Selectivity for three-dimensional contours and surfaces in the anterior intraparietal area

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Neurons in AIP also respond selectively to disparity-defined 3-D shapes, and this selectivity is preserved across positions in depth (between −0.5 and +0.5 deg average disparity) and positions in the frontoparallel plane (between −2.5 and +2.5 deg in the horizontal and vertical direction) (Srivastava et al. 2009). These AIP neurons signal differences in the depth profile much earlier than IT neurons, but the 3-D shape representation in AIP is coarser (less sensitive to the presence of disparity discontinuities in the surface) and less categorical compared with IT. The stimuli used in Srivastava et al. (2009) were 3-D shapes in which both the textured surface and the boundary of the stimulus were curved along the vertical axis. However, for many graspable objects (e.g., a stapler), information about their depth profile must be extracted from the disparity variations along their boundaries because of a lack of texture information on the surface that can carry depth information. Hence, the first goal of this study was to investigate the selectivity of AIP neurons for 3-D shapes in which the disparity variation merely ran along the boundary or along the surface of the stimulus. By using the same stimuli and recording procedures as in the IT studies, we could compare the properties of 3-D shape-selective AIP neurons with the properties of 3-D shape-selective IT neurons (Janssen et al. 2001).

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THE VISUAL SYSTEM EXTRACTS relevant information with respect to the three-dimensional (3-D) profile of objects from binocular horizontal disparity, which results from the slightly different positions of the images on the two Retinas (Cumming and DeAngelis 2001). Disparity selectivity is ubiquitous in the visual system (Neri 2005), found in early visual areas (Poggio and Poggio 1984; Thomas et al. 2002), in the dorsal visual stream (Genovesio and Ferraina 2004; Gnadt and Mays 1995; Maunsell and Van Essen 1983; Roy et al. 1992; Shikata et al. 1996), and in the ventral stream (Hinkle and Connor 2002; Janssen et al. 1999; Uka et al. 2000; Yamane et al. 2008). The posterior parietal cortex plays an important role in the processing and integration of visual information to control and direct voluntary movements (Andersen and Buneo 2002). Successful grasping depends on extracting the 3-D properties of an object to select the proper hand configurations (Castiello and Begliomini 2008), and the anterior intraparietal area (AIP) is a key area for transforming the intrinsic visual properties of an object into an appropriate grasp (Sakata et al. 1995, 1997, 1998). AIP neurons respond to the presentation of 3-D objects during visual fixation and grasping (Murata et al. 2000), and most neurons encode both object orientation and grip type (Bau- mann et al. 2009). Human functional magnetic resonance imaging (fMRI) studies have shown activations in the putative homolog of area AIP during the presentation of 3-D objects, as well as during grasping compared with reaching (Cavina-Pratesi et al. 2007; Culham et al. 2003, 2006).

Very few studies have addressed the neural representation of 3-D objects in the primate brain. A subdivision of inferotemporal (IT) cortex lying in the rostral lower bank of the superior temporal sulcus (STS) and partially corresponding to anatomically defined areas TEa and TEM (Seltzer and Pandya 1978) was functionally defined as area TEs because of a high proportion of neurons encoding the direction of curvature (concave-convex) in 3-D shapes consisting of random-dot stereograms (Janssen et al. 1999, 2000a, 2000b). One-third of these IT neurons preserved their selectivity for convex and concave stimuli in which the texture elements defining the 3-D surface had been removed and only the boundaries were curved in depth, whereas two-thirds of neurons were selective for concave and convex surfaces in the absence of boundary disparities (Janssen et al. 2001). Furthermore, most TEs neurons discriminated between surfaces curved along the vertical axis and surfaces curved along the horizontal axis.

Neurons in AIP also respond selectively to disparity-defined 3-D shapes, and this selectivity is preserved across positions in depth (between −0.5 and +0.5 deg average disparity) and positions in the frontoparallel plane (between −2.5 and +2.5 deg in the horizontal and vertical direction) (Srivastava et al. 2009). These AIP neurons signal differences in the depth profile much earlier than IT neurons, but the 3-D shape representation in AIP is coarser (less sensitive to the presence of disparity discontinuities in the surface) and less categorical compared with IT. The stimuli used in Srivastava et al. (2009) were 3-D shapes in which both the textured surface and the boundary of the stimulus were curved along the vertical axis. However, for many graspable objects (e.g., a stapler), information about their depth profile must be extracted from the disparity variations along their boundaries because of a lack of texture information on the surface that can carry depth information. Hence, the first goal of this study was to investigate the selectivity of AIP neurons for 3-D shapes in which the disparity variation merely ran along the boundary or along the surface of the stimulus. By using the same stimuli and recording procedures as in the IT studies, we could compare the properties of 3-D shape-selective AIP neurons with the properties of 3-D shape-selective IT neurons (Janssen et al. 2001).
Furthermore, real-world objects contain disparity gradients along both the vertical and the horizontal axes. We therefore wanted to determine whether AIP neurons code not only for curvatures along the vertical axis (as demonstrated by Srivastava et al. 2009) but also for curvatures along the horizontal axis.

The trial-to-trial correlation between neural activity and perceptual choice (choice probability) arises early and during perceptual decision formation in area TEs, but late and after the perceptual decision has been formed in AIP (Verhoef et al. 2010). The close correspondence between depth percept and neural activity in TEs has also been illustrated using anticorrelated disparity, in which the contrast polarity of the dots in one eye has been reversed with respect to the dots in the other eye and for which no depth structure can be perceived (but see Doi et al. 2011; Tanabe et al. 2008). TEs neurons do not signal depth from disparity in anticorrelated images (Janssen et al. 2003), and neuronal sensitivity for anticorrelated disparities is weak in ventral area V4 (Tanabe et al. 2004). In contrast, neurons in middle temporal (MT)/V5 and medial superior temporal (MST) areas of the dorsal visual stream often exhibit sensitivity for anticorrelated random-dot stereograms (Krug et al. 2004; Takemura et al. 2001), similar to neurons in primary visual cortex (Cumming and Parker 1997). Therefore, the possibility exists that sensitivity for anticorrelated disparity may distinguish dorsal stream visual areas from ventral stream areas (Parker 2007). The second goal of our study, therefore, was to assess neuronal selectivity for anticorrelated curved surfaces in area AIP, one of the end-stage areas of the dorsal visual stream.

