure 1C](#)).

Importantly, the defining feature of the EBA is its body-shape selectivity versus objects, faces, and textures or

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Activation for body-shapes: Inter-subjects consistency

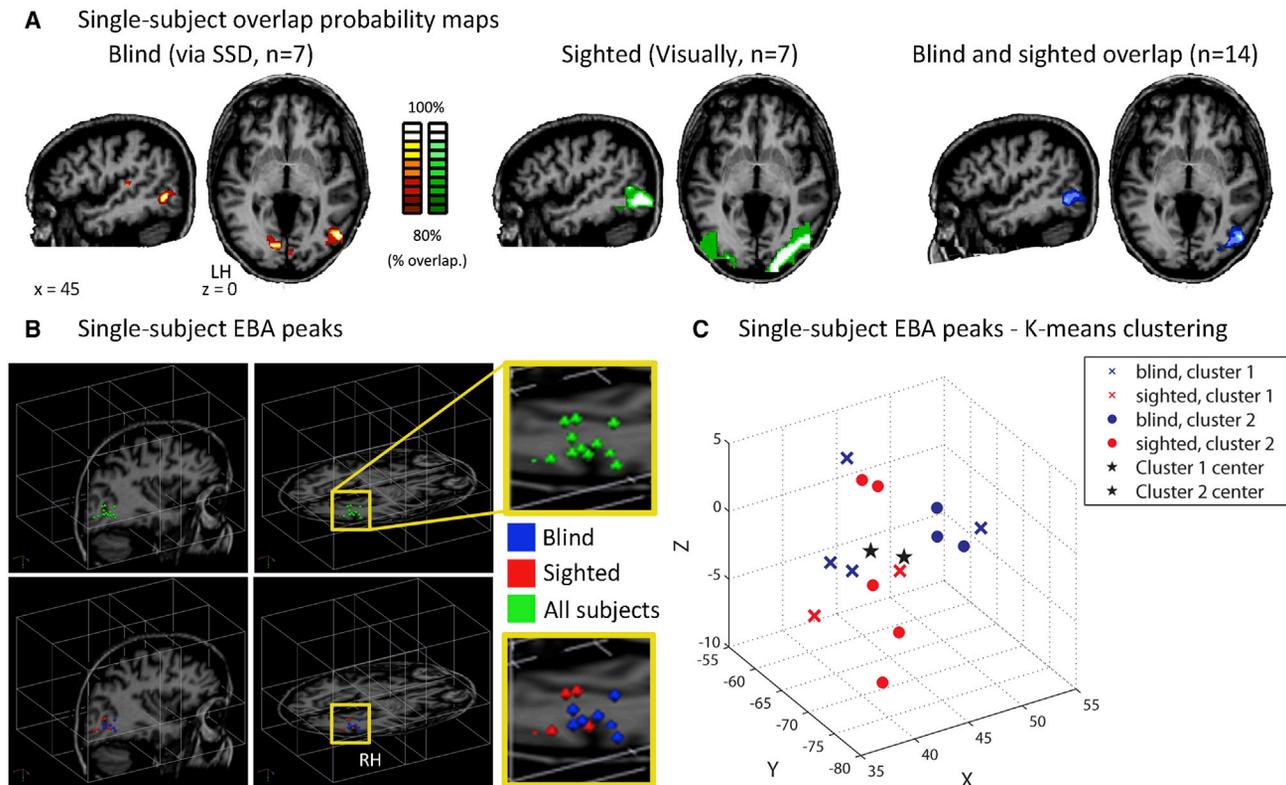


Figure 1. Extrastriate Individual Subject Activation Peaks for Full-Body Perception in the Congenitally Blind and Sighted

