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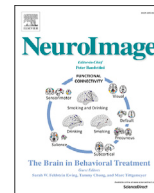
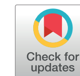


Shape responses in a macaque frontal area connected to posterior parietal cortex



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ABSTRACT

The primate dorsal visual stream processes object shape to guide actions involving an object, but the transmission of shape information beyond posterior parietal cortex remains largely unknown. To clarify the information flow between parietal and frontal cortex, we applied electrical microstimulation during functional Magnetic Resonance Imaging (fMRI) in a shape-selective patch in the posterior part of the Anterior Intraparietal area (pAIP) to chart its connectivity. Subsequently, we recorded single-unit responses to images of objects in the fMRI activation in prefrontal cortex, corresponding to area 45B, elicited by pAIP microstimulation. Neurons in area 45B had properties similar to neurons in pAIP, responding selectively to shape contours and to very small shape fragments measuring less than one deg at exceedingly short latencies. However, contrary to the prevailing view on the hierarchical organization of cortical areas, neurons in area 45B preferred even smaller shape fragments and had smaller receptive fields than neurons in pAIP. These findings provide the first evidence for ultra-fast shape processing in prefrontal cortex, and suggest that the pathway from pAIP to area 45B may not be important for object grasping.

Introduction

The primate visual system analyzes object shape in the ventral visual stream – for the purpose of object recognition – but also in the dorsal stream, where the object representation can guide actions involving objects such as grasping (Janssen and Scherberger, 2015). A key dorsal stream area for grasping in rhesus monkeys is the Anterior Intraparietal area (AIP) (Gallese et al., 1994) in the anterior lateral bank of the Intraparietal Sulcus (IPS). Neurons in AIP respond selectively to real-world objects during grasping and passive fixation (Baumann et al., 2009; Murata et al., 2000), and encode the three-dimensional (3D) structure of curved and tilted surfaces defined by binocular disparity in a manner distinct from neurons in inferotemporal cortex (Srivastava et al., 2009; Theys et al., 2012b). Moreover, a subset of neurons primarily located in the more posterior subsector of AIP (pAIP) are also selective for (flat) images of objects, silhouettes and outline shapes (Romero et al., 2012, 2013). Surprisingly, most of these pAIP neurons also respond to very small fragments of outlines spanning 1–1.5 deg (Romero et al., 2014), and this preference depends heavily on small positional changes within the receptive field (RF). A follow-up study (Romero and Janssen, 2016) reported that the RFs of pAIP neurons exhibit a wide range of sizes and profiles, from small and purely foveal to very complex with multiple local maxima, and that the RF profile can depend on the stimulus used to map the RF, similar to neighboring area LIP (Janssen et al., 2008). In humans, the overall organization of the IPS areas is most likely similar to that of the macaque monkey, but this region may also comprise uniquely human areas (Arcaro et al., 2011; Culham et al., 2003; Fabbri et al., 2016; Konen and Kastner, 2008; Orban, 2016).

To clarify the connections of shape-selective sites in AIP, Premereur et al. (2015) electrically stimulated shape-selective patches during fMRI (electrical microstimulation during functional magnetic resonance imaging, or EM-fMRI) in monkeys after single-cell recordings had identified the two subsectors in AIP (aAIP and pAIP). While EM-fMRI in aAIP primarily activated a set of visuomotor areas in parietal (Medial Intraparietal area or MIP, and PFG) and frontal (F5a) cortex, the pAIP subsector was effectively connected to caudal IPS areas (CIP and PIP) and aAIP in parietal cortex, and to both the anterior (AIT) and the posterior (PIT) inferotemporal cortex. In addition, EM-fMRI in pAIP activated the anterior bank of the inferior ramus of the arcuate sulcus, which corresponds to area 45B. EM-fMRI allows to chart the effective connectivity of

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physiologically-defined cortical areas or subsectors of areas *in vivo* (Ekstrom et al., 2008; Moeller et al., 2008; Premereur et al., 2012), so that subsequent electrophysiological recordings can clarify how representations change in interconnected areas.

One of the major advantages of charting the effective connectivity of functionally defined patches *in vivo* is that we can investigate the properties of neurons in connected but remote areas in the same animals. This approach can furnish unique information on how neural representations change along the hierarchy of cortical areas in far-extrastriate cortex and beyond. Here, we first applied EM-fMRI in pAIP, and recorded from single neurons in the activated region of frontal cortex using the same stimuli as in (2016); Romero et al. (2014). Analogous to the ventral stream, in which higher processing stages encode larger shape features (Tanaka et al., 1991), we hypothesized that 45B neurons may prefer larger shape fragments than pAIP neurons. Contrary to our expectations, however, neurons in area 45B showed an even stronger preference for the smallest line fragments and smaller RFs compared to pAIP, suggesting that the pAIP–45B pathway may not be involved in guiding grasping movement towards objects. These findings may also reveal the neural basis of ultra-rapid coarse shape processing in the visual system (Thorpe et al., 1996; Wu et al., 2015), and clarify the flow of visual information in parietofrontal networks that support perception and action.

