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Responses to two-dimensional shapes in the macaque anterior intraparietal area

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Abstract

Neurons in the macaque dorsal visual stream respond to the visual presentation of objects in the context of a grasping task and to three-dimensional (3D) surfaces defined by binocular disparity, but little is known about the neural representation of two-dimensional (2D) shape in the dorsal stream. We recorded the activity of single neurons in the macaque anterior intraparietal area (AIP), which is known to be crucial for grasping, during the presentation of images of objects and silhouette, outline and line-drawing versions of these images (contour stimuli). The vast majority of AIP neurons responding selectively to 2D images were also selective for at least one of the contour stimuli with the same boundary shape, suggesting that the boundary is sufficient for the image selectivity of most AIP neurons. Furthermore, a subset of these neurons with foveal receptive fields generally preserved the shape preference across positions, whereas for more than half of the AIP population the center of the receptive field was at a parafoveal location with less tolerance to changes in stimulus position. AIP neurons frequently exhibited shape selectivity across different stimulus sizes. These results demonstrate that AIP neurons encode not only 3D but also 2D shape features.

Introduction

The primate visual system analyses object shape for a variety of purposes, including object recognition, categorization, and action planning (Ungerleider & Mishkin, 1982; Goodale *et al.*, 1991). A large body of literature exists on the shape representation in the ventral visual stream (Desimone *et al.*, 1984; Gallant *et al.*, 1993; Logothetis & Sheinberg, 1996; Tanaka, 1996; Anzai *et al.*, 2007; Pasupathy & Connor, 1999; Brincat & Connor, 2004). Neurons in the inferior temporal cortex (ITC), the end-stage of the ventral visual stream, exhibit properties that are believed to be crucial for object recognition, i.e. both selectivity and invariance. Many ITC neurons respond selectively to images of objects, and this shape preference (i.e. the selectivity) is preserved across changes in retinal size, position (Schwartz *et al.*, 1983; Ito *et al.*, 1995; Op De Beeck & Vogels, 2000; DiCarlo & Maunsell, 2003), the visual cue defining the shape (Sáry *et al.*, 1993), and occlusion (Kovacs *et al.*, 1995). Importantly, the neural selectivity of ITC neurons is preserved across different stimulus transformations, whereas the absolute responses can change dramatically (Sato *et al.*, 1980; Schwartz *et al.*, 1983; Tovée *et al.*, 1994; Ito *et al.*, 1995; Logothetis *et al.*, 1995; Logothetis & Sheinberg, 1996; Op De Beeck & Vogels, 2000; DiCarlo & Maunsell, 2003; Li *et al.*, 2009; Kayaert *et al.*, 2011).

Much less is known about the shape representation in the dorsal stream. Neurons in the lateral intraparietal area (LIP) show shape-selective responses to two-dimensional (2D) images (Serenó & Maunsell, 1998; Sereno & Amador, 2006), but this shape representation appears to be radically different from that in the ITC – LIP neurons are, on average, less selective than ITC neurons (Lehky & Sereno, 2007), and – more importantly – the shape selectivity of LIP neurons shows much less invariance over changes in stimulus size and position (Janssen *et al.*, 2008). Moreover, the receptive field (RF) profile of many LIP neurons can be highly irregular and depend on the shape used in the test.

Adjacent to the LIP in the lateral bank of the intraparietal sulcus (IPS) is the anterior intraparietal area (AIP), an area that is critically involved in grasping (Gallese *et al.*, 1994). Neurons in the AIP respond selectively to real-world objects during manipulation and grasping (Sakata *et al.*, 1995; Murata *et al.*, 2000; Baumann *et al.*, 2009), but also to three-dimensional (3D) surfaces defined by binocular disparity (Srivastava *et al.*, 2009; Verhoef *et al.*, 2010, 2011). Previous monkey functional magnetic resonance imaging (fMRI) studies have revealed stronger activations for images of objects than for scrambled images in the AIP (Denys *et al.*, 2004; Durand *et al.*, 2007). However, it is unknown to what extent AIP neurons are also selective for 2D images of objects and, if so, what aspects of these images are being encoded in this area. Furthermore, the degree of selectivity invariance for changes in size or position of 2D images has never been investigated in the AIP, and no study has mapped the RF of AIP neurons.

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Materials and methods

Surgical and recording procedures

The experimental protocol was similar to that described previously elsewhere (Janssen *et al.*, 2008; Srivastava *et al.*, 2009). All technical procedures were performed in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals, and approved by the Ethical Committee at the Katholieke Universiteit Leuven Medical School.

One male and one female rhesus monkey (monkey H, 6.5 kg; monkey M, 6 kg) were trained to sit in a primate chair. Next, a head post (Crist Instruments for monkey H; custom-made for monkey M) was implanted on the skull with ceramic screws and dental acrylic. For this and all other surgical procedures, monkeys were kept under isoflurane anesthesia (1%) and strict aseptic conditions. Intensive training in passive fixation started after 6 weeks of recovery. Once the monkeys had acquired an adequate level of performance, a craniotomy was made, guided by anatomical magnetic resonance imaging (MRI) (Horsley-Clark coordinates, 2P 12L) over the right hemisphere in monkey M, and over the left and right hemispheres in monkey H. Recording cylinders (Crist Instruments) were implanted vertically above the IPS (Fig. 1A). An ultrasound cylinder was also attached in the coronal plane of the left and right hemispheres, respectively, of monkeys H and M. This cylinder, located orthogonal to the one used for recordings, allowed real-time imaging of the electrode tip in the lateral bank of the IPS by means of high-resolution ultrasound (Philips HDI 5000 SonoCT; scan frequency, 17 MHz; resolution, 0.5 mm). In order to verify the recording positions, glass capillaries were filled with a 2% copper sulfate solution and inserted into a recording grid at several positions while structural MRI was performed (slice thickness, 0.6 mm).