(A) Activation for full-body silhouettes is shown in comparable experiments in the sighted controls (middle panel; using vision) and in the congenitally blind (left panel; using SSD soundscapes). The blind participants in this study were enrolled in a novel training program (described in detail in [6]) in which they were taught how to effectively extract and interpret high-resolution visual information from the complex soundscapes generated by the vOICE SSD. The average training duration of the participants here was 73 hr, during which they were taught how to process two-dimensional still (static) images, including images of body postures, faces, objects, and textures. Each condition in the fMRI experiment included 10 novel soundscapes representing unfamiliar images from the trained object category. During body-shape epochs, the subjects heard soundscapes of three body-shape silhouettes (2 s per stimulus), each repeated twice (see [Supplemental Experimental Procedures](#)). The sighted subjects performed a visual localizer version of the experiment by using the same images. The Tel-Aviv Sourasky Medical Center Ethics Committee approved the experimental, and written informed consent was obtained from each subject. Overlap probability maps across the individual blind subjects (left panel) were derived from single-subject activation contrast maps at a restrictive threshold of $p < 0.001$, corrected for multiple comparisons. The blind reproducibly activated the extrastriate body area (EBA) for body shapes. The blind subjects' activation was as consistent as in the normally sighted controls (middle panel), in that all the individual subjects (100%) across both groups (right panel) showed full activation overlap solely in the extrastriate cortex.

(B) Plot of individual peak activations, demonstrating the spatial reproducibility of extrastriate body activation in the blind and sighted subjects. In the top panel, all subjects' peaks (both blind and sighted) are represented by green diamonds. In the lower panel, there is a group tag (blind or sighted; blue and red diamonds, respectively) for each individual. Note the overlap of the two groups of subjects.

(C) For purposes of illustration of the spatial consistency between the blind and the sighted, we conducted a k-means clustering analysis. K-means is designed to partition n observations (in our case the Talairach coordinates of the EBA peaks of 14 individual subjects: 7 sighted, 7 blind) into k clusters (in our case $k = 2$) in which each observation belongs to the cluster with the nearest mean so as to minimize the within-cluster sum of squares [8, 9]. Blue and red represent blind and sighted individuals, respectively; circles and Xs represent the two resulting clusters; a black star marks the center of each cluster. Both clusters contain peaks for both the blind and the sighted. This analysis further supports the anatomical consistency of the extrastriate body activation between the blind and the sighted.

scrambled images [2, 5, 10–12]. Indeed, our control sighted group showed such a preference in the ITS bilaterally (Figure 2A; right panel), peaking, as previously reported, in the right hemisphere. Surprisingly, the blind showed a comparable preference for body shapes versus objects, faces, or textures in the right ITS, in a location slightly more posterior to the selectivity peak of the sighted (Figure 2A; left panel; the location difference between the groups' selectivity peaks was 1.25 cm, or four functional voxels). The more posterior location of the selectivity peak in the blind is comparable to the location of haptic body selectivity as seen in the normally sighted, which is found posteriorly to the classical visual EBA [11, 14]. Furthermore, similar to previous reports [5, 12], the EBA

response was nearly twice as large for body shapes as for faces, objects, and textures in both groups (Figure 2A; although absolute values of the GLM parameter estimation for the blind were lower than those for the sighted). Thus the preference effect strength was also similar in both groups. Next we directly compared the activation generated by body shapes with those of each one of the other visual categories separately and independently, across the entire brain. In the sighted, all contrasts revealed significant bilateral extrastriate visual activations, whose intersection peaked in the right ITS (Figure 2B; right panel). In the blind, this peak was the only one across the entire brain to show full category selectivity for body shapes, as compared to each one of the other

