Processing of Kinetic Boundaries in Macaque V4

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Mysore, Santosh G., Rufin Vogels, Steve E. Raiguel, and Guy A. Orban. Processing of kinetic boundaries in macaque V4. J Neurophysiol 95: 1864–1880, 2006. First published November 2, 2005; doi:10.1152/jn.00627.2005. We used gratings and shapes defined by relative motion to study selectivity for static kinetic boundaries in macaque V4 neurons. Kinetic gratings were generated by random pixels moving in opposite directions in the neighboring bars, either parallel to the orientation of the boundary (parallel kinetic grating) or perpendicular to the boundary (orthogonal kinetic grating). Neurons were also tested with static, luminance defined gratings to establish cue invariance. In addition, we used eight shapes defined either by relative motion or by luminance contrast, as used previously to test cue invariance in the infero-temporal (IT) cortex. A sizeable fraction (10–20%) of the V4 neurons responded selectively to kinetic patterns. Most neurons selective for kinetic contours had receptive fields (RFs) within the central 10° of the visual field. Neurons selective for the orientation of kinetic gratings were defined as having similar orientation preferences for the two types of kinetic gratings, and the vast majority of these neurons also retained the same orientation preference for luminance defined gratings. Also, kinetic shape selective neurons had similar shape preferences when the shape was defined by relative motion or by luminance contrast, showing a cue-invariant form processing in V4. Although shape selectivity was weaker in V4 than what has been reported in the IT cortex, cue invariance was similar in the two areas, suggesting that invariance for luminance and motion cues of IT originates in V4. The neurons selective for kinetic patterns tended to be clustered within dorsal V4.

INTRODUCTION

Although the importance of relative motion for breaking camouflage was recognized very early on (Helmholtz 1962) and extensive psychophysical experiments have documented the ability of primates (humans and monkeys) to perceive kinetic boundaries (Britten et al. 1992; De Weerd et al. 1996, 2003; Lauwers et al. 2000; Marcar and Cowey 1992; Regan 1989; Regan and Hamstra 1992; Rivest and Cavanagh 1996; Sary et al. 1994, 1995), the cortical substrate involved in processing this signal is still the subject of investigation.

Motion-defined boundaries can be generated by differences in either speed or direction, these boundaries themselves can either be moving or static (Regan and Hamstra 1992), and the motion that defines a boundary can be parallel or orthogonal to that boundary. This study explored selectivity to static boundaries defined by opposed motion, boundaries that have been shown to be as perceptually distinct as those defined by luminance (Regan 1989; Regan and Hamstra 1992). When motion is orthogonal to the boundary, that boundary is defined by two cues: one consisting of the relative motion of dots in the neighboring bars and the other by the appearance and disappearance of dots at the boundary providing a dynamic occlusion cue (Regan 1989; Regan and Hamstra 1992; Sary et al. 1994). The latter flicker cue alone is sufficient to perceive the boundary, although orientation discrimination thresholds for this cue are higher than for the orthogonal kinetic boundaries, because the latter contain relative motion in addition to the flicker as cue (Sary et al. 1994). Opposed motion parallel to the boundary might therefore be considered to define the purest form of a kinetic boundary because the boundary information is defined solely by the relative motion.

Single cell recording has established the cue-invariance of shape selectivity in monkey infero-temporal (IT) neurons (Liu et al. 2004; Sary et al. 1993; Tanaka et al. 2001; Vogels and Orban 1996), including selectivity for shapes defined by relative motion. Initially (Marcar and Cowey 1992; Regan et al. 1992), these kinetic IT responses were presumed to reflect an injection of dorsal stream motion information from area MT/V5 (Van Essen et al. 1981; Zeki 1974) into the ventral stream, which culminates in area IT. However, this proposal received little support from the single cell study of Marcar et al. (1995) or from the lesion study of Lauwers et al. (2000). Indeed, MT/V5 cells did not show orientation selectivity for kinetic boundaries (Marcar et al. 1995), and judgments about kinetic boundary orientation were only weakly affected by MT/V5 lesions (Lauwers et al. 2000). In a subsequent single cell study of early areas V1 and V2, Marcar et al. (2000) reported that ~10% of the population of V2 neurons studied were selective for the orientation of kinetic edges. However, the longer response latencies in the population of neurons selective for kinetic boundaries compared with those that were not selective, combined with negative evidence concerning MT/V5, suggested that the signal originated from some region higher in the ventral stream, possibly area V4. Thus the first aim of this study was to investigate whether V4 neurons show selectivity for kinetic stimuli.