MATERIALS AND METHODS

Subjects, recording procedure, and stimuli. Three rhesus monkeys served as subjects for extracellular microelectrode recordings. The surgical and recording procedures were similar to those of Srivastava et al. (2009). Briefly, in monkeys under isoflurane anesthesia, an MRI-compatible head fixation post and recording well were implanted vertically over the parietal lobe (Horsley-Clarke coordinates: A1, L15, D35). Implantation of the recording chamber over area AIP was stereotactically guided using preoperative MRI. All surgical techniques and veterinary care were performed in accordance with the NIH Guide for the Care and Use of Laboratory Animals and were approved by the local ethical committee of the Katholieke Universiteit Leuven. The animals were trained to perform a passive fixation task, keeping the gaze of both eyes inside a 1-deg fixation window. Horizontal and vertical eye movements were recorded using an infrared-based 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 a reward. Since the receptive field (RF) of 3-D shape-selective AIP neurons includes the fovea, and given the tolerance of AIP neurons for shifts in stimulus position of at least 5 deg (Srivastava et al. 2009), no attempt was made to map the RF. Stimuli were dichoptically presented using ferroelectric liquid crystal shutters (Displaytech) operating at a frequency of 60 Hz each and synchronized with the vertical retrace of the display monitor (20-in. monitor equipped with ultra-fast P46 phosphor; Vision Research Graphics) at a frequency of 120 Hz and a viewing distance of 86 cm. As previously reported (Srivastava et al. 2009), no cross talk was measured between the images presented to the two eyes.

The stimulus set was virtually identical to the one used in previous experiments (Janssen et al. 2001, 2003). Stimuli were static random-dot stereograms consisting of 50% white and 50% black dots presented on a dark background (luminance of black dots and background = 0.06 cd/m², luminance of white dots = 2.5 cd/m²). These disparity-defined 3-D shapes were generated by combining a 2-D contour and a depth profile (concave or convex). Ten 2-D contours (Fig. 1A) measuring 6.2 × 6.3 deg² were used in the basic stimulus set. Because AIP neurons respond more strongly to larger disparity amplitudes (Srivastava et al. 2009), we chose to set the disparity amplitude in our stimuli to 0.65 deg (dot density = 50%, dot size = 0.032 deg). Different Gaussian depth profiles were created by varying disparity along the surface of the stimulus, along the boundary, or along both surface and boundary (Fig. 1B). Stimuli with opposite curvatures were created by interchanging the monocular images between the eyes (concave surfaces become convex and vice versa).

To describe our stimuli and analogous to Janssen et al. (2001), we reserve the term “3-D shape” for stimuli that have disparity gradients on both surface and boundaries and “3-D surface” for stimuli that have a disparity gradient on their surface and zero disparity on their boundaries. The terms “solid” and “rim” refer to stimuli that only contain boundary disparities (termed “boundary stimuli” in the text). The terms “vertical” and “horizontal” refer to the direction of the disparity gradient (along the vertical or along the horizontal axis). The “vertical 3-D shape” (Fig. 1B, top left) contained a disparity variation on the surface and on the boundary along the vertical axis of the shape, as in a horizontally oriented cylinder (Janssen et al. 2000b; Srivastava et al. 2009). In the “vertical solid” stimulus, the random-dot texture of the correlated vertical 3-D shape was replaced by a uniform white surface, yielding a percept of a textureless surface in which depth was entirely specified by the disparity variation along the contours (luminance = 2.5 cd/m²). In the “vertical rim” stimulus, the central area with the surface dots was left blank, reducing the stimulus to a thin (0.1-deg diameter) contour of random dots. The latter two stimuli consisted entirely of boundary disparities. The “horizontal 3-D shape” (Fig. 1B, middle left) contained disparity variations on the surface and boundary along the horizontal axis of the shape, as in a vertically oriented cylinder. To remove the texture density stripes resulting from disparity variations in the horizontal direction (Cobo-Lewis 1996), we randomly removed dots such that the 50% texture density was restored. This manipulation rendered ~20% of the dots uncorrelated between the eyes (i.e., these dots were present in one eye but not in the other). The “horizontal solid shape” and the “horizontal rim” stimuli were constructed in a manner similar to their vertical counterparts. In the “restricted surfaces,” the depth profile was a 2-D Gaussian with the maximum disparity in the center of the shape smoothly approaching zero toward the boundaries along the vertical axis and the horizontal axis (Fig. 1B, bottom). The disparity reached zero at a distance of 0.2 deg from the outer contour of the shape and the half-maximum disparity (0.31 deg) was located at 1.8 deg from the contour, which is well within the RF of AIP neurons. In the “large surfaces,” the 3-D profile in the center was identical to the “restricted surface,” but the pattern extended beyond this area, covering a 13 × 13-deg square. In this way, the original 2-D contour was replaced by a large square. Finally, anticorrelated surfaces were created by inverting the contrast polarity of the random dots in one of the monocular images of the restricted surfaces (Janssen et al. 2003). All stimuli were presented at the same mean disparity, which corresponded to the center position in the position-in-depth test.

Testing procedure. For extracellular recordings, tungsten microelectrodes (FHC or MicroProbes) were inserted through a guide tube placed in a standard grid (Crist Instruments). MRI using glass capillaries filled with a 1% copper sulfate solution inserted into key grid positions confirmed correct positioning of the electrode in the anterior part of the lateral bank of the intraparietal sulcus (IPS), similar to the recording positions of Srivastava et al. (2009). These grid locations were situated anterior to the lateral intraparietal (LIP) area, since no saccadic activity could be recorded (Srivastava et al. 2009).
Using a passive fixation task, we searched for responsive neurons while disparity-defined curved surfaces with different 2-D contours were presented at the fixation point. In this “search test,” which was identical to that used in Janssen et al. (2001), we presented a set of 30 stimuli. Each of the ten 2-D contours appeared with one of the three 3-D profiles: the concave vertical 3-D shape and the concave and convex restricted surfaces. Based on the responses in this test, the optimal 2-D contour was selected for all subsequent tests. As in previous studies (Janssen et al. 2000b), a pair of 3-D stimuli consisted of a single 2-D contour (Fig. 1A) combined with two depth profiles (concave and convex). The two members of a pair of 3-D stimuli were composed of the same monocular images: the convex profile was created by simply interchanging the monocular images of the concave profile between the eyes. The image for the left eye differed slightly from the image presented to the right eye due to the disparity on the boundaries (Fig. 1B). Thus the two members of a pair of 3-D stimuli only differed in the signs of their disparity gradients (concave vs. convex) but utilized the same monocular images. In the “disparity test,” we presented the optimal 2-D contour with four depth profiles: the concave and convex vertical 3-D shapes (i.e., the first pair of 3-D shapes) and the concave and convex restricted surfaces (i.e., the second pair of 3-D shapes), together with monocular presentations of the same stimuli. Selectivity for 3-D shape was assessed by comparing the responses to the two members of a pair of 3-D shapes relative to the responses to monocular presentations of the same stimuli. When stereo selectivity was present, we assessed the selectivity for higher order disparity with a “position-in-depth test” (for further details, see Janssen et al. 2000b) in which concave and convex 3-D stimuli were presented at five positions in depth, ranging from \(-0.50\) deg (near) to \(+0.50\) deg (far) in steps of 0.25 deg.