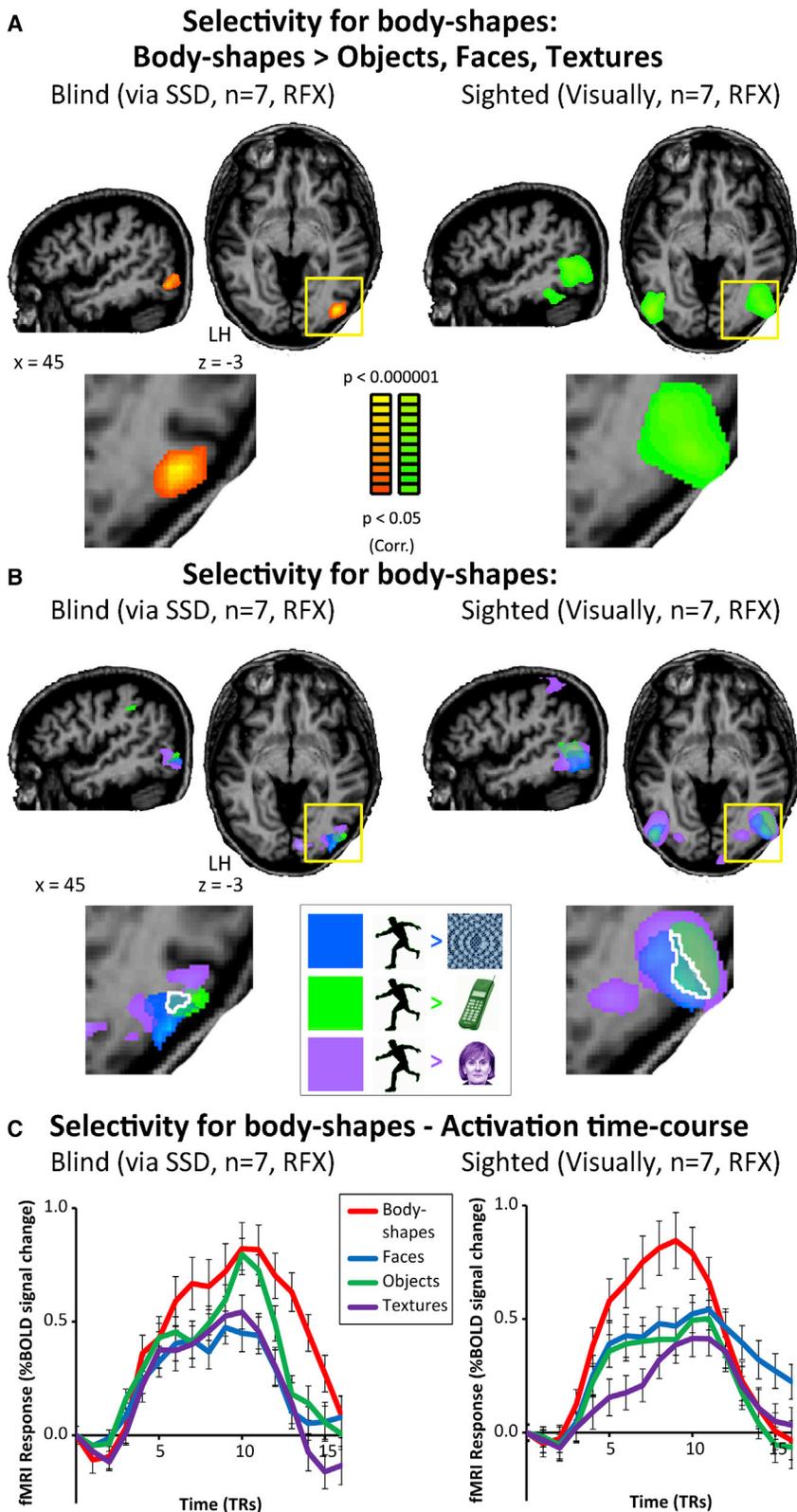


Figure 2. Extrastriate Body Selectivity without Visual Experience

(A) The preference for body shapes over other visual categories was tested in a direct contrast (versus objects, faces, and textures) in each of the groups (random-effect general linear model [GLM] analysis [13], $p < 0.05$ corrected for multiple comparisons). The maps show a highly significant activation in the inferior temporal sulcus (ITS; enlarged) in both groups. For demonstrative purposes, we also sampled the activation GLM parameter estimates (and activation time courses, see Figure 2C) for each experimental condition (body-shapes, faces, objects, and textures) in the selectivity peaks for body shapes in both groups in a region-of-interest (ROI) group level random-effect analysis. This analysis also shows clear and significant body-category selectivity in both groups, although with slightly less differentiation between body and object responses in the blind compared to the sighted. In line with previous reports, the magnitude of the response of the EBA in both groups was nearly twice as large for body shapes as for faces, objects, and textures. In the sighted group, the peak showed a GLM parameter estimate of 1.6 for bodies but only 0.74, 1, and 0.78 for faces, objects, and textures, respectively, with an average selectivity effect size of 53%. In the blind, the selectivity peak showed a parameter estimate of 0.72 for bodies but only 0.43, 0.5, and 0.45 for faces, objects, and textures, respectively, with an average selectivity effect size of 64%. Thus, despite the difference in absolute activation, the preference effect strength was similar in both groups.

(B) The overlap of the preference maps for body shapes versus each one of the other visual categories independently (textures in blue, everyday objects in green and faces in purple) is depicted for each group. The full body-shape preference is unique to the right ITS (Talairach coordinates $-38, -77, -6$) of the blind across the entire brain. The sighted group (right panel) shows bilateral selectivity for body shapes in a nearby location (although more significant in the right hemisphere). Each map is a random-effect GLM contrast at $p < 0.05$, corrected for multiple comparisons.

(C) Activation time course sampled for demonstrative purposes from the peaks of selective activation (peaks of the maps depicted in A, at $p < 0.005$) further supports the similar selectivity for body shapes in both groups. Error bars represent the SEM.