Neurons in area V4 respond selectively to the orientation of luminance defined gratings (Desimone and Schein 1987; Gallant et al. 1998). They are also selective for form as well as color (Desimone et al. 1985; Zeki 1973, 1983). Several studies have shown that V4 neurons respond selectively to features more complex than lines or edges. Kobatake and Tanaka (1994) reported that V4 neurons were selective for both simple and complex shape features. Other studies suggested that V4 neurons respond to curves, angles, or other subfeatures or parts of shapes (Gallant et al. 1993, 1996; Pasupathy and Connor 1999, 2001, 2002). Given the known selectivity of V4 neurons for gratings and/or shapes, these experiments studied both types of selectivity for motion defined stimuli, using square
wave gratings and the set of eight shapes used in the IT study of Sary et al. (1993), respectively.

The study of Sary et al. (1993) not only established that IT neurons are selective for shapes defined by relative motion, but that shape selectivity in IT is cue invariant. Thus the second aim of the study was to investigate cue invariance of those V4 neurons selective for kinetic patterns. Therefore selectivity for grating orientation and for shapes was compared for kinetic and luminance defined patterns.

Functional imaging and lesion studies have established that, in humans, a cortical region, designated the kinetic occipital (KO) region, is sensitive for kinetic contours, as well as luminance contours (Dupont et al. 1997; Nawrot et al. 2000; Orban et al. 1995; Tootell and Hadjikhani 2001; Van Oostende et al. 1997; Zeki et al. 2003). The macaque homolog of KO is still under study, but preliminary results of 2-deoxy glucose (Nelissen et al. 2000) and functional MRI (fMRI) studies (Fize et al. 2001) have suggested that dorsal V4, or parts of it, may exhibit kinetic selectivity similar to that of human KO. In these functional imaging studies, activity in the visual system of human and nonhuman primates is compared for kinetic patterns and control stimuli. Because the imaging results depend equally on experimental and control conditions, it is important to determine single cell responses to these control stimuli, as much as to the experimental stimuli. Thus the third aim of this study was to compare V4 neuronal responses to kinetic stimuli and the control stimuli used in fMRI studies: moving random dots and transparent motion displays.

METHODOLOGY

Subject and surgery

We recorded single neurons in dorsal area V4 from two awake, behaving monkeys (Macaca mulatta) weighing between 5 and 6 kg. The head post and the recording chamber (3 cm diam) were implanted under isoflurane anesthesia under sterile conditions. We localized dorsal V4 in each monkey with an anatomical MRI scan before implanting the recording chamber. A craniotomy of ~3 mm diam was drilled at the start of a recording series. This hole would be used until the dura thickened and became impenetrable to the electrodes. The use of antimitotic agent 5-fluorouracil (Sigma-Aldrich) in monkey V enabled us to prolong the useful duration of each craniotomy for ≥8–9 wk (Spinks et al. 2003). All the experimental procedures were in accordance with the national and European guidelines and were approved by the K.U.Leuven ethical committee.

Both subjects performed a passive fixation task. Eye movements were tracked using an infrared camera (ISCAN). Monkeys maintained stable fixation in a window centered on a red dot (fixation window diameter 1.5 × 1.5° for monkey V and 2 × 2° for monkey I) and were rewarded with a drop of apple juice for maintaining fixation throughout the trial duration. Standard extracellular recording technique was used, which is described in detail elsewhere (Schoups et al. 2001; Vogels and Orban 1990). In this experiment, we used glass-coated tungsten electrodes with an impedance of ~1 MOhm. Spikes were isolated from the filtered (460–5,000 Hz) signals using a window discriminator, and spike times were sampled at the rate of 1,000 Hz.

Stimuli

All the stimuli were stored as 640 × 480-pixel image sequences and were presented for 600 ms as a continuous “movie” of frame sequences on an image monitor at a frame rate of 60 Hz while the subjects viewed the screen from a standard distance of 75 cm.