If the neuron was judged to be higher order disparity selective, the cell was further tested in the “boundary-surface test.” In this test, different convex and concave depth profiles were shown for the optimal 2-D contour. As in the disparity test, we compared the responses to pairs of concave and convex stimuli that were composed of the same monocular images. The depth profiles varied along the boundary of the stimulus (vertical 3-D rim and vertical solid), along the surface of the stimulus (restricted surface and large surface), or along both boundary and surface (vertical 3-D shape). We also tested the neurons using horizontal disparity variations along the surface and the boundary (correlated horizontal 3-D shape) and along the boundary only (horizontal rim and horizontal solid). As a final test, we compared the selectivity for convex and concave restricted surface stimuli with the selectivity for their anticorrelated counterparts (anti-correlation test). Because anticorrelated vertical 3-D shapes would still contain important depth information along their boundaries, we only tested the effect of stimulus anticorrelation with restricted surface stimuli lacking boundary disparities.

Data analysis. Matlab (MathWorks) was used for data analysis. Net neural responses were calculated by subtracting the mean activity in the 400-ms interval preceding stimulus onset from the mean activity between 50 and 450 ms after stimulus onset. Response latencies were calculated by identifying the first of three consecutive 20-ms time bins in which the population response to the preferred stimulus was significantly higher than in the preceding time bin (Student’s t-test P value < 0.05). For comparison with the IT study (Janssen et al. 2001), the latency of the neural selectivity was computed as the first of three consecutive 20-ms time bins in which the population response to the preferred 3-D shape significantly exceeded the response to the nonpreferred 3-D shape. We also calculated population selectivity latencies using 5-ms time bins. In addition, we calculated the response latency of the individual neurons using Poisson statistics (Janssen et al. 2008; Maunsell and Gibson 1992). We quantified the degree of stereo selectivity by means of three indexes used in previous studies (Janssen et al. 1999, 2000b, 2001; Srivastava et al. 2009). In the disparity test, we computed a stereo difference index (SDI), defined as \(SDI = |\text{difference in response to concave and convex}|\) / \(1 + |\text{difference in response to concave and convex}|\).
convex stimuli in the stereo condition — summed difference in response to the monocular presentations)/(difference in response to concave and convex stimuli in the stereo condition + summed difference in response to the monocular presentations) (Janssen et al. 1999). The SDI compares the response difference in the stereo condition with the response difference in the monocular conditions. As in our previous studies, the neural selectivity was considered to arise from binocular mechanisms if the SDI was >0.5, corresponding to a 3-fold difference in the stereo condition compared with the monocular conditions. As in previous studies (Janssen et al. 1999, 2000a, 2000b, 2001, 2003; Srivastava et al. 2009), neurons were classified as responsive to the spatial variation of disparity if the response to the nonpreferred shape compared with the lowest response of the preferred shape across all positions in depth, indicating the differential response normalized to the highest response for a given pair of 3-D shapes. To compare 3-D shape selectivity across different types of 3-D stimuli, we computed the normalized response difference (NRD) between convex and concave stimuli for every stimulus type separately (i.e., vertical and horizontal 3-D shape, vertical and horizontal solid stimulus, vertical and horizontal rim stimulus), defined as NRD = [(net response to the preferred 3-D shape — net response to the nonpreferred 3-D shape)/net response to the nonpreferred 3-D shape/x/maximal response of the neuron]. The NRD gives the differential response to convex and concave stimuli normalized to the highest response to any of the stimuli in the test (Janssen et al. 2001). This index also takes into account the absolute response levels of the neuron, not merely the degree of selectivity expressed as a percentage response difference.

To assess the representation of 3-D boundary stimuli in the neural space of AIP, we calculated the Euclidean distances between the stimuli based on the following formula: distance between stimulus $i$ and stimulus $j$ = $(\sum (R_{i}^j - R_{j}^i)^2)^{1/2}$, in which $R_i$ is the mean response of neuron $i$ to stimulus 1 and $n$ is the number of neurons tested. Subsequently, we employed nonmetric multidimensional scaling in Statistica (StatSoft) using a matrix of these distances between each pair of stimuli as input. The optimal number of dimensions for the resulting stimulus configuration was chosen by examining the scree plot for a significant reduction in stress of the configuration by adding an extra dimension.

**RESULTS**

We recorded the responses of 147 single AIP neurons showing significant selectivity for concave vs. convex surfaces that could not be explained by the monocular responses. The majority of these disparity-selective neurons (107/147, 73%) preserved their selectivity across positions in depth, indicating higher order disparity selectivity (Fig. 2A). Binocular eye position traces recorded during the position-in-depth test showed only marginal deviations (on average, 0.1 deg of vergence) between the nearest and furthest positions in depth, much smaller than the range of disparities in the position-in-depth test (1 deg, Fig. 2B). These small vergence eye movements became significant ~200 ms after stimulus onset (t-test, $P < 0.05$). In contrast, the neural selectivity for concave and convex was already significant within 50 ms after stimulus onset. Furthermore, no significant differences in vergence movements were present between the convex and concave conditions at any position in depth (t-test, no significance). Hence, as previously demonstrated (Srivastava et al. 2009), eye movements cannot explain the neural selectivity to 3-D stimuli in AIP. Of these higher order neurons, 96 neurons were further tested in the boundary-surface test.