of the EBA of the blind. We found that the EBA of the blind showed highly significant functional connectivity to the contralateral location (comparable to the left EBA of the sighted), as well as to a vast region in the visual cortex, including the fusiform gyrus. Intriguingly, outside the occipital cortex, the EBA was most connected to the posterior superior temporal sulcus (pSTS)/temporal-parietal junction (TPJ; Figure 3), to areas which are considered an integral part of the body-image network that are also involved in Theory-of-Mind (ToM) tasks [3, 16, 17]. Additionally, the EBA was functionally connected to a small cluster in the parietal lobe (left posterior intraparietal sulcus; IPS), which

categories (Figure 2B; left panel). The activation time course sampled for demonstrative purposes (Figure 2C) further supported the similar selectivity for body shapes in both groups.

Finally, we inspected the network functional connectivity (by using intrinsic, rest state [15] functional-connectivity analysis)

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Functional connectivity of EBA in the blind (n = 13, RFX)

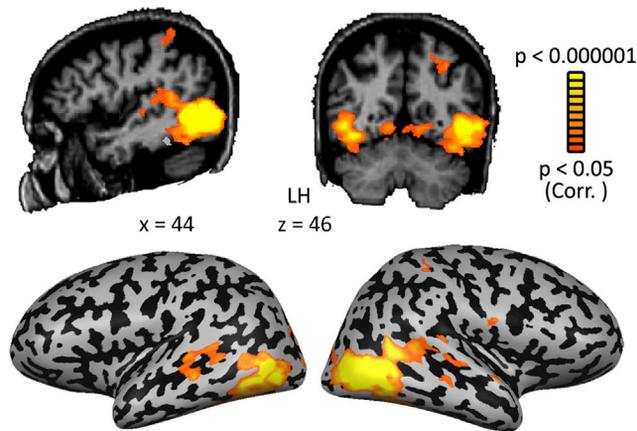


Figure 3. Functional Connectivity of the EBA in the Blind

The intrinsic functional connectivity [15] of the right EBA in the blind was investigated with a data set of spontaneous BOLD fluctuations from a group of 13 congenitally blind subjects (see Table S1). Functional connectivity was computed from a seed ROI in the peak of intersubject-consistent body-shape activation in the blind group (100% overlap) in the right ITS, which also overlapped with the activation in the sighted (see Figure 1A). Individual time courses from this seed ROI were sampled from each of the participants, z-normalized, and used as individual predictors in a group analysis using a GLM in a hierarchical random effects analysis. The minimum significance level of the results was set to $p < 0.05$ corrected for multiple comparisons, using the spatial extent method. This analysis revealed EBA functional connectivity to both the contralateral extrastriate cortex and the fusiform gyrus, as well as several areas in the body-image network, such as the pSTS/TPJ and IPS.

has been linked to multisensory and visuomotor integration of information related to body movements, and specifically to coding of the peripersonal space [18].