To study kinetic boundary selective cells in V4, we used both grating and shape stimuli. Kinetic gratings were generated by a random texture pattern (50% bright and black pixels, 2.9 × 2.9 min. arc in size) moving in the fronto-parallel plane at a standard speed of 3°/s. Luminance of bright dots measured 39.5 cd/m², with a contrast close to 100%. We used two classes of kinetic gratings as in Marcar et al. (2000) and Sary et al. (1995): one in which the pixels of the random texture moved parallel to the orientation of the boundary (KGP) and another in which the pixels moved orthogonal to the orientation of the boundary (KGO; Fig. 1A). By comparing the apparent orientation selectivity to these two stimuli, we were able to distinguish cells showing genuine orientation selectivity for kinetic gratings from those cells responding to just the direction of the motion component. Cells selective for local motion direction will have their apparent orientation selectivity for KGP and KGO shifted by 90° with respect to one another (Marcar et al. 2000), whereas a cell selective for kinetic orientation show the same orientation tuning for both KGP and KGO. In addition to these kinetic grating stimuli, we tested two control stimuli that had been previously used in fMRI experiments devoted to kinetic contour processing: uniform motion and transparent motion stimuli (Fize et al. 2001; Van Oostende et al. 1997). The transparent stimuli were similar to KGP except that the “gratings”

FIG. 1. Schematic representation of the grating (A), shape (B), and control stimuli. In A, left to right: horizontal luminance grating, KGP, KGO gratings, and transparent (transp) and uniform (uni) motion in horizontal direction. In B, 1 of the 8 shapes (arrow) is shown in kinetic shape vertical, kinetic shape horizontal, luminance shape black on white (B/W), and luminance shape white on black (W/B) versions along with the 4 control stimuli. Black arrows indicate direction of motion.
were but a single pixel in width. These lines moved in opposite directions, creating the impression of two sets of dots moving in opposite directions without apparent boundaries. In the uniform motion stimuli, all pixels moved back and forth along the same axis at the same speed as the pixels in our kinetic grating stimuli and transparent motion stimuli. For all motion stimuli, a static random textured pattern was present before motion onset to eliminate any static onset response. The start of a moving stimulus was defined as the onset of the first frame showing displacement of this random texture pattern; thus coherent motion was present from the first frame of the stimulus sequence in both kinetic grating and control stimuli.

The luminance-defined gratings consisted of static square-wave gratings. For each cell tested, we used the same stimulus size and spatial frequency and the same intervening static texture pattern as that in the kinetic gratings for each of the cells tested. We imposed a 20% random pixel noise on the luminance gratings (i.e., 1 of 5 pixels had the “wrong” contrast polarity) to reduce their saliency. We tested the dorsal V4 neurons by displaying the grating and motion control stimuli in a circular aperture of the optimum size on a uniform gray background (21.3 cd/m² luminance, 37.2° diam). The median diameter of the circular aperture was 3.72°. Because the median spatial frequency tested equaled 1.24 cycles/°, on average, at least three cycles of the grating were visible in the circular aperture.

We also tested V4 neurons with the eight shapes used in the IT cue-invariance study of Sary et al. (1993). Shapes were available in five sizes ranging from 1.03 to 25.70 deg², and the size was adapted to the size of the receptive field (RF) of the neuron. Median size quartiles were 5 and 10, respectively). If the cell recording remained stable after the kinetic grating test, we continued testing with our shape stimuli. Alternatively, if there were no apparent responses in the short grating test, we tested the cell immediately with the shape stimuli consisting of eight shapes defined by either relative motion or by luminance. Here too, the shape size was chosen based on the estimated size of the RF. The shape test included a total of 36 conditions including the control stimuli (4 types × 8 shapes + 4 controls). Neurons included in the sample were tested with at least five presentations of each stimulus of the shape test (median 6 presentations; 1st and 3rd quartiles were 5 and 10, respectively).

In both tests, after 1,000 ms of stable fixation, stimuli were presented for 600 ms followed by 300 ms of poststimulus static random textured patterns, and this sequence was repeated as long as the subject retained fixation. The subject was given a juice reward at the end of each poststimulus static pattern presentation.