During the experiment, we recorded single-unit activity at several grid positions with standard tungsten microelectrodes (impedance of 1 M Ω at 1 kHz; FHC) inserted vertically through the dura by means of a 23-gauge stainless-steel guide tube and a hydraulic microdrive (FHC). The neural activity was amplified and filtered between 300 and 5000 Hz. Spike discrimination was carried out on-line by using a dual time window discriminator, and displayed with LABVIEW and custom-built software. The positions of both eyes were monitored with a binocular infrared-based camera system (Eye Link II; SR Research) sampling the pupil at 500 Hz. Stimuli were presented on a monitor (M21L-67S01; Vision Research Graphics) equipped with a fast-decay P46-phosphor (Vision Research Graphics) and operating at 120 Hz. 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 the monkeys' view) in the first video frame containing the stimulus. All recorded signals (eye position, neural activity, and photocell pulses) were digitized and processed at 20 kHz with a digital signal processor (DSP; C6000 series; Texas Instruments).

We searched for visually responsive neurons during the presentation of object images at the fixation point (passive fixation task). Especially in the first recording sessions, the ultrasound cylinder was filled with sterile conductive gel (Pharmaceutical Innovations) to allow visualization of the electrode across the different structures. The active-silent transitions observed between the white matter, medial bank, sulcus and, finally, the lateral bank of the IPS were useful for identification of the recording area. To exclude the possibility that some cells were accidentally recorded in the most anterior region of the LIP, we searched for saccade-related activity in monkey H, considering all recording positions of the present study. Ten recording sessions performed while the monkey made visually guided saccades to 10 targets in the contralateral visual hemifield did not show any

FIG. 1. Methods. (A) Anatomical magnetic resonance image and lateral view of the macaque brain, indicating the reconstructed recording positions in the AIP. (B) Stimuli in the search test. All stimuli in the search test (faces, hands, natural objects, and artificial objects) were presented with congruent and incongruent disparity. (C) Stimuli in the shape test. The surface stimulus was a 2D image presented binocularly. The silhouette, outline and line-drawing stimuli were reduced renderings of the surface stimuli lacking surface information.

saccade-related activity in any of the recording positions tested. As in previous studies (Srivastava *et al.*, 2009; Theys *et al.*, 2012), we defined AIP functionally as the area in the anterior lateral bank of the IPS, where no responses to saccadic eye movement are present (as opposed to the LIP, which is located more posteriorly in the lateral bank of the IPS). The absence of saccadic responses, combined with the presence of selectivity for 3D stimuli presented at the fixation point, confirmed that the recording area was located in the AIP (Srivastava *et al.*, 2009).

Stimuli and tests

In the passive fixation task, each trial started with the onset of a small square in the center of the screen (fixation point; 0.2×0.2 deg). If both eyes remained within a 1-deg square electronically defined window around the fixation point for at least 500 ms, a visual stimulus was presented in the center of the display for the next 800 ms. Trials were considered to be correct when the monkeys kept a constant fixation until the offset of the stimulus, receiving a drop of water as reward.

The first stimulus set consisted of 24 stereoscopic images of natural and artificial objects, including faces, hands, fruits, branches, and several artificial graspable objects (monocular images in Fig. 1B). For each stereoscopic stimulus, we obtained left and right eye images by taking two photographs from slightly different viewpoints, matched to the interocular distance of the monkeys. The stimuli were presented stereoscopically by alternating the left and right eye images on the display, in combination with two ferroelectric liquid crystal shutters operating at 60 Hz each in front of the monkeys' eyes and synchronized to the vertical retrace of the monitor (two superimposed shutters in front of each eye; Displaytech). The use of the fast-decay phosphor and the two superimposed shutters prevented any measurable crosstalk between the eyes. For every stimulus in the first stimulus set, the pattern of binocular disparity was congruent with the disparity gradients present in the real-world objects (congruent stereo mode). In a second stimulus set, the stimuli were identical to those in the original set but contained the opposite disparity pattern, by exchange of the two images between the eyes (incongruent stereo mode). We searched for responsive neurons during the presentation of stimuli from both stimulus sets at the fixation point. All binocular stimuli in this search test differed in size (range of vertical and horizontal diameter, 1–9.8 deg) and surface area (range, 6.9–109.3 deg²).

For all subsequent tests, we equalized the surface area between the stimuli (both 3D and 2D). Because of the large variation in surface area in our stimuli, we first split the original stimulus set into two categories (round and elongated stimuli; see Fig. 1B, 'R' and 'E' labels), and then resized the monocular images to the same value, depending on the stimulus category to which the stimulus belonged (surface area for round stimuli, 34.4 deg²; surface area for elongated stimuli, 25.7 deg²). A third set of stimuli consisted of binocularly presented, area-equalized 2D (i.e. no disparity present) versions of the original set. For this third set, both shutters opened and closed simultaneously, synchronized to the appearance of either the left or right eye image on the display (no-stereo mode, termed 'surface' in Fig. 1C). Finally, we created a set of 2D area-equalized (6 deg in diameter) contour stimuli consisting of silhouette, outline and line-drawing versions of each stimulus with PHOTOSHOP 8.0 (Adobe) and MATLAB routines (Fig. 1C). All contour stimuli were presented binocularly without disparity. Because the silhouette stimuli were area-equalized, the total luminance of these stimuli was identical within the stimulus category (round or elongated). For the outline stimuli, the surface area included by the outline was identical within the stimulus category (round or elongated), but, because of the variation in the shape of the contour, the total number of bright pixels fluctuated between by approximately $\pm 3.5\%$ between stimuli. The luminance measured in a 6.5×6.5 window around the center of the stimuli equaled 1.4 cd/m² for the surface stimuli, 5 cd/m² for the silhouettes, 0.4 cd/m² for the outlines, and 0.8 cd/m² for the line-drawings. The stimuli appeared randomly interleaved on a black background at the fixation point (mean luminance, 0.46 cd/m²) and at a viewing distance of 86 cm.

We searched for responsive AIP neurons during the presentation of stereo stimuli with congruent and incongruent disparity at the fixation point. If the neuron was responsive to at least one of the stimuli, we selected the object image evoking the strongest response (termed the preferred image) and a different object image to which the neuron responded weakly (termed the nonpreferred image) for subsequent testing. Both of these images belonged to the same stimulus category (round or elongated), so that their surface areas were equal in all subsequent tests. Neurons showing object-selective responses were next studied in the shape test, which included the presentation of the preferred and nonpreferred object images in congruent, incongruent and no-stereo mode (2D images), and the three contour versions (silhouette, outline, and line-drawing). The response differences between the congruent, incongruent and no-stereo mode conditions will be presented in a separate study, and will therefore not be discussed further.

