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Caudal Intraparietal Sulcus and three-dimensional vision: A combined functional magnetic resonance imaging and single-cell study

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ABSTRACT

The cortical network processing three-dimensional (3D) object structure defined by binocular disparity spans both the ventral and dorsal visual streams. However, very little is known about the neural representation of 3D structure at intermediate levels of the visual hierarchy. Here, we investigated the neural selectivity for 3D surfaces in the macaque Posterior Intraparietal area (PIP) in the medial bank of the caudal intraparietal sulcus (IPS). We first identified a region sensitive to depth-structure information in the medial bank of the caudal IPS using functional Magnetic Resonance Imaging (fMRI), and then recorded single-cell activity within this fMRI activation in the same animals. Most PIP neurons were selective for the 3D orientation of planar surfaces (first-order disparity) at very short latencies, whereas a very small fraction of PIP neurons were selective for curved surfaces (second-order disparity). A linear support vector machine classifier could reliably identify the direction of the disparity gradient in planar and curved surfaces based on the responses of a population of disparity-selective PIP neurons. These results provide the first detailed account of the neuronal properties in area PIP, which occupies an intermediate position in the hierarchy of visual areas involved in processing depth structure from disparity.

Introduction

The primate visual system needs to reconstruct the third dimension (depth) from a range of depth cues, among which binocular disparity – formed by positional differences between retinal images in the two eyes – is one of the strongest. The neural underpinnings of stereoscopic vision have been extensively studied in early visual cortex (Cumming and DeAngelis, 2001; Parker, 2007). A large number of studies have investigated the representation of 3D object structure defined by gradients of binocular disparity in the macaque inferotemporal (Janssen et al., 1999, 2000a, b; Yamane et al., 2008), posterior parietal (Srivastava et al., 2009; Theys et al., 2012b) and ventral premotor cortex (Theys et al., 2012a, 2013). In humans, a highly similar network has been described using fMRI (Ban and Welchman, 2015; Durand et al., 2009; Georgieva et al., 2008). More recently, considerable progress has been made in charting the anatomical connectivity of 3D-structure selective cortical regions in macaques (Premereur et al., 2015), in causally relating neural activity to perceptual performance in 3D structure categorization (Van Dromme et al., 2016; Verhoef et al., 2012), and even in clarifying the flow of visual information in this 3D-structure network (Janssen et al., 2017; Van Dromme et al., 2016). However, we know much less about the neural representation of 3D surfaces in intermediate areas of the dorsal and ventral visual stream (Orban, 2016). Detailed knowledge concerning neuronal properties in these mid-level areas may aid in understanding how these high-level representations are computed at the end-stages of the dorsal and ventral visual streams.

A previous monkey fMRI study (Durand et al., 2007) observed no significant 3D-structure related activations in the caudal Intraparietal Sulcus (IPS), although (Tsao et al., 2003) had reported strong disparity-evoked activations in this region evoked by near-far checkerboard stimuli. Recently however, another monkey fMRI study by Van Dromme et al. (2016) measured robust 3D-structure related activations in the caudal IPS in monkeys trained to discriminate 3D structure (concave vs convex). The activations related to 3D structure defined by disparity were even more pronounced in the medial bank (area PIP) than in the lateral bank (area CIP). Moreover, the 3D-structure-selective patch in posterior AIP is effectively connected to both CIP and PIP (Premereur et al., 2015). Except for a few sporadic single-cell recordings (Sakata et al., 2005; Taira et al., 2000; Tsutsui et al., 2001), no study has investigated the properties of PIP neurons to date.

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We combined fMRI-guided invasive electrophysiological recordings with advanced analytical methods to investigate the neural properties of the macaque area PIP in the medial bank of the caudal IPS. While a sizeable fraction of PIP neurons encoded the 3D orientation of planar surfaces (first-order disparities), only a very small proportion of PIP neurons exhibited selectivity for curved surfaces (i.e. second-order disparities). A linear support vector machine classifier could reliably decode the sign of curvature from a population of disparity-selective PIP neurons independent of position in depth, indicating that the population of PIP neurons contained significant information about 3D object structure. These results provide the first single-cell evidence regarding the role of area PIP in processing disparity gradients.

Materials and methods

Surgical procedures and animals

Three adult rhesus monkeys (two males and one female, ranging between 6.5 and 7.5 kg) served as experimental subjects for single-unit extracellular recordings. The monkeys were first implanted with an fMRI-compatible head post using dental acrylic and ceramic screws, under isoflurane anesthesia (Van Dromme et al., 2016). Monkeys were trained in a passive fixation task and a 3D-structure discrimination task previously described by (Verhoef et al., 2012). Two monkeys (R. and A.) were scanned during passive fixation of curved and flat surfaces, together with control stimuli for each condition (Van Dromme et al., 2016). We then implanted a recording chamber vertically above the caudal part of the intraparietal sulcus, centered on the fMRI activation evoked by curved surfaces (contrast [*curved – control*] – [*flat – control*]) in monkeys R. and A., and at a similar anatomical position (Horsley-Clarke coordinates −10A and 8.5 L) in monkey B. Recordings were obtained from the left hemisphere of monkeys R and B and the right hemisphere of monkey A. Animal care and experimental procedures complied with the national and European guidelines (Directive, 2010/63/EU) and were approved by the ethical committee of KU Leuven. Structural magnetic resonance imaging (MRI, 0.6 mm slice thickness), using glass capillaries filled with a 1% copper sulfate solution inserted into several grid positions, together with the pattern of grey to white matter transitions, confirmed that the recordings were made in the caudal part of the medial bank of the IPS, corresponding to area PIP. In addition, we obtained an anatomical MRI with the electrode in one of the recording positions for monkey A. (Fig. 2A).