**Analysis of neuronal activity**

A split-plot ANOVA analysis (within-trial factor: baseline-response; between-trial factor: orientation) comparing firing rates during the 600 ms before the stimulus (baseline) and the 600-ms stimulus periods (shifted 50 ms to account for response latency) was carried out (main effect of the within trial factor) to establish whether or not the neuron gave a significant response (P < 0.05) during the stimulus periods. We applied this analysis separately for each of the grating sets (luminance, KGP, and KGO), as well as for the transparent control stimulus used in the grating test. For the uniform motion stimulus, we compared the firing rates during the 300 ms before the stimulus (baseline) with the first 300 ms of the response period to determine the response to the forward direction of motion and the later 300 ms to determine response to backward direction of motion also by using a split-plot ANOVA. The selectivity of the cell to the grating orientation was established by performing a one-way ANOVA on the net (after subtraction of baseline activity) responses (P < 0.05) for each grating type separately.

Similarly, for the cells tested with shape stimuli, a split plot ANOVA was used to determine their responsiveness to the shapes. A one-way ANOVA examining the net responses to each of four shape types separately determined whether shape was a significant factor (P < 0.05).

Selectivity for the kinetic boundary was assessed by comparing responses to the KGP and KGO stimuli using regression analysis (Marcar et al. 2000; Movshon and Newsome 1996; Movshon et al. 1985). The correlation coefficient was first calculated between the net responses to the parallel and orthogonal versions of each of the eight orientations of the kinetic grating stimuli. Because the directions of motion are perpendicular to one another at a given orientation for the two types of kinetic gratings, a positive correlation conveys selectivity for the orientation of the boundaries and not for the motion component of the stimuli. The opposite hypothesis was also tested—that the responses to these two orientations were negatively correlated and that their apparent orientation selectivity was 90° apart—by calculating the correlation coefficients between the KGP and KGO responses shifted by 90° (Marcar et al. 2000). These two sets of correlations were tested for significance both with respect to differing from zero and with respect to being different from one another (Zar 1974).

Tunings for orientation or for axis and direction of motion were analyzed with circular statistics using net responses. The preferred angle or preferred orientation, $a$, for those cells which were selective for grating stimuli (significant ANOVA) were calculated as the circular mean, defined as

$$\tan a = \frac{\sum_{i=1}^{n} S_i \times \sin(2a_i)}{\sum_{i=1}^{n} S_i \times \cos(2a_i)}$$
Selectivity index (SI) for kinetic or luminance-defined gratings, which is a measure of the degree of orientation selectivity, was determined by the formula

\[ SI = \sqrt{\sum_{i=1}^{n} S_i \times \sin(2\alpha_i)} + \sum_{i=1}^{n} S_i \times \cos(2\alpha_i) \]

where \( n \) is the number of orientation tested, \( S \) is the response elicited by the stimulus \( i \), and \( \alpha_i \) is the angle specifying the orientation of a given stimulus (Batschelet 1981). Similar formulas were used to calculate the SI for axis of motion of the uniform motion or transparent motion stimuli. To calculate SI for direction of motion, the same formula was used except that the angle \( 2\alpha \) was replaced by \( \alpha \).

Latencies of responses to our stimuli were calculated using a Poisson spike train analysis the details of which have been published by Hanes et al. (1995). This analysis determines the probability that a number of events within a specific time interval occurs by chance. This is achieved by comparing the actual number of spikes in a given trial to the predicted number obtained by the Poisson distribution that is derived in turn from the mean discharge rate during the entire length of the trial. This measure of probability is expressed as a Surprise Index (SUl) (Hanes et al. 1995; Legendy and Salcman 1985) where higher index values convey lower probability that the elevation in discharge rate occurred by chance. SUl is given as

\[ SUl = -\log P \]

\( P \) is determined by the Poisson’s formula

\[ P = e^{-n} \sum_{i=0}^{n} (iT/i!) \]

Just as in Hanes et al. (1995), \( P \) is the probability that, given mean discharge rate \( r \), a time interval \( T \) contains \( n \) or more spikes. We applied the spike train analysis to individual trials. However, we chose only the most responsive condition in each of our stimulus types for this analysis. We first measured the mean discharge rate (step 1, Hanes et al. 1995) and defined the \( T \) that in turn determined the end and the beginning of the “burst” (steps 2 and 3 Hanes et al. 1995). We chose a significance level of \( P < 0.01 \). Finally, the onset of response was determined working backward from the beginning of the “burst” (step 4, Hanes et al. 1995).

