What Body Parts Reveal About the Organization of the Brain

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<td>Published Version</td>
<td>doi:10.1016/j.neuron.2010.10.021</td>
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What body parts reveal about the organization of the brain
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In this issue of Neuron, Orlov et al. show that the human occipito-temporal cortex contains regions responding preferentially to body part categories, such as upper limbs (hand, elbow), torsos, or lower faces (mouth, chin). This organization may reflect differences in the connectivity of these regions with other brain regions, to support the efficient processing of the different types of information different body parts provide.

The visual analysis of others’ faces and bodies is one of the most developed visual skills we possess, reflecting the extreme importance these stimuli have throughout our lives. For example, we can instantly recognize thousands of highly similar faces (at least those of our own species), and extract a multitude of emotions and mental states from subtle facial expressions. Whole-body postures and body gait provide information about personality characteristics, gender, age, identity, and mental states. In paintings, sculptures, and dance, artists please our highly developed aesthetic sense of the body and its movements. Waist-hip-ratio, among other body cues, is used as an indicator of reproductive health and attractiveness. Hands are used to communicate, to accentuate speech, and to manipulate objects and tools. From the above examples, it becomes clear that information from the human body is rich and diverse, with some types of information provided by multiple body parts, but others primarily by one body part (e.g., identity is most effectively recognized from the face). It is not surprising then, that the brain contains multiple dedicated regions to process these diverse types of body cues efficiently. Human functional brain imaging and neurological patient studies have provided evidence for brain areas that are selectively involved in the perception of people. Within the occipito-temporal cortex (OTC), distinct regions have been described that are selective for faces (Kanwisher et al., 1997; Moro et al., 2008), bodies (Moro et al., 2008; Peelen and Downing 2007), or hands (Bracci et al., 2010).

In a study published in this issue of Neuron, Orlov et al. (2010) present important new data about the processing of faces and bodies in OTC. They show an orderly and highly consistent (both within and between participants) map of regions responding preferentially to specific parts of the human body. This finding raises new questions about the neural mechanisms supporting person perception, and about the functional organization of OTC more generally.

In a first experiment, participants' brain activity was measured while they were presented with a continuous sequence of images belonging to one of five different body parts: upper limbs (hand and elbow), lower limbs (leg and foot), trunks, lower faces (mouth and neck), and upper faces (eyes and nose). Using a phase-encoding approach (a technique frequently used for mapping the visual field
preference of voxels in early visual cortex), the authors then correlated the time course of the brain activity with the time course of the presentation sequence to establish which of the body parts most reliably activated a given voxel. The resulting map of preference values showed that surprisingly many OTC voxels had a significant preference for one body part relative to the others. Notably, these preferences were not randomly distributed, but were neatly clustered in distinct regions, with a gradual transition between neighboring regions. Each of the five body parts was selectively represented in at least one region. Furthermore, the locations of these regions were consistent across participants. The upper and lower face regions were located next to each other, in parts of the ventral OTC where previous studies had described face-selective responses. The upper-limbs region was located in the lateral part of OTC, where previous studies found hand and body-part selective responses. The regions selective for lower-limbs and trunks were more distributed across the lateral and ventral OTC, and fell outside regions previously implicated in body and face processing. These findings were replicated in a second experiment using a more traditional block design.

To what extent is this map specific to body stimuli? Does it simply reflect the differences in shape between the body parts? To address these questions, the authors carried out several clever control experiments. First, they showed that no orderly map emerges for other objects (cellos, cars) when these are split up into parts. Second, they showed that the body part map is consistent for different parts of the five body-part categories. For example, the response in the upper-limbs region was selective to both the elbow and the hand, despite their difference in visual appearance. Similarly, the selectivity in the lower face region was found for both the lips and the chin. This provides important evidence that these regions are not selective to particular shapes but instead contain a higher-level, shape-invariant representation of body parts. Finally, an experiment that included non-body objects, in addition to the body parts, showed that most of the regions were also selective for their preferred body part relative to non-body objects. In sum, Orlov et al. provide convincing evidence for a large-scale body-part map in OTC, indicating that different body parts activate at least partly different neural mechanisms.