To assess the RF near the fovea of neurons showing object-selective responses in the previous tests, we presented the preferred and nonpreferred area-equalized object images in their optimal configuration (congruent, incongruent or no-stereo mode) at nine different positions in the visual field spaced 5 deg apart around the fixation point (position test). Finally, a size test was also performed, for comparison of responses to the preferred and the nonpreferred images in their optimal configuration (congruent, incongruent or no-stereo mode) during foveal presentations with different sizes (12, 9, 6 and 3 deg).

Data analysis

All data analyses were performed in MATLAB (Mathworks). For each trial, the baseline firing rate was calculated from the mean activity recorded in the 400-ms interval preceding the stimulus onset. Net neural responses were then calculated by subtracting the baseline from the mean activity observed between 50 and 450 ms after the onset. We used *t*-tests on the responses to the preferred and nonpreferred surfaces, silhouettes, outlines and line-drawings to assess the significance of the shape selectivity for each of these stimulus types. The identification of the preferred and nonpreferred silhouette, outline and line-drawing stimuli was based on the responses to the corresponding 2D surface stimuli. To compare the shape selectivity across different types of stimuli in the shape test, we calculated the normalized response difference (NRD) for every stimulus type (surface, silhouette, contour, and line-drawing) separately, defined as $(R_{\text{preferred image}} - R_{\text{nonpreferred image}}) / (R_{\text{preferred surface}})$. The NRD takes into account the absolute response levels of the neuron, not merely the degree of selectivity expressed as a percentage response difference. For example, a neural response of 40 spikes/s to the preferred surface and 4 spikes/s to the nonpreferred surface, but 20 spikes/s to the preferred silhouette and 2 spikes/s to the nonpreferred silhouette, would yield NRDs of 0.9 and 0.45 for the surface stimuli and the silhouettes, respectively.

Response latencies were computed as the first of three consecutive time bins after stimulus onset (bin size, 20 ms) showing a significantly increased response as compared with baseline (*t*-test, $P \leq 0.05$).

For the position test, contour plots were constructed by 2D linear interpolation of the mean responses to the preferred and the nonpreferred images. The global RF maximum and additional local maxima were determined with MATLAB routines (Image toolbox). To provide a worst-case estimate of the shape preference across all positions tested, we calculated the maximum normalized response to the worst (i.e. nonpreferred) image (MNRW) (Janssen *et al.*, 2008). The MNRW is simply the strongest response of the neuron to the

nonpreferred image normalized to the highest response in the test (i.e. the response to the preferred image at the optimal position), and thereby indicates how much the neural selectivity was diminished in the position test (an MNRW of 0 indicates that the neuron did not respond to the nonpreferred shape at any position; an MNRW of 1 indicates that the neuron lost its selectivity at some position in the test). In order to compare the selectivity between the different positions, we calculated a selectivity index (SI), defined as $SI = (R_{\text{preferred image}} - R_{\text{nonpreferred image}}) / R_{\text{preferred image}}$, for each position tested. The preferred and nonpreferred images were defined on the basis of the cell responses at the fixation point.

To quantify the degree of position invariance, we computed the separability between position and shape. A separability index (SPI) was obtained by calculating the correlation between the observed and the predicted responses, assuming perfect dissociation between the two dimensions (Brincat & Connor, 2004). The predicted responses were the product of the marginal sums for each stimulus and position tested. An index of 1 indicated perfect separability of shape and position, whereas an index of 0 indicated marked differences in neural selectivity across positions. A similar SPI was calculated for the size test.

Results

We recorded the activity of 177 AIP neurons that were responsive to the images in the search test in two monkeys. Thirty-eight neurons (21.5%) showed visual responses that were not selective for any of the stimuli in the search test and were not further studied. The remaining 139 AIP neurons responded selectively to at least one of the stimuli in the search test (102 neurons in monkey H; 37 neurons in monkey M). Structural MRI and high-resolution ultrasound imaging were used to verify the recording positions (see Materials and methods), and confirmed that neurons were localized in the lateral bank of the anterior IPS (Fig. 1A). In monkey H, we recorded from both hemispheres ($N = 47$ in the left hemisphere and $N = 55$ in the right hemisphere), but no consistent differences in neuronal properties were observed between the two hemispheres.

Shape test

The neuron in Fig. 2A responded significantly more strongly to the 3D image of a tangerine (preferred image) than to that of a key (nonpreferred image) at the fixation point, and this image selectivity was almost identical for the area-equalized images without binocular disparity ('surface'). Moreover, all three contour versions of the same stimulus (silhouettes, outlines, and line-drawings) evoked significant and robust image selectivity (t -tests, $P < 0.01$). Note that although the boundary information was clearly sufficient to evoke selective responses in this neuron, the absolute responses to the contour and the line-drawing stimuli were significantly lower than the response to the surface stimuli (t -test, $P < 0.01$). The neuron in Fig. 2B responded significantly more to the image of a human hand than to that of a face, both with (3D) and without ('surface') disparity gradients. However, this selectivity was only present for the images containing surface information, as the responses to the different contour stimuli did not show any clear preference for the hand over the face image [t -test, not significant (NS)]. Therefore, the boundary information was not sufficient for this second example neuron.

