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TACTILE OBJECT CATEGORIES CAN BE DECODED FROM THE PARIETAL AND LATERAL-OCCIPITAL CORTICES

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Abstract—The visual system classifies objects into categories, and distinct populations of neurons within the temporal lobe respond preferentially to objects of a given perceptual category. We can also classify the objects we recognize with the sense of touch, but less is known about the neuronal correlates underlying this cognitive function. To address this question, we performed a multivariate pattern analysis (MVPA) of functional magnetic resonance imaging (fMRI) activity to identify the cortical areas that can be used to decode the category of objects explored with the hand. We observed that tactile object category can be decoded from the activity patterns of somatosensory and parietal areas. Importantly, we found that categories can also be decoded from the lateral occipital complex (LOC), which is a multimodal region known to be related to the representation of object shape. Furthermore, a hyperalignment analysis showed that activity patterns are similar across subjects. Our results thus indicate that tactile object recognition generates category-specific patterns of activity in a multisensory area known to encode objects, and that these patterns have a similar functional organization across individuals. © 2017 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: tactile, somatosensory, perception, multivariate pattern analysis, object recognition, object category.

INTRODUCTION

The ventral stream of the cortical visual system contains neural representations of visual objects such as faces, animals, and inanimate objects. Thus, an organizing principle of the visual system is the neural encoding of abstract categories of behaviorally relevant objects

(Kiani et al., 2007; Meyers et al., 2008; Freeman and Simoncelli, 2011; Lehky et al., 2014; Aparicio et al., 2016). It is well established that these neuronal representations are invariant to changes in low-level physical characteristics such as luminance, contrast, angle of view, location, or size. Moreover, it has been observed that some of these circuits encode representations that are invariant to the sensory modality used to recognize the objects, i.e., a given object elicits similar patterns of neuronal activity irrespective of the object being recognized by visual, auditory, or tactile cues (Amedi et al., 2001; Grill-Spector et al., 2001; Ghazanfar and Schroeder, 2006; Kassuba et al., 2011; Man et al., 2015). These unified neuronal representations correspond closely with the unified and stable subjective perception that we have of the objects around us.

In the somatosensory system, the different physical attributes that define a tactile object, such as texture, curvature, or edge orientation, are encoded in the neuronal activity of numerous parietal areas that show varying degrees of selectivity for those features (Bodegård et al., 2001; Iwamura, 1998; Sathian, 2016; Yamada et al., 2016; Yau et al., 2009, 2016). Peripheral receptors and areas 1 and 3b, for example, contain neurons that are selective for the orientation of edges (Bensmaia et al., 2008; Pruszynski and Johansson, 2014; Peters et al., 2015); area SII contains neurons that show orientation selectivity across several finger pads (i.e., they show positional invariance; Fitzgerald et al., 2006), and there is evidence that edge curvature is represented in area 2 (Yau et al., 2013).

However, it is not clear if these variate tactile attributes, which are encoded in separate neuronal populations at early processing stages, converge in upstream association areas to generate a unified representation of tactile objects. Moreover, it is important to know if such tactile category encoding is located within the somatosensory system itself or whether it is located within a multisensory association area. There is strong evidence that the object representations along the temporal lobe can be activated by more than one sensory modality (Kim and Zatorre, 2011; Lacey and Sathian, 2014; Podrebarac et al., 2014; Snow et al., 2014), and we know that visual information can transfer to the tactile modality and viceversa (Yildirim and Jacobs, 2013). In particular, the lateral occipital complex (LOC) has been shown to encode objects that are identified by touch or sight (Amedi et al., 2002; Peltier et al., 2007; Stilla and Sathian,

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Abbreviations: BOLD, blood-oxygen-level-dependent; fMRI, functional magnetic resonance imaging; LOC, lateral occipital complex; LSVM, linear support vector machine; M1, primary motor; MVPA, multivariate pattern analysis; SMA, supplementary motor area; V1, primary visual.

2008; Lucan et al., 2010; Masson et al., 2015; Erdogan et al., 2016). Pietrini and colleagues showed that the inferotemporal cortex generates neuronal representations of tactile objects and that these representations are similar to those generated by visually identifying the same objects (Pietrini et al., 2004).