**Selectivity for vertical 3-D boundaries and surfaces.** A large majority of the neurons we recorded in AIP (83/96, 86%) showed a significant selectivity for the vertical 3-D shapes. In Fig. 3, an example neuron is shown with robust 3-D-shape selectivity and a preference for the convex profile. In the position-in-depth test, this neuron preserved its 3-D shape preference across all five positions in depth (Fig. 2A). Both boundary stimuli (the vertical 3-D rim and vertical 3-D solid shape) evoked equally strong selectivity: the interaction be-
tween depth profile (convex, concave) and stimulus type (vertical, rim, boundary) was not significant (ANOVA, *P* > 0.05). In contrast, no significant response or selectivity was present for the restricted or the large surface. Because the surface stimuli were curved along the vertical and the horizontal axes (MATERIALS AND METHODS), whereas all the boundary stimuli were curved only along the vertical axis, the possibility exists that the presence of an additional disparity gradient along the horizontal axis may have been inhibitory for the neuron, rendering the neuron unselective for surfaces curved along the vertical and horizontal axes. Therefore, it cannot be concluded that the boundary in depth was necessary for this neuron. However, the neuron’s response was clearly driven to a large degree by the disparity variation on the boundary of the stimulus: the removal of all surface information had little effect on the response and on the selectivity. In line with the IT study (Janssen et al. 2001), we designated neurons for which a boundary in depth was sufficient to evoke 3-D shape-selective responses “boundary neurons.”

The majority of AIP neurons in our sample encoded the depth profile of at least one of the 3-D boundary stimuli: for 67% of the vertical 3-D shape-selective neurons (56/83), curved boundaries in depth were sufficient for 3-D shape selectivity, even after removal of all surface information. Most of these boundary neurons (53/83, 64%) were selective for the vertical solid shape, whereas a smaller fraction (41/83, 49%) showed selectivity for the vertical rim. Figure 4A shows the population response of all 3-D shape-selective neurons (*n* = 83). For the vertical 3-D shape, the median SI = 0.79, meaning that the response to the preferred depth profile was a factor of 4.8 times larger than the response to the other member of that pair, consisting of the same monocular images but opposite depth profiles. Similarly large differences in neural responses to concave and convex stimuli were evident for the vertical rim (median SI = 0.71) and the vertical solid shape (median SI = 0.61). These results were highly similar if we restricted our analysis to neurons showing significant selectivity at every mean disparity in the position-in-depth test (*n* = 23, median SI = 0.78, 0.73, and 0.70 for the vertical 3-D shape, solid, and rim stimuli, respectively). In line with Srivastava and colleagues (Srivastava et al. 2009; Srivastava S and Janssen P, unpublished observations), the response latency for the vertical 3-D shape stimuli was remarkably short (percentile 10 = 50 ms, percentile 50 = 90 ms). Moreover, the neural selectivity for the vertical 3-D shape pair in the population response also emerged 50 ms after stimulus onset. For the boundary stimuli, the response differences between preferred and nonpreferred 3-D shapes emerged as early as 70 ms after stimulus onset. These latency differences were confirmed by a separate analysis using 5-ms bins (selectivity latency = 50–55 ms for the vertical 3-D shape, 65–70 ms for the vertical solid shape, and 75–80 ms for the vertical rim). Figure 4B plots the normalized response differences for the population of neurons selective to the vertical 3-D shape (*n* = 83) against the normalized response differences for the concave and convex boundary stimuli (rim and solid) (correlation coefficient *R* = 0.67, *P* < 0.01). Many data points cluster near or even above the diagonal, illustrating once more that for many AIP neurons, curved boundaries represent very effective 3-D stimuli. A large subset of neurons (34/83, 41%) even demonstrated similar selectivity for the vertical 3-D shape compared with the boundary stimuli [2-way ANOVA with depth profile (concave, convex) and stimulus type (vertical, solid, rim) as factors, interaction *P* > 0.05]. Although the disparity information carried by the random-dot texture elements of the surface was not required by most AIP neurons, the presence or absence of a uniform surface (carrying no depth information, as in the solid shape) tended to affect the neuronal responses: almost one-half of the boundary neurons (26/56, 47%) distinguished between the preferred vertical solid and the vertical rim (significant main effect of stimulus type in a 2-way ANOVA with depth profile and stimulus type as factors, *P* < 0.05), and 20% of the boundary neurons showed a significant difference in selectivity for solid vs. rim stimuli (ANOVA, interaction between depth...
A small fraction of AIP neurons (31/96, 32%) were selective for many restricted surfaces as vertical 3-D shapes, a relatively "surface neurons." Although our search test contained twice as much information about the presence of a particular 2-D contour was not crucial (rightmost large-surface stimuli indicates that, at least for this neuron, the robust response difference between the convex and concave rightmost columns with the large-surface stimuli were effective in terms of selectivity. Note that for the neuron in Fig. 5, selectivity for the curved boundary stimuli were effective in terms of selectivity. The slight weaker selectivity for curved surfaces compared with the vertical 3-D shapes in AIP, together with the smaller number of surface neurons in the AIP sample, could partially account for these latency differences. However, random sampling of 31 AIP neurons from the population of 83 neurons selective for the vertical 3-D shape yielded a median selectivity latency of 50 ms (percentile 90 = 70 ms) for both the original 3-D shapes and for the 3-D boundaries.

The restricted surface contained disparity variations along both the vertical and the horizontal axes, whereas the vertical 3-D shape contained a disparity variation only along the vertical axis. The neural sensitivity to horizontal disparity variations will be discussed separately. In Fig. 6B, the SI for the restricted surface is plotted against the SI for the large surface for the population of surface neurons in AIP (n = 51) (R = 0.21, P = 0.25). The presence or absence of a 2-D contour had a pronounced effect on most AIP neurons: 20 neurons were selective for the restricted surface but not for the large surface, and another 20 neurons showed selectivity for the large surface but not for the restricted surface. Only a minority of AIP neurons (11/51 surface-selective neurons) displayed significant selectivity for both the restricted and the large surfaces. Hence, even for 3-D surface-selective AIP neurons, the mere presence or absence of a 2-D contour was generally important.

In the group of neurons selective for the vertical 3-D shape (n = 83), 19 cells also showed selectivity to the restricted surface stimulus. Conversely, 12 neurons selective for the restricted surface were not selective for the vertical 3-D shape. The presence or absence of vertical 3-D shape selectivity was not statistically independent of the presence or absence of

Fig. 4. Population analysis of vertical 3-D shape-selective anterior intraparietal (AIP) neurons. A: population response of neurons selective for the vertical 3-D shape (n = 83). The average responses to the preferred (black) and nonpreferred (gray) vertical 3-D shape (left), vertical solid (middle), and vertical rim stimuli (right) are plotted as a function of time. The thin vertical line indicates the first bin in which the response to the preferred shape significantly exceeded the response to the nonpreferred shape. Vertical calibration bar, 40 spikes/s. B: scatterplot comparing the selectivity for the vertical 3-D shape stimuli with that for the vertical 3-D boundary stimuli. For the population of all vertical 3-D shape-selective neurons (n = 83), the response differences between concave and convex stimuli for the vertical 3-D shapes normalized to the highest response of the cell (normalized response differences, NRD) are plotted against the NRD for the vertical solid stimuli (circles) and the vertical rim stimuli (diamonds).