Analysis of eye movements

During the single cell recordings, eye positions were not saved, but we observed that the two monkeys fixated quite well, keeping their gaze well within the fixation window most of the time. To substantiate these informal observations, after completion of the single cell recordings, we analyzed a number of position records obtained during the presentation of the stimuli of the grating or shape test. We simulated 150 grating tests (median 8 presentations; 75 tests with each monkey) and 64 shape tests (median 8 presentations; 34 tests with monkey I and 30 with monkey V). For each trial, we used the 600-ms response and baseline periods to calculate the SD of horizontal (\( x \)) and vertical (\( y \)) eye positions. The SD was subjected to a split plot ANOVA exactly as done with the firing rates. In addition, one-way ANOVAs were performed to test the effects of orientation in KGO, KGP, and LG, stimuli, axis of motion in uniform and transparent motion stimuli, and shape of the four stimulus types in the shape tests. Only 2 of 900 ANOVAs tested on 150 grating tests reached significance (\( P < 0.05 \)). We also calculated the average SD, by first taking the mean over the eight presentations and calculating the median and quartiles of those means over the 600 conditions sampled. The median (1st and 3rd quartiles) values during the grating test were 0.12 (0.11 and 0.12°) and 0.11° (0.11 and 0.12°) for the horizontal direction in monkeys I and V, respectively. For the vertical direction, these values were 0.1 (0.09 and 0.1°) and 0.1° (0.09 and 0.12°). Very similar results were obtained for the shape test.

We further analyzed the eye movement data to examine whether the eye movements of the subjects correlated with the kinetic grating orientation. First, we calculated a mean eye position (for \( x \) and for \( y \) coordinates) during the 600-ms baseline period preceding each stimulus presentation. We analyzed the eye movement data during the stimulus presentation in two ways. First, we calculated the average \( x \) and average \( y \) positions over the entire duration of stimulus presentation, giving us the mean \( x \) and \( y \) positions that we used for the analysis. In addition, we binned the \( x \) and \( y \) eye movement data during the stimulus presentation into 12 bins of 50 ms each, calculated the mean \( x \) and \( y \) positions in each of the bins, and analyzed the bins individually. Using mean \( x \) and \( y \) positions derived from the entire stimulus presentation, we computed an eye movement vector with a direction component and a length component for each trial. The origin of this vector in each trial was the mean \( x \) and \( y \) positions obtained from the baseline period, and endpoint of the vector was the mean \( x \) and \( y \) positions during the stimulus presentation. For the binning analysis, we obtained one vector per bin in each trial with the mean \( x \) and \( y \) positions of baseline as the origin, and the mean \( x \) and \( y \) positions in each bin as the endpoint of each vector.

Although our stimulus orientations spanned 0 to 180°, each orientation of the kinetic grating stimulus contained movement in opposite directions. Because eye movement directions span 360°, we first flipped the \( x \) and \( y \) positions so that the direction of these vectors lay within 180° (e.g., 270° will become 90°). Then we doubled both the stimulus orientation and the direction of the eye movement vectors and calculated the circular correlation (Batschelet 1981) between stimulus orientation and the eye movement direction. Instead of averaging the direction of the eye movement vector across trials for a given orientation, we used all trials belonging to a particular orientation in the analysis. Correlations were calculated for LG, KGP, and KGO stimuli separately. When we computed circular correlations over the 600-ms stimulus presentation of each trial, of the 150 grating tests, only 3, 5, and 4 tests were significant (\( P < 0.05 \)) for Lum, Par, and Orto, respectively. Overall, median (1st and 3rd quartiles) \( P \) values for the correlations in three stimulus types were 0.72 (0.32–0.89), 0.70 (0.23–0.76), and 0.76 (0.19–0.81), respectively. Results were similar when correlations were calculated for separate 50-ms bins. This shows that there was no significant correlation between the orientation of the stimulus and the direction of the subjects’ eye movements. We also computed a circular–linear correlation (Batschelet 1981) between the orientation of the stimulus and the lengths of the eye movement vectors. This analysis revealed no correlation between the stimulus orientation and the lengths of eye movement vectors (median and quartiles \( P \) values for the correlations 0.74, 0.26–0.74; 0.79, 0.19–0.79; and 0.78, 0.2–0.83 for LG, KGP, and KGO, respectively).