Ninety-six image-selective AIP cells were evaluated in the shape test (63 in monkey H; 33 in monkey M). The overwhelming majority of those neurons [91/96 (95%); 97% in monkey H; 91% in monkey M] showed significant selectivity (t -test, $P < 0.05$) for at least one of the 2D

FIG. 2. Example neurons in the shape test. (A) Peristimulus time histogram of an example neuron showing selectivity for the 2D surface stimuli (top row, preferred shape; bottom row, nonpreferred shape), and contour selectivity for the silhouette, outline and line-drawing stimuli. The horizontal bar indicates the duration of stimulus presentation (800 ms). (B) Example neuron responding selectively to the 2D surface stimuli but not to any of the contour stimuli. Same conventions as in (A).

area-equalized object images lacking disparity (surfaces, silhouettes, outlines, or line-drawings). The surface stimuli evoked significant selectivity (t -test, $P < 0.05$) in 75 of 96 (78%) AIP neurons, but an even larger number of AIP neurons [80/96 (83%); 83% in monkey H; 85% in monkey M] were selective for one or more of the contour stimuli (t -test, $P < 0.05$ corrected for multiple comparisons). Conversely, 16 neurons were selective for at least one of the contour stimuli but not for the surface stimuli. The silhouette stimuli evoked selective responses in 62% of the neurons, as compared with 56 and 40% for the outline and line-drawing stimuli, respectively. Thus, for the large majority of AIP neurons, boundary information was sufficient to evoke selective shape responses. We termed neurons showing selectivity for at least one of the contour stimuli boundary neurons.

Figure 3A shows the scatter plot relating the NRD obtained for the 2D surface images to the NRD for the silhouette stimuli. A large

FIG. 3. Shape test scatter plots. The NRD for the 2D surface stimuli is plotted against the SI for the silhouette (A), outline (B) and line-drawing stimuli (C), together with a histogram of the distribution of the NRDs. The diagonal indicates the line of equality.

number of cells showed strong selectivity for both surface and silhouette stimuli (data points around the diagonal), and a sizeable proportion of AIP neurons were even more selective for the silhouette than for the 2D surface stimuli (upper left quadrant). (The clustering of

data points in the top right corner was caused by clipping the higher NRD values to 1.5 for purposes of illustration.) Only a small fraction of neurons ($N = 14/91$, 15%) responded weakly or not selectively ($\text{NRD} < 0.2$) to the silhouette stimuli. Because the neural selectivity for the silhouette stimuli could be either weaker or stronger than that for the surface stimuli (almost equal number of data points above and below the diagonal), the correlation between the surface NRD and the silhouette NRD was relatively weak ($r = 0.36$, $P < 0.05$). Thus silhouette stimuli can be sufficient to evoke selective responses, but certain features inside the surface stimuli appeared to be inhibitory for a sizeable fraction of the AIP neurons (i.e. those neurons with a higher NRD for the silhouette than for the surface stimuli). Figures 3B and C show the NRD for 2D surface images plotted against the NRD for the outline and the line-drawing versions, respectively. Although many neurons shared high selectivity for the 2D surface, outline and line-drawing stimuli, a larger number of cells selective for the 2D surface stimuli exhibited weak selectivity ($\text{NRD}, < 0.2$) for the outline ($N = 20/91$, 22.0%) and line-drawing ($N = 18/91$, 21.0%) stimuli. As for the silhouette stimuli, the correlation between the NRD for surface stimuli and the NRD for contour and line-drawing stimuli was relatively weak (Pearson correlation coefficient, $r = 0.19$ and $r = 0.28$, respectively, $P > 0.05$). It should be mentioned that our line-drawings were more complex than the outlines and silhouettes for most of the stimuli, as the boundary of the stimulus was combined with small shape elements inside the figure (see, as an example, the nonpreferred shape in Fig. 2B). The significantly lower incidence of selectivity with the line-drawing stimuli than with the outline stimuli (z -test, $P < 0.05$) suggests that these internal shape elements might exert an inhibitory influence in a subpopulation of AIP neurons.

In Fig. 4, the time course of the neural selectivity is illustrated by plotting the difference in the average population response to the preferred and nonpreferred images for all selective AIP neurons recorded in the shape test. To compare the neural selectivity between stimulus types, only cells exhibiting significant selectivity for a particular type of stimulus (2D surfaces, silhouettes, outlines, and line-drawings) were included, even though the same analysis performed on all 96 neurons tested yielded virtually identical results (data not shown). The differential response in our population of image-selective AIP neurons was similar for the 2D surface and silhouette stimuli, and considerably weaker for the outline and line-drawing stimuli. Neurons started to signal the difference between the preferred and nonpreferred 2D surface stimuli at approximately 60–80 ms after the stimulus onset (t -test on the population response, $P < 0.05$), consistent with Srivastava *et al.* (2009). The fastest latencies were observed for the silhouette stimuli (40–60 ms), which had the highest mean luminance, whereas the outline (60–80 ms) and line-drawing (80–100 ms) stimuli evoked selectivity at considerably longer latencies. A cell-by-cell analysis of the selectivity latencies based on t -statistics (20-ms time bins, $P < 0.05$) yielded similar results for all four types of 2D image (percentile 10 = 60 ms and percentile 50 = 80 ms for surface, silhouette, outline and line-drawing stimuli). Thus, our data demonstrate that AIP neurons respond selectively to 2D images of real-world objects, and that this selectivity can be preserved for stimuli that contain only boundary information. Only a very small minority of AIP neurons appear to require surface information carried by texture, shading and inner shape elements.

Position and size test

We recorded the responses of 49 AIP neurons in the position test (33 in monkey H; 16 in monkey M), almost all of which were contour neurons [45/49 (92%); 91% in monkey H; 93% in monkey M] as determined in the shape test. We used the stimulus type that evoked the strongest

response in the neuron tested (judged online), either with (21/49, 43%) or without (28/49, 57%) disparity gradients (i.e. 3D or 2D).

FIG. 4. Shape test population analysis. The average response difference between the preferred and nonpreferred images is plotted as a function of time (20-ms bins) for surface (green), silhouette (purple), outline (orange) and line-drawing (cyan) stimuli. Each plot shows the average response difference for all AIP neurons showing selectivity for that stimulus type.