Stimuli

The animals were trained to maintain the gaze of both eyes inside an electronically defined 1° fixation window during the passive fixation task. Horizontal and vertical eye movements were recorded using an infrared camera system sampling at 500 Hz (EyeLink II; SR Research). After a 400 ms fixation period, the stimulus was presented for 600 ms at the fixation point (which remained visible), and if fixation had been maintained, a drop of juice was given as reward. During training and the single-cell recording experiments, stimuli were presented dichoptically using a double pair of ferroelectric liquid crystal shutters (optical rise/fall time about 35 μS, Displaytech) operating at a frequency of 60 Hz each and synchronized with the vertical retrace of the display monitor (20-in. P46 fast-decay phosphor; Vision Research Graphics), operating at a frequency of 120 Hz and at a viewing distance of 86 cm (Srivastava et al., 2009). Stimulus luminance measured behind the shutters (operating at 60 Hz) was 0.8 cd/m^2 with no measurable cross talk between the images presented to the two eyes. All monkeys showed excellent stereopsis as demonstrated in an earlier 3D structure categorization test, in which concave and convex surfaces at different disparity coherences (ranging from 40 to 100% coherence) had to be discriminated by means of eye movements to the left or right (Verhoef et al., 2012).

We used a basic stimulus set consisting of 32 pairs of disparity-defined curved surfaces, which was identical to that used by (Srivastava et al., 2009), together with eight planar surfaces (first-order stimuli). The first-order stimuli (Fig. 1A) were presented in two different sizes (8.3° and 18.7°, except for monkey B where we used only the 8.3° planar stimuli), and consisted of squares with linear disparity gradients either along the vertical or horizontal axis of the stimulus (50% dot density). The surfaces in which disparity varied along the vertical axis (30° rotation along the horizontal axis) could have the top tilted either towards (profile A) or away from the observer (profile B). Similarly, the surfaces in which disparity varied along the horizontal axis could have the right side towards (profile A) or away from the observer (profile B). The two profiles were derived from the same monocular images by simply interchanging the images presented to each eye. To avoid texture-density cues in surfaces with disparity variations along the horizontal axis, we randomly removed dots with each change in disparity, as in previous studies (Janssen et al., 2001). The curved (second-order) surfaces (Fig. 1B) were constructed by combining four pairs of depth profiles (half-sine, inclined, Gaussian, S-shape) with eight two-dimensional (2D) shapes, filled with a 50% density random-dot pattern. The combination of a 2D contour and a depth profile generates a 3D stimulus. The two members of each 3D surface pair used the same two monocular images, since interchanging the monocular images between eyes yielded two 3D surfaces that differed only in the signs of their disparity gradients (convex surfaces become concave and vice versa). The curved surfaces measured 6.6° vertically, dot size was 2 arcmin, and stimulus contrast was 4.6 (ΔI/I). In the case of the curved stimuli, disparity varied only along the vertical axis of the stimulus.

fMRI experiment: scanning procedures and stimuli

All scanning procedures have been described in Van Dromme et al. (2016). We trained monkeys A. and R. to sit in a sphinx position inside an MRI-compatible plastic chair, which was placed inside the horizontal bore of the magnet. Stimuli were projected using a digital projector (Barco 6300 LCD) onto a translucent screen positioned 57 cm in front of the monkey. A pair of red/green stereo-glasses were placed in front of the monkey's eyes to provide dichoptic presentations of the stimuli. We used a 3.0 Tesla full body scanner (Trio, Siemens), and a radial transmit-only surface coil and custom-built eight-channel phased-array receive coil were positioned closely around the monkeys' head. A contrast agent (monocrystalline iron oxide nanoparticle or MION; Feraheme, AMAG pharmaceuticals) was injected to enhance the signal-to-noise ratio and spatial selectivity of the MR signal (Zhao et al., 2006). We used a gradient-echo single-shot T2 – weighted echo-planar imaging sequence (40 horizontal slices, TR = 2 s, TE = 17 m, 1.25 mm isotropic). A pupil/corneal reflection tracking system (Iscan, operating at 120 Hz) was used to monitor the position of one eye. Monkeys were required to maintain fixation on a dot on the center of screen within a 1.5° electronically-defined window.

We used a 2 by 2 block design with factors *curvature* (curved versus flat) and *disparity* (stereo versus control). In the curved stereo condition, we presented a subset of the curved surfaces (four 2D shapes and three pairs of depth profiles, Van Dromme et al., 2016) at two positions in depth. In the flat stereo condition, we presented flat surfaces (with the same 2D contours) at 12 positions in depth such that the disparity content (i.e. the sum of all disparities) was identical to the one in the stereo curved condition. The curved-control and flat-control conditions consisted of the presentation of one of the monocular images of the corresponding stereo conditions to both eyes simultaneously.

Single-cell experiment

During all single-unit recording sessions, eye position signals from both eyes, neural activity, and photocell pulses were digitized and processed at 20 kHz on a digital signal processor (DSP) (C6000 series; Texas Instruments). Extracellular neural activity was recorded by means of