Additionally, a two-dimensional Kolmogorov–Smirnov (Williams et al. 2003) test was used to compare the distributions of the eye positions for orthogonal orientations of the different grating stimuli (4 pairs of orthogonal orientations for each stimulus type). We compared distributions both test by test and by pooling all the grating test data (\( n = 150 \)), separately for each stimulus. In the analysis of the entire 600-ms stimulus presentation, none of the four orthogonal comparisons in the pooled data or the test by test analysis yielded significantly different distributions (\( P < 0.05 \)). Only six comparisons (6/144) were significant (\( P < 0.05 \)) when we analyzed each bin separately for the pooled data. These results indicate that the two monkeys who participated in this study fixated quite well when presented with the stimuli used in the study and that there was no correlation between their eye movement directions and the orientation of the stimuli presented.
RESULTS

We sampled 512 single neurons in dorsal area V4 from two awake, behaving monkeys (332 cells from monkey I and 180 cells from monkey V). Of these, 482 cells were tested with the grating test, and 256 of the 482 cells were subsequently tested with the shape test. Thirty-nine cells were tested only with the shape test. The quality of single unit isolation was excellent as indicated by the small percent of instances in which a spike was detected in the 2-ms interval after the previous spike occurrence. In 294 (57%) neurons, not a single spike was detected in the 2-ms interval, in an additional 204 (40%) neurons such an event was rare (<1% of the intervals). In the 23 neurons for which a “spike” was detected within 2 ms of a previous spike in >1% of the intervals, this was generally caused by the complexity of the spike waveform.

Grating stimuli

We tested 482 single neurons in dorsal area V4 from two awake, behaving monkeys (316 cells from monkey I and 166 cells from monkey V) with the grating test. The majority of these neurons gave significant responses (ANOVA, \( P < 0.05 \)) to the kinetic and luminance-defined stimuli: 353 (73%), 351 (73%), and 429 (89%) neurons responded to the KGP, KGO, and luminance-defined gratings, respectively. All 482 neurons had RFs in the lower visual field with the eccentricities of the estimated centers ranging from 1.3 to 25° (median 5.81°, 1st and 3rd quartiles 3.83 and 8.82°, respectively). We performed anatomical MRI of both subjects before implanting the recording chambers, enabling us to localize the dorsal V4 region. Anatomical MR images taken in between recording sessions using reference glass tubes filled with copper sulfate, verified that the recordings were in the prelunate gyrus. Furthermore, RF size as well as the topography of the neurons matched with the previously reported experiments in dorsal V4 (Desimone and Schein 1987; Gattass et al. 1988).

Kinetic grating orientation selectivity in V4

Figure 2A shows the PSTHs plotting the responses (response significance, \( P < 1.0 \times 10^{-6} \) for KGP, KGO, and luminance gratings, ANOVA) of cell j26_2_6 to the stimuli of the grating test. Responses to the control stimuli were not significant for this cell. The PSTHs indicate that the cell preferred horizontal orientations for both types of the kinetic and the luminance gratings. A polar plot of the responses to the different orientations is shown in Fig. 3. Orientation selectivity was evident for both kinetic and luminance stimuli as shown by the significance of the factor orientation in one-way ANOVA (\( P < 0.05 \) for KGP, KGO, and LG responses) and by high SI values, 0.62, 0.67, and 0.56 for KGP, KGO, and luminance gratings, respectively. Figure 2, B and C, shows the PSTHs of two other representative neurons preferring horizontal (cell v5_1_2; Fig. 2B) and vertical (cell o16_1_6; Fig. 2C) orientations of the grating stimuli. Clearly selectivity for orientation was observed for different levels of responsiveness to the kinetic gratings.