The level of abstraction that follows object representation is object category, i.e., the representation of a group of objects that share a high-level attribute such as function (e.g., spoons or pens) or behavioral relevance (e.g., faces or animals). These categories have been described in the prefrontal, temporal and occipital lobes (Ishai et al., 2000; Kourtzi and Connor, 2011; Watanabe et al., 2012; McKee et al., 2014; Proklova et al., 2016). We seek to gather evidence on whether the cortical activity could be used to decode the category of an object explored with the sense of touch.

Recognizing and classifying the objects we touch is a fundamental cognitive skill that allows not only naming those objects, but more importantly, allows recovering stored relevant information related to the objects around us. Although objects vary considerably in their specific physical characteristics, classifying them into perceptual categories simplifies and organizes the sensory world around us. It allows planning our behavior and executing the motor commands to adequately interact with those objects. It is well established that subjects can correctly identify and categorize objects explored only with the sense of touch (for a recent review see Sathian, 2016). This can also be done by congenitally blind individuals, indicating that a visual representation of objects is not needed for identification or classification. A relevant question is thus what are the neuronal correlates of tactile object identification and, moreover, the neuronal correlates of tactile object categories.

The existence of neuronal representations of tactile categories would be consistent with the idea that the somatosensory system uses similar processing algorithms and strategies as the visual system, which hierarchically encodes object properties such as texture, form, object identity and finally, object category.

We performed a multivariate pattern analysis (MVPA) on block-design functional magnetic resonance imaging (fMRI) data to identify the cortical areas that contain enough information to decode tactile object categories significantly above chance (Hanke et al., 2009; Haxby et al., 2014). We probed the whole cortex with a searchlight analysis that selected the voxels within a sphere (radius = 3 voxels) to train a linear support vector machine (LSVM) to classify the activity associated with 10 types of objects that were explored with the right hand. Our results revealed voxel clusters in the parietal and the LOC from which the category of the touched objects could be decoded.

EXPERIMENTAL PROCEDURES

Stimuli and task design

Participants explored a total of 120 objects grouped into 10 categories comprising spoons, stuffed toys, bottles, pens, books, balls, strings, drinking glasses,

pseudorandom 3D shapes, and square sandpapers with different roughness (12 different objects per category). The objects were explored for 3 s with the right hand, and participants performed a one-back repetition detection task in which they had to indicate whether the object they explored was the same or different from the previous one. After the 3-s exploration period the object was removed and the participants had a 1-s window to press one of two buttons with their left hand to indicate whether the object was the same or different from the previous one.

A block consisted of six stimuli of the same category (Fig. 1). Blocks of different object categories were selected in pseudo-random order, lasted 24 s each, and were separated by a 12-s baseline. The stimuli in each block were selected with a 50% chance of being the same as the previous one. A presentation of 10 different blocks defined a run, and subjects performed 12 repetition runs that lasted 372 s each. Participants were given a 15 min break after six runs.

Subjects lay within the scanner with their right palm up and the experimenter handed them the objects following instructions from a computer monitor about the time and the object to be handled. The participants were instructed to close their eyes within the scanner and held a button pad with their left hand to press one of two buttons to indicate whether the current object was the same or different from the previous one. The objects we used were visible to the participants before and after completion of the scans. We did not attempt any systematic selection of object categories, and our criterion was straightforward: we selected common objects that could be comfortably manipulated with one hand and that were compatible with MRI. Only one category (the 3D random shapes that we used in a previous study, Rojas-Hortelano et al., 2004) contained non-familiar objects. We measured volume, weight and compliance (using von Frey filaments) of each object. Mean object volume was 251 cm³, mean weight 60 g, and mean compliance of non-rigid objects was 2 N.

Subjects and Image acquisition

Ten healthy right-handed subjects (5 women, age range 27–36 yr) underwent fMRI on a 3-T Phillips Achieva TX scanner (Best, The Netherlands) using an echo planar imaging gradient echo (EPI-GRE) sequence with a repetition time (TR) of 2 s and an echo time (TE) of 27 ms. Functional volumes consisted of 32 axial slices covering the whole brain with a voxel size resolution of 2 × 2 × 3.5 mm³. On each of the 12 repetition runs 190 volumes were acquired. Subjects gave written consent and were compensated for their time. Experimental procedures were approved by the institutional Research Ethics Committee and were in accordance with the Declaration of Helsinki.

Data preprocessing and pattern analysis

Data preprocessing was performed with FSL (FMRIB's Software Library; www.fmrib.ox.ac.uk/fsl). Each run was motion-corrected to the first volume of each participant.

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