Discussion

The absence of visual experience poses a unique challenge to the creation of the brain’s representation of bodies because it greatly limits the ability to perceive others’ body postures and motion or to read cues indicative of their actions and intent from their body shape, details which are available in the blind solely by touching people in their proximity, and in the case of our subjects, by using SSD sound input for ~10 hr. We show here that despite the lack of any visual experience with body shapes from external sources, when using SSDs the blind can not only perceive whole-body images (Movie S1; Supplemental Experimental Procedures) but also process them in the dedicated “visual” neural network, because the activation and selectivity for body shapes in the congenitally blind was found not in the somatosensory or auditory cortices, but rather in the visual cortex, overlapping the EBA location and peaking in very close proximity to the sighted EBA peak. This result was verified in several converging analyses at the group level (Figure S1; Figure 2) between the subjects in each group and in their overlap (Figure 1A; probability maps), as well as when inspecting single subjects’ activation peaks and their clustering (Figures 1B and 1C). Functional-connectivity analysis (Figure 3) further showed that the EBA was not only activated by body-shape processing but also that it is connected to two key components in the body-image network: the pSTS/TPJ and IPS, regions that have been implicated in mediating the spatial

unity of the self and body (embodiment), interpreting the motions of a human body in terms of goals, and the ability to reason about the contents of mental states of others (ToM) [3, 16–18].

In addition to previous findings regarding the preservation of functional properties of components of the mirror system, the ToM [19, 20], and processing of action verbs [21] in blind people, to which we show that the EBA is functionally connected, our data suggest that despite vastly different life experiences and some differences in the blind body-image [22], the blind brain still contains many aspects of the neural network for the perception and processing of others’ external body-images.

Our study suggests there is another key task and/or function (body-image-shape analysis) that demonstrates retention of function in “visual” areas in the brains of the congenitally blind [23–25]. Other studies have argued for similar theoretical implications concerning the perception of motion (hMT+; [26]), general object shapes and tools (lateral-occipital complex, [27–29] inferior-temporal gyrus [30], and parietal lobe; [31]), spatial location (middle-occipital gyrus; [32, 33]), and reading (visual word-form area; [6, 9]). However, besides adding a new retained domain to “vision,” the current study is unique in another aspect: this is the first time visual cortex functional preservation is reported for a percept normally inaccessible to the blind. Location, motion, small palpable objects, and script, which have been the targets of previous studies, are as available to the blind as they are to the sighted, albeit via other senses. Blind children learn to read Braille at the age of 6, and haptic object recognition and auditory localization are available to the blind early in life as the brain develops. In contrast, blind people’s experience of the full body configuration of others is highly restricted, and the SSD used here was learned in adulthood for a limited time. Nevertheless, despite the vast plasticity of the visual cortex to process other sensory inputs and other cognitive tasks [25, 34], our data show activation of the extrastriate “visual” cortex of the blind during the perception of full body shapes, which thus suggests retention of functional specialization in this same region (showing high anatomical consistency of the extrastriate visual cortex peaks between the two groups). This supports the existence of innately determined constraints for the emergence of the EBA that are sensory independent but domain specific [23], task or computational specific [35, 36] (similar concepts have also been referred to as metamodal, amodal, or supramodal [26, 30, 37]). Such constraints might arise from the connectivity [23] of the extrastriate cortex to other parts involved in higher-order perception and integration of the body image, such as the pSTS/TPJ and IPS (Figure 3). Such functional connectivity (likely following anatomical connectivity) may be speculated to affect cortical organization during development even in the complete absence of bottom-up visual information, driving the organization of the right extrastriate cortex toward deciphering the geometric shape of the body. This specialization may begin very early and might even exist from birth, as infants (as early as three months) already show differential brain responses to natural versus distorted body configurations [38].