Materials and methods

Subjects and surgery

The experimental protocol was similar to that previously described (Romero et al., 2014; Romero et al., 2012). All technical procedures were performed in accordance with the National Institute of Health's *Guide for the Care and Use of Laboratory Animals* and EU Directive 2010/63/EU, and were approved by the Ethical Committee at the Katholieke Universiteit Leuven. Two male rhesus monkeys (*Macaca mulatta*; monkey C, 6.5 kg; monkey D, 6.5 kg) were trained to sit in a primate chair. Next, a head post (Crist Instruments) was affixed to the skull with ceramic screws and dental acrylic. After training in passive fixation, we implanted an MRI-compatible recording chamber (Crist Instruments) over parietal cortex to allow access to area AIP. For this and all other surgical procedures, monkeys were kept under propofol anesthesia (10 mg/kg/h) and strict aseptic conditions.

Electrical microstimulation during fMRI

In both animals, we first identified the posterior subsector of area AIP (pAIP) by recording single-cell selectivity to images of objects, silhouettes and outlines during passive fixation (Romero et al., 2014). Subsequently, we ran a contrast-enhanced EM-fMRI experiment with the electrode in pAIP (visible on an anatomical MRI in Fig. 1A) to identify the part of area 45B that is activated when stimulating pAIP (Premereur et al., 2015). We sedated the animals with a mixture of ketamine and medetomidine, lowered the electrode to one of the recording positions, and alternated between stimulation (1 mA at 200 Hz during 250 ms every 3 s, pulse duration 0.48 ms) and no-stimulation blocks (each lasting 40 s), with each experimental run lasting 490 s (monkey D: 2 sessions, 15 runs, monkey C: 3 sessions, 23 runs). We calculated the contrast *stimulation – no stimulation*, and displayed the T-values on each animal's own anatomical scan with the electrode positioned at the prefrontal registration position. We used as a threshold $p < 0.001$ (uncorrected for multiple comparisons), as in our previous studies (Premereur et al., 2015; Van Dromme et al., 2016).

Electrophysiological recordings in area 45B

We implanted a second recording chamber over frontal cortex, centered on the fMRI activation elicited by electrical microstimulation in pAIP (Fig. 1B and C, Horsley-Clark coordinates 29–30 A and 19–20L). We recorded single-unit activity with standard tungsten microelectrodes (impedance, 1 MΩ at 1 kHz; FHC) inserted through the dura by means of a 23 gauge stainless-steel guide tube and a hydraulic microdrive (FHC). Neural activity was amplified and filtered between 300 and 5000 Hz. Spike discrimination was performed online using a dual time-window discriminator, and displayed with LabView and custom software. We continuously monitored the position of the right eye with an infrared-based camera system (Eye Link II, SR Research) sampling pupil position at 500 Hz. The stimuli were presented on a monitor (resolution, 1280 × 1024 pixels; Vision Research Graphics) equipped with a fast-decay P46-phosphor operating at 120 Hz at a viewing distance of 86 cm (46 pixels per degree) on a dark background (luminance 8 cd/m^2). A photocell attached to the stimulus display in the lower right corner detected the onset of a white square (covered with black tape to obscure it from view) in the first video frame containing the stimulus. All

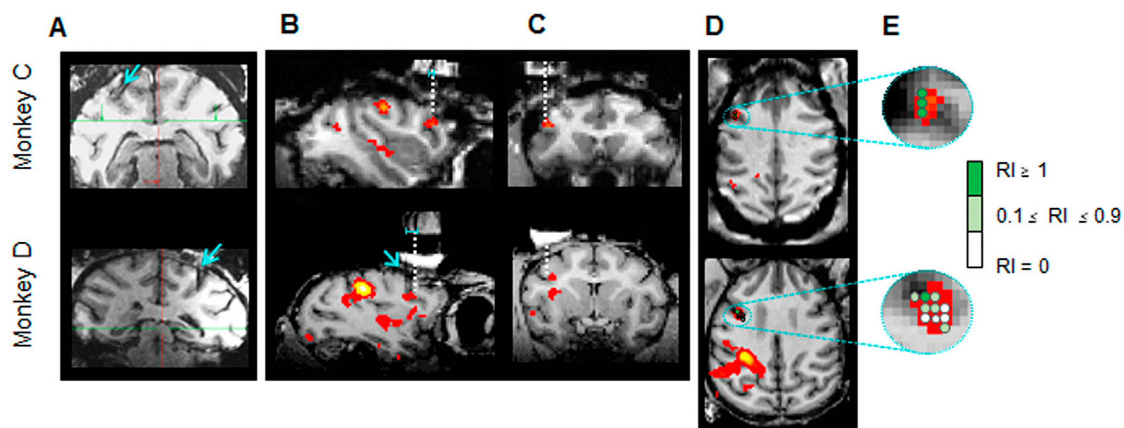

Fig. 1. FMRI activations during microstimulation in AIP and recording sites. A. Coronal MR image of the microstimulation position in AIP (the light-blue arrow represents the electrode). B-D. Sagittal (B), coronal (C) and horizontal (D) sections of the fMRI activations in area 45B of both monkeys mapped onto each animal's own anatomical MRI with the recording chamber and an electrode in one of the recording positions (in monkey D the light-blue arrow indicates a second electrode, in the most posterior site of recording). The dotted line in B and C illustrates one of the recording tracks. In Figure D, the dark green circles represent the best position in the grid, where we found the highest number of selective cells. E. Projected recording positions and Responsivity index RI (circles). The dark green circles indicate the best recording sites in each monkey (Responsivity Index RI ≥ 1, indicating 1 selective neuron or more recorded per session). The light green circles and the white circles indicate moderate (RI = 0.1–0.9 selective neurons recorded per session) or a complete lack of selectivity (RI = 0), respectively.

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