The neuron in Fig. 5A (the same as in Fig. 2A) fired selectively in response to the image of a tangerine when presented in the center of the screen ($SI = 0.83$) and to a lesser extent at two other positions (5 deg contralateral on the horizontal meridian and 5 deg down on the vertical meridian). The other six positions tested did not evoke any significant responses (t -test pre-stimulus vs. post-stimulus epoch, NS). Much weaker responses occurred when the nonpreferred shape (key) was presented at any of the positions tested. Thus, this example neuron showed three distinct characteristics: it responded at a limited number of positions, the RF center was located at the fixation point, and the response to the nonpreferred shape never exceeded 50% of the maximal response to the preferred shape at any of the positions tested ($MNRW < 0.50$; see Materials and methods). Figure 5C shows another highly selective neuron ($SI = 1.39$), but in this case the excitatory response occurred exclusively when the preferred shape (human hand holding a marker) appeared at the foveal location, whereas all other presentations of the same shape evoked strong inhibitions below the baseline firing rate (note the different scale bars in Fig. 5A and C). Similarly, presentations of the nonpreferred shape (human face) evoked inhibitory responses across all positions tested. The neuron in Fig. 5C did not tolerate any change in position for the preferred shape, the RF center was located at the fixation point, and the response to the nonpreferred shape never exceeded 50% of the maximal response to the preferred shape. Note that both example neurons (Fig. 5A and C) were selective at every position that elicited significant responses. The SPIs between shape and position equaled 0.87 for the neuron in Fig. 5A and 0.94 for the neuron in Fig. 5C.

FIG. 5. Example neurons in the position and size tests with the highest response at the fixation point. (A) Example neuron (the same neuron as in Fig. 2A) showing invariance of the image selectivity across position. The graph is a 2D-interpolated map of the average responses to the preferred image (left) and the nonpreferred image (right). Colors indicate the strength of the neural response (varying between 0 and 48 spikes/s). [0,0] is the central position (at the fixation point), and +5 deg azimuth is contralateral. The red dots indicate the stimulus positions tested; the dot indicating the central position at [0,0] has been omitted for clarity. The smallest size for which selectivity was observed is plotted at the fixation point. (B) The same neuron as in (A) tested in the size test. Average responses (mean $\pm$ SEM) to the preferred image (black) and nonpreferred image (gray) are plotted for the four sizes. (C) Example neuron in the position test showing excitatory responses to the preferred image at a single position (the central position), and inhibitory responses below baseline for all other positions (left) and for the nonpreferred image at every position tested (right). Same conventions as in (A). (D) The same neuron as in (C) in the size test. Same conventions as in (B).

FIG. 6. Example neurons in the position and size tests showing the highest response at a parafoveal position. (A) Example neuron with an RF profile that differs between the preferred shape (left) and the nonpreferred images (right). (B) Same neuron as in (A) in the size test. (C) Example neuron with a parafoveal RF for the preferred image (left) and the nonpreferred image (right). (D) Same neuron as in (C) in the size test. Same conventions as in Fig. 5.

The example neurons in Fig. 5 were also tested with the preferred and nonpreferred images and a range of stimulus sizes (3–12 deg) at the fixation point. The shape preference was preserved across all sizes tested in both neurons (Fig. 5B and D; ANOVA with shape and size as factors, main effect of shape $P < 0.05$, size $P > 0.05$, interaction NS for both neurons). The SPIs between shape and size were 0.98 for the example neuron in Fig. 5B and 0.93 for the neuron in Fig. 5D, confirming that the shape selectivity did not interact with the effect of the stimulus size. The observed size invariance for stimuli up to 12 deg makes it highly unlikely that the shape selectivity of the neuron in Fig. 5C – which did not tolerate any change in position – arose from an accidental interaction between a local shape element and the RF of the neuron. Thus, these two AIP neurons gave the strongest response at the fixation point, with limited (Fig. 5A) or no (Fig. 5B) tolerance for changes in position and robust tolerance for changes in stimulus size.

However, a sizeable proportion of AIP neurons did not respond maximally at the fixation point. The neuron in Fig. 6A fired vigorously in response to the image of the spoon at almost all positions tested, but most strongly at the lower position on the vertical meridian. The image of a branch, which was highly similar in orientation and aspect ratio, evoked almost no response at the fixation point ($SI = 0.80$), but was surprisingly effective in driving the neuron at seven out of eight parafoveal positions (Fig. 6A, right panel). The selectivity at the position where the neuron gave the maximal response (5 deg below the fixation point, $SI = 0.19$, t -test on the difference between the net responses, NS) was much lower than that observed at the fixation point ($SI = 0.80$), indicating that the degree of shape selectivity was strongly overestimated in the shape test, where the stimulus was presented at the fixation point. Although this example neuron tolerated changes in position of the preferred shape much more than the neurons in Fig. 5, it fired in response to the nonpreferred shape at more than 75% of the maximum response in the test (position 5 deg down on the vertical meridian, $MNRW = 0.81$), indicating a

loss of shape selectivity. In addition, at the worst position for the preferred shape (5 deg ipsilateral on the horizontal meridian), the neuron also showed no selectivity ($SI = -0.04$, t -test on the difference between the net responses, NS) despite the robust responses to both

FIG. 7. Position test population averages. (A) Average response of all neurons with foveal RFs. (B) Average response of all neurons with parafoveal RFs. The color codes the average response normalized to the highest response of each neuron, averaged across neurons. Otherwise, same conventions as in Figs 5 and 6.

the preferred and the nonpreferred shapes (on average, 25 spikes/s for the preferred shape). The strongest responses were measured at the same position for both stimuli (i.e. 5 deg below the fixation point on the vertical meridian), but the RF profile as determined with the spoon (preferred shape) differed markedly from the RF profile for the branch (nonpreferred shape), mainly because of the weak responses to the image of the branch at the fixation point. Thus, in contrast to the example neurons in Fig. 5, this AIP neuron responded maximally at a parafoveal position, and lost its shape selectivity at positions that still evoked strong shape responses. Note that the center-surround organization of the RF as determined with the nonpreferred shape (Fig. 6A, right panel) represents the opposite pattern to the RF of the neuron in Fig. 5C (i.e. excitatory center and suppressive surround).

Despite the profound effect of position on shape selectivity for the neuron in Fig. 6A, tolerance to changes in size was very robust, as the shape preference was preserved across all sizes tested (Fig. 6B; ANOVA with shape and size as factors, main effect of shape $P < 0.05$, size $P < 0.05$, interaction NS). However, the 6-deg image of the nonpreferred shape evoked significantly less response than the 3-deg and 9-deg images, which might suggest that specific contour elements of the 6-deg branch image – not present in the image of the spoon – encroached on a suppressive area within the RF surrounding the fovea. Although this type of AIP neuron may respond to particular shape elements presented in its RF, the strongly reduced shape selectivity at parafoveal positions suggests that it does not encode object shape independently of position.