A: vertical 3-D shape, vertical solid, vertical rim
B: NRD for vertical 3-D boundary vs. NRD for vertical 3-D shape

Profile and stimulus type, P < 0.05. Thus the inner surface of the 2-D contour had a pronounced effect on most AIP neurons: 20 neurons were selective for the restricted surface but not for the large surface, and another 20 neurons showed selectivity for the large surface but not for the restricted surface. Only a minority of AIP neurons (11/51 surface-selective neurons) displayed significant selectivity for both the restricted and the large surfaces. Hence, even for 3-D surface-selective AIP neurons, the mere presence or absence of a 2-D contour was generally important.
selectivity for the restricted surface ($\chi^2 = 4.2, P < 0.05$): relatively fewer neurons than expected by chance were selective for both types of stimuli. This statistical dependency could be due either to the absence of 3-D boundary information in the surface stimuli or to the presence of both a vertical and a horizontal gradient in the surface stimuli (discussed below). Most surface neurons ($n = 36/51, 71\%$) responded selectively to one of the surface stimuli and to at least one of the boundary stimuli (rim or solid), indicating that for these neurons, both a pure surface and a boundary in depth was sufficient for 3-D shape selectivity. Twenty-four percent of these neurons were selective for one of the surface stimuli and to at least one of the boundary stimuli but showed no selectivity for the original vertical 3-D shape pair. Only a minority of neurons ($n = 5$) were selective for both the restricted surface stimulus pair and the vertical 3-D shape pair, while at the same time showing no selectivity for any of the boundary stimulus pairs.

**Selectivity for horizontal 3-D shapes.** All higher order disparity-selective AIP neurons were also tested with disparity gradients along the horizontal axis. Almost one-half of these AIP neurons ($47/96, 49\%$) showed selectivity for disparity variations along the horizontal axis. This proportion is likely to be an underestimation of the true proportion of horizontal 3-D shape-selective neurons in AIP, because the horizontal gradient stimuli were not present in our search test. Similar to the vertical 3-D shape, the majority ($35/47, 75\%$) of these neurons showed selectivity for at least one of the horizontal boundaries. In Fig. 7, an example of a horizontal boundary neuron is shown with selectivity to the original horizontal 3-D shape and a similar selectivity to the boundary stimuli, as evidenced by a significant main effect of depth profile ($P < 0.05$) and a nonsignificant interaction between stimulus type and depth profile (2-way ANOVA, horizontal 3-D rim and solid, $P > 0.05$). The restricted and large surfaces did not evoke any differential response ($t$-test, $P > 0.05$; Fig. 7, right). Similar to the example neuron in Fig. 3, the neural selectivity appeared to be largely driven by the disparity variation on the boundary of the stimulus. Figure 8A shows the average response to the preferred and the nonpreferred horizontal 3-D shapes of all neurons selective for the horizontal 3-D shape ($n = 47$). The median SI was 0.86, comparable to the SI of the vertical 3-D shape, and selectivity for the horizontal 3-D shape emerged as early as 60 ms after stimulus onset (65–70 ms with 5-ms bins; response latencies: percentile 10 = 60 ms, percentile 50 = 80 ms). The median SI was 0.54 and 0.64 for the horizontal rim and horizontal solid, respectively, and the response latency for the horizontal boundary stimuli was highly comparable to the latency for the vertical 3-D boundary stimuli (percentile 10 = 60 ms, percentile 50 = 80 ms). In the population response, the selectivity latency for horizontal solid and the horizontal rim stimuli equaled 70 ms (70–75 ms with 5-ms bins), comparable to the latency for the original horizontal 3-D shape and also comparable to those for the vertical stimuli.

Most information about the depth profile of the horizontal solid shapes has to be extracted from the upper and lower contour segments, since the vertical contour segments on the left and right remain at zero disparity. Because depth is derived from horizontal shifts between the images in the two eyes, a horizontal upper and lower contour (as in shapes 6 and 9 in Fig. 1A) does not contain any depth information (Tyler and Kontsevich 2001). Because most of our shapes contained horizontal segments, particularly in the middle of the contour where disparity should be maximal (see shapes 4, 5, 7, and 10 in Fig. 1A), our horizontal boundary stimuli created a much weaker depth percept compared with the vertical boundary stimuli. In this respect the robust and fast encoding of horizontal curved boundaries is remarkable. (Gradients of horizontal disparity along the vertical axis do not create this ambiguity because every point in one eye can be matched with another point in the other eye.) The normalized response differences

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**Fig. 5. 3-D surface selectivity: example neuron.** In this surface-selective neuron, selectivity is shown for the convex vertical 3-D shape (left) and for the convex surface stimuli (right: restricted and large surface). Selectivity is absent for the vertical boundary stimuli (middle: rim and solid). Vertical calibration bar, 50 spikes/s. Bin width, 40 ms.
for the population of neurons selective for the horizontal 3-D shape pair (n = 47) are plotted as a function of the normalized response difference for the boundary stimuli (rim and solid) in Fig. 8B. Similar to the vertical 3-D shape (Fig. 4B), many AIP neurons (22/47, 47%) displayed comparable selectivity for the horizontal boundary stimuli and the horizontal 3-D shape (ANOVA, interaction between depth profile and stimulus type, P < 0.05).