Taking this one step further, Orlov et al. next asked whether the body-part specificity might extend to unseen motor-actions, performed with different body parts. This question was inspired by previous work that showed activity overlapping body-selective regions in OTC when participants performed unseen movements with their hands or feet (Astafiev et al., 2004; Peelen and Downing, 2005). Furthermore, recent work using multivariate pattern analysis, indicated shared representations of observed and executed hand actions in lateral OTC (Oosterhof et al., 2010). To test the body-part specificity of movement-related activity in OTC, Orlov et al. asked participants to perform unseen movements of different body parts – hands, feet, buttocks, and tongue. Remarkably, although movements of the hands, feet, and buttocks (but not the tongue) all activated the lateral OTC, the differential activation during these movement conditions positively correlated with the visual body-part selectivity. For example, activity in the upper-limbs regions was stronger when subjects moved their hands than when they moved their buttocks. Control experiments indicated that this selectivity was not
related to the visual imagery of the movements. This result suggests that some of the body-part preferences in (lateral) OTC are driven by both visual and motor (or proprioceptive) input. Future studies should test the functional significance of these cross-modal responses, for example by using TMS. One possibility is that the movement-related activity in OTC is related to an automatic spread of activation within a body-part network without any direct functional relevance. Alternatively, the endogenous action commands may serve as prediction or attention signals, priming the relevant body-part selective area to expect a particular change in the moved body part, thereby facilitating perceptual processing, although this explanation seems less likely for the rarely observed buttocks movements.

The body part map described by Orlov et al. spans large parts of ventral and lateral OTC, extending beyond known face- and body-selective regions. Does this mean that most of OTC is exclusively involved in the analysis of faces and bodies? No, probably not. What is shown here is the preference of voxels for one body part relative to other body parts and non-body objects. Each voxel reflects the average activity of many thousands of neurons, and it is likely that the response properties of these neurons are considerably heterogeneous. As long as a reliably higher percentage of neurons respond preferentially to one body part relative to the other body parts, the voxel will be assigned to a body part in the body-part map. Responses to non-body objects and non-preferred body parts were generally well above baseline, and sometimes approached levels comparable to those of a region's preferred body part. Furthermore, it cannot be excluded that another (yet untested) stimulus, for example visual motion, will turn out to be the most effective stimulus for some of these regions. Therefore, the results of Orlov et al. are best explained not in terms of a set of body-part modules, each exclusively involved in processing one body part, but rather in terms of a broad landscape of moderately clustered body-part preferring neurons, intermixed with neurons processing other types of visual input.

What could be the function (or functions) performed by the body-part preferring regions and what drives the organization of the body-part map? One possibility is that these regions all perform a similar function (e.g., visual recognition) on different inputs. An alternative possibility is that multiple types of computations are performed within the body-part map. Different body parts provide different types of information – hands and feet are linked to action, faces are optimal for conveying identity and emotions, and the trunk may be important for assessing physical attractiveness. Orlov et al. report strong responses to lower limbs in the upper-limb region and vice versa; both these body parts are important for action perception. Similarly, neighboring regions responded to lower and upper face parts, and strong responses were observed to upper face parts in the lower-face region and vice versa, perhaps indicating a common role in identity or emotion perception. Anatomical connectivity of the different regions may play an important role in shaping the specificity and organization of these regions (Mahon and Caramazza, 2009). Once information is extracted from the visual input, it propagates to other areas where the information is further processed, integrated with information from other modalities, and linked to previous experiences. For example, understanding mental states is thought to involve a network of regions including the
medial prefrontal cortex, and action understanding depends on a large-scale fronto-parietal network. Different parts of the OTC (e.g., ventral versus lateral OTC) may be differentially connected with these other parts of the brain, which then shapes their functionality and body-part preference.

In sum, the study by Orlov et al. (2010) provides convincing evidence for an orderly map of body-part selective regions in occipito-temporal cortex. The selectivity of these regions was not related to the specific visual shapes of the body parts, as it was found for multiple sub-parts within a category. Furthermore, the non-face body-part regions, mostly in lateral OTC, showed cross-modal selectivity. We suggest that the organization of the body-part map may be related to the specific connectivity of these regions with other brain structures, to support the efficient processing of the diverse types of information extracted from different body parts. These findings open up many interesting questions regarding the functionality of these regions, their mutual interactions, and their connectivity with the rest of the brain.

REFERENCES