Finally, image selectivity could also be strongly overestimated at the fixation point, because this central position appeared to be located at the edge of the RF. At the fixation point, the example neuron in Fig. 6C responded to the image of the cables but not to the image of a key (SI = 0.97). The maximal response of the neuron was measured for the image of the cables presented in the upper contralateral hemifield (SI = 0.23), but presentations of the nonpreferred image (the key) in the upper contralateral hemifield also evoked strong responses (mean response to the nonpreferred shape = 20 spikes/s; MNRW = 0.77; t -test on the difference between the net responses, $P < 0.05$). In the size test, the neuron was selective for the 6-deg, 9-deg and 12-deg stimuli, but not for the 3-deg stimuli, and the responses to the preferred and the nonpreferred images increased monotonically with stimulus size (Fig. 6D). Thus, the results of the size test were consistent with the hypothesis of accidental interactions between the parafoveal RF and the stimuli, as the larger stimulus sizes stimulated the upper contralateral visual field more than the smaller stimulus sizes.

Figure 7A plots the average responses for all AIP neurons with the maximum response at the fixation point, normalized to the highest response in the test [$N = 19/49$ (39%); 39% in monkey H; 38% in monkey M]. Changes in the stimulus position within the central 10 deg had a profound impact on the neural response to the preferred shape (e.g. ipsilateral and upper visual field positions; ANOVA on the responses to the preferred shape at all positions, $P < 0.05$ for 90% of the neurons). On average, the cells with foveal RFs responded significantly to the preferred shape at only three of nine positions (median number of positions with t -test $P < 0.05$ on the average response post-stimulus vs. pre-stimulus onset). Remarkably, a subgroup of highly selective AIP neurons (4/19, 21%) only responded to the preferred image at a single position in the visual field, i.e. at the fixation point (example neuron in Fig. 5B). Although the absolute response of these AIP neurons was strongly affected by stimulus position, the shape preference was generally preserved, as the nonpreferred shape elicited, on average, weak responses at every position tested (Fig. 7A, right panel). To provide a worst-case estimate for the strength of the shape preference across all positions tested, we calculated the MNRW. The median MNRW for this population of AIP neurons was 0.44, and only three

neurons (16%) showed an MNRW of > 0.75 , indicating that AIP neurons with foveal RFs tended to respond more weakly to the nonpreferred image at any of the positions tested. Overall, 12 of 19 (63%) AIP neurons with foveal RFs showed an MNRW of < 0.75 (i.e. shape preference) and significant shape selectivity at more than one position (i.e. tolerance to changes in position). In other words, at those positions where the AIP neurons responded to the preferred image, the shape selectivity was generally preserved.

The subpopulation of AIP neurons that responded maximally at parafoveal positions is plotted in Fig. 7B [$N = 30/49$ (61%); 61% in monkey H; 63% in monkey M]. The position of the preferred shape affected the average response in almost all neurons (ANOVA on the responses to the preferred shape at all positions $P < 0.05$ for 90% of the neurons), and, on average, four of nine positions elicited significant responses to the preferred image (median number of positions with t -test $P < 0.05$ on the average response post-stimulus vs. pre-stimulus onset), which was significantly more than for the AIP neurons with foveal RFs (two-tailed t -test $P < 0.05$). Although these neurons were also highly selective at the fixation point (Fig. 7B; average SI = 1.14 at the fixation point), one or more positions outside the center evoked stronger responses to the preferred shape and – in contrast to the AIP neurons with foveal RFs – frequently also strong responses to the nonpreferred shape (e.g. lower contralateral position in the right panel of Fig. 7B). On average, the highest response to the nonpreferred image reached 74% of the maximum response to the preferred shape (median MNRW of 0.74), and 57% of the neurons showed an MNRW of > 0.75 . Therefore, in AIP neurons with parafoveal RFs, the preferred image may have elicited more activity at the fixation point because it overlapped more with the parafoveal RF than the nonpreferred image. Note that we did not observe any clear clustering in the recording position of AIP neurons with foveal or parafoveal RFs. Thus, in general, AIP neurons showed limited tolerance to changes in stimulus position; AIP neurons with foveal RFs preserved their shape selectivity at those positions where the neurons responded, whereas AIP neurons with parafoveal RFs did not preserve their shape selectivity at parafoveal positions.

We calculated the image selectivity for each position on the basis of the average responses of all AIP neurons tested ($N = 49$). The average image selectivity was statistically significant (t -test, $P < 0.05$ corrected for multiple comparisons) at all positions tested except for the ipsilateral lower and contralateral upper positions, indicating that, as a population, the AIP preserves its image selectivity across a range of positions.

For the example neuron in Fig. 6A, the RF profile as determined with the preferred shape differed markedly from the RF profile determined with the nonpreferred shape. We quantified the correspondence between the RF profiles as estimated with both the preferred and the nonpreferred shapes for all neurons that showed an MNRW of $> 50\%$ ($N = 37$). The average 2D correlation coefficient obtained was 0.51, indicating that the RF profile depended substantially on the shape tested. Similarly, the median overlap in the RF profiles (calculated as the proportion of pixels in the interpolated RF maps for which the response was more than 50% of the maximum response to both the preferred and the nonpreferred shapes) was only 61%. Although the RF profile could depend heavily on the shape used in the test (see neuron in Fig. 6A), the best position for the preferred shape corresponded to the best position for the nonpreferred shape in 35% (17/49) of the neurons.

The mean SPI for shape and position in our population of AIP neurons was 0.86 ± 0.02 , which is similar to values reported for the ITC (Brincat & Connor, 2004). However, the mean SPI was similar for AIP neurons with foveal (mean SPI, 0.83 ± 0.06) and parafoveal (mean SPI, 0.87 ± 0.026) RFs. For the neurons in Fig. 6A and C, whose shape selectivity clearly depended on position, the SPIs were

0.81 and 0.82, respectively. Because the maximum response to the preferred shape was measured at the same position as the maximum response to the nonpreferred shape, the separability between shape and position was relatively high. Therefore, in some cases, the SPI may not capture the dependence of shape selectivity on position, and tends to overestimate the degree of position invariance.