We also wanted to determine to what extent AIP neurons can signal the direction of curvature along the vertical and horizontal axes of a shape. Figure 9 plots the SI for the horizontal 3-D shape pair as a function of the SI for the vertical 3-D shape pair. Note that for both the horizontal and the vertical 3-D shape pairs, the SI was set to zero for net responses to the preferred 3-D shape below 5 spikes/s to avoid spuriously large indexes. The preferred depth profile was determined based on the responses to the vertical 3-D shape; hence, a negative index for the horizontal 3-D shapes indicates inverted selectivity compared with the vertical 3-D shape (e.g., a neuron could prefer convex for the vertical but concave for the horizontal 3-D shape). The largest subpopulation of AIP neurons was selective for the vertical but not for the horizontal 3-D shape (44%, or 42/96 neurons), which can be accounted for by the absence of horizontal 3-D shapes in the search test. However, it is noteworthy that a large subpopulation of AIP neurons was selective for the vertical 3-D shape pair but responded only weakly to the horizontal 3-D shapes (zero SI for the horizontal 3-D shape pair in Fig. 9). Note also that very few neurons showed no selectivity for the vertical 3-D shape (zero SI for the vertical 3-D shape in Fig. 9). This observation can also be explained by our search test, which consisted of vertical 3-D shapes and 3-D surfaces, and by our requirement that every neuron should show selectivity for either the vertical 3-D shape or the surface stimulus to be tested further in the boundary-surface test. A small subset of neurons (n = 5) showed an inverse selectivity for the horizontal and vertical 3-D shapes, such as in a saddle surface. Importantly, the selectivity for vertical 3-D shapes was not statistically independent of the selectivity for horizontal 3-D shapes (χ² test, P = 0.015): for example, neurons that preferred a concave vertical 3-D shape tended not to prefer a concave horizontal 3-D shape, and relatively more neurons than expected by chance showed selectivity for only one of the two types of 3-D shapes. The simultaneous presence of both a vertical and a horizontal gradient in the surface stimuli may have reduced the responsiveness to the surface stimuli in some AIP neurons, which could partially account for the lower proportion of surface neurons in AIP.

**Multidimension scaling analysis.** To investigate how AIP neurons represent vertically and horizontally curved surfaces and boundaries, we used multidimensional scaling (MDS) to visualize the interstimulus distances, derived from the average net responses of all 96 AIP neurons. Because in the IT study of Janssen et al. (2001) not all neurons were tested with the vertical rim and the horizontal solid and rim stimuli and the MDS solution could depend on the stimuli included in the test, we included only the responses to the vertical and horizontal 3-D shapes and the responses to the vertical solid stimuli (i.e., stimuli used in both areas). A 2-D solution of this MDS analysis is shown in Fig. 10A. The first dimension (dimension 1) distinguishes vertical convex stimuli from vertical concave stimuli: vertical concave stimuli cluster on the left and vertical convex stimuli on the right. The second dimension (dimension 2) discriminates between horizontal concave stimuli (top) and horizontal convex stimuli (bottom). Clearly, the 3-D shape representation in AIP considers the boundary stimuli to be very similar to the original 3-D shapes, as evidenced by the close proximity of the solid shapes to their respective 3-D shape counterparts in the MDS solution. Including the responses to the horizontal solid shapes and the rim stimuli in the MDS analysis yielded a very similar result, with the rim stimuli located very close to the solid shapes and the horizontal solid shapes located close to the horizontal 3-D shapes (data not shown). Adding a third dimension improved the goodness of fit only slightly (stress value = 0.10 for 3 dimensions, compared with 0.13 for 2 dimensions): this third dimension distinguished the rim stimuli from all other stimuli (data not shown). Although we did not search for responsive neurons with horizontal 3-D shapes, the large distance between the concave and convex horizontal 3-D shapes on dimension 2 illustrates the robust selectivity for horizontal disparity variations in AIP. Furthermore, vertical disparity gradients are distinct from horizontal disparity gradients, since these two types of 3-D stimuli occupy very different positions in the neural space of AIP.
These results suggest that AIP neurons are highly sensitive to the direction of curvature in 3-D shapes. In Fig. 10B, the MDS solution of the neural space of IT (using the data of Janssen et al. 2001) is shown for comparison. IT neurons discriminate more clearly between boundary stimuli and the original 3-D shapes, since the solid shapes are further removed from their 3-D shape counterparts. In contrast, the direction of curvature appears to be less well represented in IT, given the relatively close proximity of the convex and concave horizontal 3-D shapes to the vertical 3-D shapes.

Responses to anticorrelated disparity. Twenty-four neurons showing selectivity for the correlated restricted surface were further studied in the anticorrelation test. Figure 11A shows the responses of a surface neuron selective for the correlated restricted surface stimulus but not for the anticorrelated restricted surface. The population responses for the correlated and the anticorrelated stimuli are plotted in Fig. 11B. Anticorrelated surfaces evoked substantially weaker responses on average (mean net response = 6 spikes/s, compared with 23 spikes/s for the restricted surfaces) and, more importantly, on average no significant difference between concave and convex surfaces. However, neuronal tuning for anticorrelated disparities can be either inverted or congruent compared with the tuning for correlated disparity (Krug et al. 2004), which could average out in the population response. Therefore, we plotted the normalized response differences for the surface stimuli as a function of the normalized response differences for the anticorrelated stimuli (Fig. 11C). No significant response modulation with respect to the anticorrelated random-dot stimuli was found. The subpopulation contained two outliers (2/24), but the response strengths of these neurons were relatively low: 16 spikes/s for preferred surface compared with 8 spikes/s for nonpreferred surface (P = 0.13), and 9 vs. 3 spikes/s, respectively, for the other neuron (P = 0.61). Note that the lack of selectivity for anticorrelated disparities cannot be accounted for by a weak selectivity for the correlated surfaces, since the average degree of selectivity for the latter stimuli was robust (median SI = 0.79) in this subpopulation of AIP neurons. Hence, unlike other dorsal
stream areas (MT/V5 and MST), AIP neurons were insensitive to anticorrelated disparities.

**DISCUSSION**

AIP neurons showed an exquisite sensitivity for disparity variations along object boundaries, but a smaller proportion of AIP neurons were selective for curved surfaces without boundary disparities. Furthermore, AIP neurons reliably discriminated between vertical and horizontal corrugations. Surfaces composed of anticorrelated disparities were ineffective in AIP.

The total surface area that was curved in depth was smaller for our surface stimuli (27.3 deg$^2$) compared with the vertical 3-D shapes (31.2 deg$^2$). Furthermore, the surface stimuli were curved along the vertical and the horizontal directions, which could also have contributed to a weaker selectivity. For these reasons, a direct comparison between the selectivity for the vertical 3-D shape and the surface stimuli is difficult. We believe that the comparison between the vertical 3-D shape, the solid shape, and the rim stimulus is valid, since the latter two stimuli are reduced versions of the first stimulus (i.e., depth information on the surface has been removed). The crucial point is that the removal of all surface depth information from the vertical 3-D shape stimuli did not abolish the selectivity of most AIP neurons. This is independent and strong evidence in favor of the interpretation that for the large majority of AIP neurons, boundary disparities are sufficient for 3-D selectivity, suggesting that the neural object representation in AIP is primarily contour based. On the other hand, across our population of AIP neurons, the selectivity for surfaces was present in a smaller percentage of neurons, was weaker, and emerged later in time compared with the vertical 3-D shape, despite the fact that we searched for responsive neurons using the convex and concave surfaces.