Importantly, the recruitment of the extrastriate visual cortex for processing body shapes reported here did not result from the fact that the stimulus was animate (despite the existence of an inanimate/animate stimulus distinction recently reported in the visual cortex of the blind [39]), as it showed a preference for body shapes over faces (Figure 2B; see body versus faces),

both of which are animate stimuli. Therefore, the blind EBA preference is specific to the representation of the body.

However, several aspects of our findings suggest that the body-perception network in the blind is not identical, or as fully developed, as that of the sighted. For instance, whereas the EBA of the blind showed both strong activation and selectivity for body shapes (Figure 2), an additional component of the body-perception network, the fusiform body area (FBA; [40, 41]), only showed activation for body shapes (although at a highly significant threshold; see Table S2) and connectivity to EBA (see Figure 3) but not selectivity for body shapes. This is consistent with the existence of selectivity for haptic perception of body parts in the right (posterior) EBA but its absence in the FBA in the sighted [11, 14]. In sighted people, such findings were explained either by the use of isolated body parts (not whole-body configurations) or the sequential nature of haptic exploration, which does not elicit whole-shape gestalt representations. Although here we used whole-body silhouettes, which are typically favored by the FBA, it may be that the blind’s lack of experience with full-body configurations, which are much less accessible than the perception of individual body parts (e.g., in shaking hands or being led by hand), caused less specialization in this part of the network. Relatedly, it was recently suggested that the ventral-medial aspect of the ventral stream serves as a gateway between perception and memory [42], perhaps generating more reliance on individual life experience and expertise missing in the blind. Similarly, although both groups showed similar selectivity effect size in the EBA, the blind showed weaker general activation strength (Figure 2A). This could suggest that the level of expertise in perceiving body shapes or visual experience in general may affect EBA recruitment. Although we cannot address this question here, it would be interesting in the future to discern the effects of the lack of visual input and the lesser expertise and experience with body shapes by further testing this group of blind subjects after more body-specific training. Similarly, the effect of our SSD longitudinal training (over several months) on body responsiveness could be investigated further. Generally, such experimental designs may also help address the ongoing visual literature debate related to the role of expertise in face processing in the fusiform face area [43]. Furthermore, although the assessment of retinotopic areas cannot be conducted in the congenitally blind, it may be interesting to investigate whether high-resolution imaging (combined with creative ways to define motion-sensitive area hMT+, e.g., by using a visual-to-somatosensory SSD to provide tactile motion stimulation; [26]) can also reveal the distinction within the EBA to multiple body-selective foci surrounding hMT+ recently reported in sighted people [44], hints of which can be found in our data (see Figure S2).

From the rehabilitation perspective, although SSDs have several advantages [45], they were never widely adopted by the blind community. The encouraging behavioral results obtained here in perceiving visual details, which are otherwise entirely unavailable to the blind and which normally convey social cues—namely, the body posture of others—as well as other capacities shown previously, such as object-type recognition, reading [6], spatial location, and navigation [46] abilities, provide a careful basis for optimism that SSDs can become useful stand-alone visual aids, especially when used in conjunction with constructed training. Regardless, SSDs may be used as “sensory-interpreters” that provide high resolution [7], instructing the perception of visual signal

arriving from lower-acuity invasive devices such as retinal-implants [47].

To summarize, our results show that the extrastriate visual cortex may develop and engage in its role in perception of body information and its functional connectivity to other key structures in understanding body images of others and their intentions in the absence of vast exposure to body-shape information and even in the full absence of visual experience. Thus, our findings join novel converging evidence, suggesting that the brain has a sensory-independent, task-selective supramodal organization rather than a sensory-specific one.

Supplemental Information

Supplemental Information includes two figures, two tables, Supplemental Experimental Procedures, and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.02.010>.

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