Although size had a significant effect on 76% of the AIP neurons tested ($N = 25/33$; 73% in monkey H; 86% in monkey M; ANOVA on the responses to the preferred shape for all sizes, $P < 0.05$), more than half of the AIP neurons recorded in the size test (19/33; 57.7% for monkey H; 50.0% for monkey M) showed significant shape selectivity for more than one stimulus size (eight of these neurons preserved their selectivity across all sizes). The shape preference of these neurons was therefore considered to be size-invariant. Conversely, a sizeable proportion of AIP neurons (14/33; 42%) were merely selective to a single size in the test, which was mostly the 3-deg size. Figure 8 shows the average responses to the preferred and nonpreferred shapes across sizes for the whole population of AIP neurons recorded in this task. Responses to the preferred shape were, on average, almost five times stronger than responses to the nonpreferred shape. As a population, the shape preference was clearly preserved for every size tested ($P < 0.05$, t -tests corrected for multiple comparisons). The mean separability of shape and size was 0.82 ± 0.03 , which is again similar to values reported for the ITC (Brincat & Connor, 2004). Moreover, robust size invariance was frequently observed in neurons that lost their shape preference at some positions, as shown for the neuron in Fig. 6A. The correlation between the degree of position invariance (measured by means of the MNRW) and the degree of size invariance (the number of sizes for which the neuron showed selectivity) was not significant (Pearson correlation coefficient – $r = -0.26$).

Discussion

Our study is the first to demonstrate selectivity for 2D images of objects in the AIP. As boundary stimuli lacking surface information were sufficient to evoke selective responses, the shape selectivity in AIP appeared to be primarily based on the contours of the images. Although most of our stimuli contained rich texture and shading information, only a very small fraction of AIP neurons required surface information. Whereas AIP neurons with foveal RFs generally preserved their shape selectivity across a (limited) number of positions, AIP neurons with

parafoveal RFs frequently did not preserve their shape selectivity across positions. As in the neighboring LIP, the RF profiles observed in AIP could depend on the shape used for testing.

Selectivity for 2D images in the AIP

All previous single-cell studies in the AIP (e.g. Sakata *et al.*, 1995; Murata *et al.*, 2000; Baumann *et al.*, 2009; Srivastava *et al.*, 2009; Verhoef *et al.*, 2010, 2011) used stimuli (real-world objects or stereograms) that contained gradients of binocular disparity. Here, we observed strong selectivity for 2D images of objects in the large majority of AIP neurons. Binocular disparity facilitates accurate grasping (Watt & Bradshaw, 2003), but the removal of binocular cues has much less effect on grip aperture scaling with a small, overtrained set of objects (Keefe & Watt, 2009). Our results demonstrate conclusively that neurons in the AIP, an area that is critical for visually guided grasping (Gallese *et al.*, 1994), do not always require disparity, and encode both 3D and 2D features. These single-cell results are in agreement with previous monkey fMRI studies (Denys *et al.*, 2004; Durand *et al.*, 2007). However, note that, because, in the traditional LOC localizer (Kourtzi & Kanwisher, 2000), images of objects – typically 9 deg in size – are always presented at the fixation point, both foveal and parafoveal AIP neurons would have contributed to the stronger fMRI activations for images of objects than for scrambled images of objects. Therefore, the fMRI studies have most likely overestimated the degree of shape selectivity in the AIP.

Our stimulus set consisted of images of natural and artificial objects containing rich texture and shading information that was highly relevant for object identity and depth structure. For example, the silhouette and outline versions of the face stimuli were hardly recognizable as faces. However, only a very small fraction of AIP neurons (approximately 10%) required this surface information for image-selective responses. Although we did not manipulate monocular depth cues explicitly, the strong emphasis on the image contour (which was sufficient for selectivity in most AIP neurons, and evoked even stronger selectivity in some AIP neurons) suggests that static monocular depth cues are relatively less important for AIP neurons. Note, however, that – similar to the situation with ITC neurons – surface information did not affect the shape preference (i.e. the difference in response to preferred and nonpreferred images) but frequently affected the response rates.

FIG. 8. Size test population analysis. The average responses to the preferred and nonpreferred images of all AIP neurons tested in the size test ($N = 33$) are shown for every size tested (black full line, 12 deg; gray full line, 9 deg; black dashed line, 6 deg; gray dashed line, 3 deg).

Effect of stimulus position on the shape preference of AIP neurons

The observation of selective responses to different contours does not necessarily imply genuine shape selectivity, as spurious shape selectivity can arise from accidental interactions between the shape and the RF profile (Janssen *et al.*, 2008). Accordingly, the results of the position test were crucial for the interpretation of the contour selectivity. On the basis of the results of the position test, only 16% of our population AIP neurons showed an MNRW of < 0.50 (i.e. shape preference) and significant shape selectivity at more than one position (i.e. tolerance to changes in position; median number of positions with shape selectivity, 4), suggesting that these neurons were actually encoding 2D shape features. For the other AIP neurons, the shape selectivity was either present at a single position (usually at the fixation point), or strongly overestimated because the nonpreferred shape evoked strong responses at a different location.

Stimulus position had a strong influence on the responses of almost all AIP neurons. Hence, we did not observe any strictly response-invariant AIP neurons for position. However, the shape preference

could be preserved across a limited number of positions in the visual field, most frequently in AIP neurons with foveal RFs. Also in the ventral visual stream, selectivity invariance is more pronounced than response invariance (Ito *et al.*, 1995; Tanaka, 1996; Logothetis & Sheinberg, 1996; Vogels & Orban, 1996; Op De Beeck & Vogels, 2000; Brincat & Connor, 2004), and Li *et al.* (2009) have shown that preserving the shape preference is more important for object recognition than preserving response magnitude (we will therefore use the term 'invariance' to describe selectivity invariance, not response invariance). Overall, the coding of 2D shape is much more dependent on position in the AIP than in the ITC, consistent with the notion that object representation in the AIP is more action-oriented than that in the ITC (Srivastava *et al.*, 2009).