We did not map the RFs of the 3-D shape-selective AIP neurons, nor did we attempt to optimize stimulus size for the neuron under study. Therefore, the possibility exists that the strong selectivity for boundary stimuli arises because of a specific sensitivity to disparity gradients at a very restricted position in the visual field (i.e., where the boundary is located).

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**Fig. 9.** Scatterplot comparing the selectivity for the vertical 3-D shape with the selectivity for the horizontal 3-D shape for the neurons in the population including all vertical and all horizontal 3-D shape-selective cells ($n = 88$). Note that for neurons with a very low response, the selectivity index is set to zero. Cells selective for the vertical but not for the horizontal 3-D shape ($n = 42$) are indicated by open diamonds.

**Fig. 10.** Multidimensional scaling (MDS) solution. Two-dimensional MDS solutions are shown based on the average neural responses to the vertical 3-D shape, horizontal 3-D shape, and vertical solid shape stimuli for AIP (A) and inferotemporal (IT) areas (B).
However, AIP neurons tolerate changes in stimulus position in the central 5 deg of the visual field (Srivastava et al. 2009), which strongly argues against the possibility of a highly localized RF subregion sensitive to disparity gradients. AIP neurons also tolerate changes in stimulus size between 3 and 12 deg (Romero MC and Janssen P, unpublished observations). Thus, the robust selectivity for boundary disparities did not arise from interactions between the RF substructure and the depth profile of the stimuli.

Area AIP is one of the end-stage areas of the dorsal visual stream that is known to be crucial for grasping (Gallese et al. 1994). Because binocular disparity is the main depth cue for the control of our grasp (Bradshaw et al. 2004), the neural representation of disparity-defined curved surfaces in AIP is likely to be important for the intricate visuomotor transformations necessary for visually guided grasping. Many real-world objects (e.g., a stapler, a computer mouse, or a pen) contain very little depth information on their surfaces because of a lack of texture elements that can carry depth information. For tree-dwelling primates, the rapid and accurate extraction of depth information from the contours of objects (such as the branches of a tree) is crucial for survival. Hence, the predominantly boundary-based nature of the 3-D object representation in AIP, available as early as 50 ms after stimulus onset, may guide the preshaping of the hand during grasping.

Sensitivity to contours in depth is ubiquitous in the primate visual system. Stereoscopic edges (zero-order disparity or position-in-depth information) are extracted at an early stage in the visual system (Burkhalter and Van Essen 1986; Poggio et al. 1988; Qiu and von der Heydt 2005; von der Heydt et al. 2000). V4 neurons encode the 3-D orientation of slanted oriented bars, in which binocular disparity varies along the bar contour (Hinkle and Connor 2002), and in the caudal intraparietal (CIP) area, neurons respond to the gradient of binocular disparity in solid-figure stereograms (Taïara et al. 2000), which are the first-order equivalent of our solid 3-D shapes. The only area known to encode second-order (curved) boundaries is area TEs, in the anterior lower bank of the STS, part of area IT (Janssen et al. 2001). Several important differences between area AIP and area IT regarding their representation of 3-D stimuli become apparent in our current data. When we compare the neuronal properties with those of area TEs, the difference between the relative proportions of surface-selective and boundary-selective cells is obvious: one-third of the neurons in area AIP showed selectivity to the restricted surface stimuli, whereas in area IT, more than two-thirds of the neurons showed a significant selectivity for restricted surface stimuli. In contrast, AIP contained twice as many vertical boundary neurons compared with IT, as well as almost twice as many horizontal 3-D shape-selective neurons. Although horizontal boundary stimuli were not tested extensively in IT, the large proportion of horizontal boundary neurons in AIP and the robustness of the selectivity for horizontal boundary stimuli may represent yet another difference between IT and AIP. Overall, the neural representation in AIP emphasizes boundaries in depth much more so than IT. The difference between IT and AIP with regard to neural sensitivities to boundary stimuli and horizontal 3-D shapes was also apparent in the MDS solution. In the neural space of AIP, the vertical solid stimulus is located very close to the vertical 3-D shape, and the distance between the concave and convex vertical solid stimuli is almost as great as the distance between the concave and convex vertical 3-D shapes. In the neural space of IT, on the other hand, the concave and convex vertical solid stimuli are located much closer to each other and at a considerable distance from their vertical 3-D shape counterparts. The stronger selectivity for horizontal 3-D shapes in AIP compared with IT is exemplified by the larger distance between the concave and convex horizontal 3-D shapes in the neural space of AIP compared with that of IT. We only investigated curvatures along the vertical axis and along the horizontal axis, as these represent the principle axes of curvature in the Koenderink shape space (Koenderink 1990). AIP neurons also became informative about the depth profile much earlier than IT neurons (as much as 40 ms earlier for the boundary stimuli), in agreement with previous findings (Srivastava et al. 2009; Verhoef et al. 2010). Intriguingly, the latencies in AIP differed substantially among the vertical 3-D shape (50 ms), the vertical boundary stimuli (70 ms), the restricted surface (110 ms), and the large surface (130 ms) stimuli, whereas in IT these latencies were much more similar: 110 ms for the vertical 3-D shapes and vertical boundaries, compared with 130 ms for the restricted surfaces (Janssen et al. 2001, 2003). These results suggest that the extraction of 3-D
boundaries is computationally less demanding and therefore more suitable for guiding actions operating under strict time constraints. The main factor underlying the longer latency for surfaces in AIP was a nonselective, transient response to the nonpreferred restricted surfaces, which was even stronger in the case of the large surfaces. Hence, AIP neurons extract or represent 3-D boundaries before 3-D surfaces. Both IT and AIP neurons were highly sensitive to the direction of curvature (vertical vs. horizontal). However, in AIP, the presence or absence of vertical selectivity was not independent of the presence or absence of horizontal selectivity, whereas in IT, the two types of selectivity were statistically independent. The interaction between vertical and horizontal curvature selectivities in AIP may partially account for the relatively weaker selectivity for the restricted and the large surface stimuli in which both gradients were present. It is tempting to relate this finding to the higher proportion of surface neurons and to the stronger surface selectivity in IT: the simultaneous presence of a vertical and a horizontal gradient in the surface stimuli may have been less inhibitory for IT neurons, which could partially explain the stronger selectivity for surface stimuli in IT compared with AIP. The second factor can be related to the absence of disparity on the contours of the surface stimuli: the overwhelming majority of AIP neurons were sensitive to boundaries in depth, and many AIP neurons even demonstrated similar selectivity for stimuli in which both the surface and the boundary were curved in depth (vertical 3-D shape) and for stimuli in which only the boundary contained disparity variations, suggesting that 3-D surface information was largely discarded. In all likelihood, the bumps and troughs of our restricted surface stimuli with zero-disparity boundaries were less “graspable,” and therefore less effective in AIP, than the vertical and horizontal 3-D shape stimuli, in which boundary and surface signal the same depth profile, as do real-world objects. Finally, the possibility exists that low-resolution magnocellular input is dominant in AIP, so the small dot size in our stimuli (0.032 deg) could also account for a difference with area IT. Boundary stimuli such as the solid stimuli, in contrast, contain more low spatial frequencies and could therefore be encoded more robustly in AIP. A strong argument against the latter interpretation comes from our data and data from previous studies (Verhoef et al. 2010, 2011), showing that the neural selectivity for pure 3-D surfaces can be substantial in AIP (Fig. 11B). The population of neurons for which a pure surface is sufficient to evoke selective responses is simply smaller than the population that responds selectively to stimuli containing curved boundaries.