We only tested position invariance in a subset of the AIP neurons recorded, almost all of them neurons for which a simple boundary stimulus was sufficient for selectivity. The position test showed that 60% of the AIP neurons responded more strongly at a parafoveal position than at a foveal position (which was used in the shape test). Although at least some of the shape selectivity that we observed in neurons with parafoveal RFs may have been caused by accidental interactions between the shape and the RF profile, the observation still holds that the large majority of AIP neurons required a simple boundary or boundary fragment for image selectivity. Furthermore, this subset of neurons was tested at a less optimal RF position, but the results of the shape test were highly similar for foveal and parafoveal AIP neurons (Supporting information). In fact, the shape boundary came very close (2 deg) to the fovea when the image was presented at the best parafoveal position. Therefore, neurons responding to the shape boundary appearing at a parafoveal location may also have had the hotspot of the RF very close to the fovea. The functional significance of parafoveal RFs in the AIP is unclear at present. Given the role of the AIP in visually guided grasping, parafoveal RFs may be important for the analysis of other elements in the vicinity of the object to be grasped, which is typically fixated while the hand is approaching the object in natural vision (Johansson *et al.*, 2001), or for coarse object analysis, when objects in peripheral vision are grasped (e.g. climbing the cage while fixating on food presented by the experimenter). Alternatively, AIP neurons with parafoveal RFs may be responsive to the sight of the own hand approaching the object, which could be important for online visual control of the grasp. In this hypothesis, position-invariant AIP neurons with foveal RFs encode object geometry (3D and 2D shape features) at the fovea, whereas AIP neurons with parafoveal RFs could encode the hand approaching the object to be grasped.

In our study, a sizeable proportion of AIP neurons (22%) showed a clear RF substructure, with either an excitatory foveal RF center combined with parafoveal positions evoking inhibitory responses, or excitatory parafoveal positions combined with no response at the fixation point. This proportion is likely to be an underestimation, given the limited range of positions in our test (which was dictated by the size of our display). Some AIP neurons only responded to the preferred shape presented at the fixation point, and showed strong inhibition for all other positions of the preferred shape and all positions of the nonpreferred shape (in addition to size tolerance across the entire range tested). Although we did not explicitly test center-surround antagonism (which would require the presentation of two shapes simultaneously in the center and in the surround), these RF profiles suggest that AIP neurons might carry information about the retinal location of shape elements relative to the fovea. Analogously to other dorsal stream areas (Duffy & Wurtz, 1997; Xiao *et al.*, 1997; Eifuku & Wurtz, 1998), the RF structure of AIP neurons could be

important for the visual analysis of multiple objects in a visual scene (segmentation) before and/or during grasping. Future studies will have to clarify the exact RF substructure of AIP neurons.

Comparison with the LIP

Several RF properties of AIP neurons resembled those of LIP neurons responsive to simple 2D shapes (Janssen *et al.*, 2008). As for the LIP, the median overlap between the RF profiles obtained for each image was relatively modest (61%, as compared with 60% for the LIP), indicating that RF profiles in the AIP, like those previously described for the LIP (Janssen *et al.*, 2008), can depend on the stimulus used for the mapping. Thus, the dependence of the RF profile on the shape used in the test appears to be a general property of shape-responsive neurons in areas at the IPS of the dorsal visual stream. In our study, a small fraction of AIP neurons (12%) showed an irregular RF, with one or more local maxima in addition to the global maximum, as compared with 20% irregular RFs in the LIP. In the LIP, almost one of five neurons responded to the nonpreferred shape at a position not overlapping with the global RF maximum as measured with the preferred shape (termed 'multifocal' neurons). In contrast, for our AIP population, only two neurons (4%) were multifocal. Unlike LIP neurons, AIP neurons frequently responded maximally at the fixation point, and these neurons also showed the highest degree of position invariance over a limited number of positions. The RF of AIP neurons with parafoveal RFs lacking position invariance was more similar to that reported for LIP neurons. As no saccadic activity was observed in any of the recording experiments, we conclude that all of our neurons were located in the AIP, although most likely near the boundary with the neighboring LIP. Finally, unlike in the LIP, we frequently observed center-surround organization of the RF in the AIP. Thus, AIP neurons share certain characteristics with neurons in the LIP (e.g. RF profile depending on the shape used in the test) but they are less often multifocal. Overall, a sizeable fraction of AIP neurons show some degree of position invariance, but at least half of the AIP neurons do not encode an abstract representation of object shapes that is tolerant to changes in position, as in the ventral stream, but rather signal a particular contour or contour fragment at a specific position.

Effect of stimulus size on the shape preference of AIP neurons

Somewhat surprisingly given the importance of object size for grip aperture, AIP neurons displayed substantial size invariance across a four-fold change in size. The observed size tolerance could be related to the limited range of sizes tested – a 1-deg shape would probably have elicited much less selectivity – but it is remarkable that the shape preference of many AIP neurons was preserved across a range of sizes that spans a large part of the object sizes that a monkey's hand can grasp. Although the range of sizes tested was slightly smaller than that used in the LIP (1–5 deg) (Janssen *et al.*, 2008), our results suggest that AIP neurons may exhibit more size invariance than LIP neurons.

Our data do not allow us to identify the critical feature for shape-selective AIP neurons (Tanaka *et al.*, 1991) – although the shape contour was sufficient for the large majority of AIP neurons, we cannot infer whether AIP neurons require the entire shape contour, or merely respond to contour fragments or smaller (combinations of) shape elements within the object images that we used. Future studies will have to employ a systematic stimulus reduction approach to elucidate the nature of the shape representation in the AIP.

Supporting Information

Additional supporting information can be found in the online version of this article:

Data S1. Foveal versus parafoveal receptive fields in AIP: tolerance to stimulus position.

Fig. S1. Shape test data for foveal and parafoveal AIP neurons.

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Abbreviations

2D, two-dimensional; 3D, three-dimensional; AIP, anterior intraparietal area; fMRI, functional magnetic resonance imaging; IPS, intraparietal sulcus; ITC, inferior temporal cortex; LIP, lateral intraparietal area; MNRW, maximum normalized response to the worst image; MRI, magnetic resonance imaging; NRD, normalized response difference; NS, not significant; RF, receptive field; SI, selectivity index; SPI, separability index.

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