The strong emphasis on the object boundaries in AIP seems to be dissociated from the known properties of 3-D surface perception. For human observers, the threshold for discriminating curved surfaces is lower by a factor of two for random-dot stereograms (with surface and boundaries in depth) compared with pure 3-D boundary stimuli, as in our vertical solid shape (Vreven et al. 2002). IT neurons, however, respond on average much less strongly to the solid 3-D shape compared with the vertical 3-D shape, in agreement with human psychophysical performance.

Previous studies have also highlighted the close correspondence between neural selectivity and 3-D perception in IT, but not in AIP. For example, AIP neurons are relatively insensitive to the sign of curvature (convex vs. concave) and to the presence of disparity discontinuities (Srivastava et al. 2009), whereas IT neurons are strongly affected by discontinuities and are highly sensitive to the sign of curvature, just as human observers are (Rogers and Cagenello 1989). Furthermore, when monkeys discriminate concave and convex surfaces, the choice probabilities in IT arise early and during perceptual decision formation, whereas in AIP, choice probabilities emerge later and after the perceptual decision has been made (Verhoef et al. 2010). The data concerning the neural coding of 3-D shape and the choice probabilities strongly suggest that the object representation in AIP is not related to 3-D object recognition. AIP neurons provide a rapid representation of specific object features that can guide the preshaping of the hand during visually guided grasping. We also recorded in 3-D shape-selective sites during a visually guided grasping task in two monkeys with a paradigm similar to that of Murata et al. (2000). The 3-D shape-selective multiunit activity in AIP frequently showed both visual object-selective as well as visuomotor responses during grasping (Theys T, Pani P, and Janssen P, unpublished observations). These observations link the current and previous studies on 3-D shape selectivity in area AIP (Srivastava et al. 2009; Verhoef et al. 2010, 2011) to earlier AIP studies using grasping tasks (e.g., Baumann et al. 2009; Murata et al. 2000) and support our interpretation of an action-oriented object representation in AIP. Furthermore, our results are relevant for any biologically inspired, artificial vision-based grasping system: a robot capable of grasping objects based on visual information may only need to extract the 3-D contours of the object to be grasped to compute the appropriate hand posture.

The most striking similarity between AIP and IT resides in the lack of neural sensitivity to anticorrelated curved surfaces. Both early visual areas (Cumming and Parker 1997) and dorsal stream areas MT/V5 (Krug et al. 2004) and MST (Takemura et al. 2001) contain large numbers of neurons sensitive to disparity in anticorrelated stereograms. Only unpublished observations exist for area CIP, in the caudal lateral bank of the IPS (Naganuma et al. 2002). In ventral stream areas, on the other hand, neural selectivity for anticorrelated disparity is absent (in IT [Janssen et al. 2003]) or strongly reduced (in V4 [Tanabe et al. 2004]). Despite our relatively small sample size, our data suggest that neurons in AIP, one of the end-stage areas of the dorsal visual stream, most likely do not signal depth in anticorrelated stereograms, in agreement with previous human fMRI data (Preston et al. 2008). These results shed new light on the processing of disparity in extrastriate visual cortex. Selectivity for anticorrelated disparities does not seem to be a distinguishing characteristic of the dorsal visual stream but seems to be a specific property of the V1-MT/V5-MST pathway. Anticorrelation selectivity in V1 can be explained by a modified disparity energy model, in which V1 neurons simply sum the inputs from each eye irrespective of contrast polarity, giving rise to inverted tuning functions for disparity (Cumming and Parker 1997). The rapid vergence eye movements elicited by anticorrelated RDS patterns (Masson et al. 1997), presumably driven by anticorrelation-sensitive MST neurons, may simply be the behavioral output of the V1-MT/V5-MST pathway that rapidly combines (absolute) disparity information from the two eyes for the continuous control of the vergence angle. The processing streams involved in object recognition (IT) and object
grasping (AIP) reject anticorrelated disparities, most likely because anticorrelation is irrelevant for these functions: for accurate object recognition and grasping, the contrast polarity of the points in the left eye and in the right eye should be taken into account. Conversely, the absence of neural selectivity for anticorrelation in a given area may not always imply a role in depth perception, since the choice probability in AIP emerges after the perceptual decision (Verhoef et al. 2010).

To conclude, we have demonstrated that AIP neurons mainly represent 3-D object boundary information and, to a lesser degree, 3-D surface information, with a strong emphasis on the axis of curvature (vertical vs. horizontal), and that AIP neurons are insensitive to anticorrelated disparities. Future studies need to address to what extent a reliable object description, capable of being exploited for visually guided grasping, can be derived from the firing of a population of AIP neurons.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: T.T., S.S., and P.J. conception and design of research; T.T. and S.S. performed experiments; T.T. and P.J. analyzed data; T.T. and P.J. interpreted results of experiments; T.T. prepared figures; T.T. drafted manuscript; T.T., J.v.L., J.G., and P.J. edited and revised manuscript; T.T., S.S., J.v.L., J.G., and P.J. approved final version of manuscript.

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