Of the cells that gave significant responses to our grating stimuli, those selective for the orientation of kinetic gratings were examined further. We considered cells as orientation selective for kinetic gratings if orientation had a significant effect (assessed by ANOVA) for both types of kinetic gratings \(( n = 82 \) or if orientation had a significant effect for one of the two types of kinetic gratings and the SI exceeded the cut-off value of 0.27 for the other kinetic grating \(( n = 5 \)). We determined this cut-off value by plotting the cumulative SI distributions of orientation selective and nonselective (as as-
sessed by ANOVA) neurons for luminance gratings. The point where two curves intersect was defined as the SI cut-off value. Eighty-seven responsive cells met these criteria. Correlation analysis of this sample (Fig. 4) determined whether they responded selectively to the orientations defined by relative motion or whether they merely responded to the direction of motion component of the kinetic grating stimuli. Each point in the Fig. 4 indicates the correlation coefficients for one cell. The abscissa represents correlation coefficients obtained by comparing net responses for KGP and KGO across equivalent orientations for a given cell. The ordinate shows the correlation coefficient values for the same cells obtained by comparing net responses to KGP and KGO shifted by 90° (see METHODS). Neurons selective for kinetic boundary orientation fall into the lower right quadrant of this plot, whereas those selective for the motion component per se cluster in the diagonally opposite quadrant. The majority of the V4 cells are concentrated in the lower right quadrant, thus showing their preference for the orientation defined by relative motion. This is clearly different from V2 (Marcar et al. 2000), where equal proportions of the neurons were direction selective for the direction of motion component and orientation selective for kinetic boundaries. Using the same criteria as in the Marcar et al. 2000 study, indicated by the shaded box in the lower right of Fig. 4, 52 (59% of the orientation selective cells) of the V4 neurons were defined as kinetic grating selective. Of these, 36 neurons gave statistically significant correlation coefficient values (outside the stippled lines in Fig. 4). An example of such a selective neuron has been shown earlier (Fig. 2). Only few cells (n = 11, 12% of the orientation selective cells) proved selective for the motion component, located in the shaded box in the upper left quadrant.

Properties of kinetic grating orientation selective neurons: cue invariance

Most of the kinetic grating selective cells (43/52) were also orientation selective for luminance gratings (assessed by ANOVA). However, a few cells (9/52) were selective exclusively for kinetic grating stimuli and not for the luminance gratings. An example of one such neuron is shown in Fig. 5. This neuron preferred similar orientations for both types of kinetic gratings, but was not selective for luminance gratings. It was responsive, although, to the luminance gratings, as were six of the nine neurons.

Figure 6. A and B, compares the preferred orientations for luminance and kinetic gratings for all the kinetic grating selective cells that were also orientation selective for luminance gratings (43/52). Each point on the scatterplot displays the preferred orientation for luminance and kinetic gratings calculated using circular statistical methods (see METHODS) for each cell. There was a significant correlation between the preferred orientations of luminance and kinetic gratings (r = 0.87 and r = 0.90 for KGP and KGO, respectively). These correlations were almost as high as that between the preferred...
orientations for KGP and KGO (Fig. 6C), which is one of the defining criteria of selectivity for kinetic grating orientation. The difference in preferred orientation between luminance and kinetic gratings is plotted as a frequency histogram along the top corner of the scatterplots. The mean of the distribution was not statistically different from zero \( P > 0.55 \) for KGP and \( P > 0.10 \) for KGO (\( t \)-test); means \(-2.23\) and \(5.94\) for KGP and KGO, respectively] and the SD was small \((28.7\) and \(26.7^\circ\) for KGP and KGO, respectively). Again, these values are close to those for the KGP and KGO: the mean difference in preferred orientation equaled \(5.29 \pm 21.2^\circ\), which was not significantly different from zero.

FIG. 6. A and B: scatterplots showing preferred orientations of KG selective cells that were also selective for luminance-defined gratings \((n = 43)\). C: similar scatterplot of preferred orientations for KGO and KGP of all KG selective neurons \((n = 52)\). Preferred orientations for KGP (A) or KGO (B) are plotted as a function of preferred orientation for luminance grating. Preferred orientations for KGO are plotted as a function of those for KGP in C (black dots, neurons also selective for luminance grating orientation; black triangles, neurons selective only for KG orientation). Correlation coefficients are indicated. Insets along the corner of scatterplots plot frequency histograms of difference between preferred orientations of KGP or KGO and luminance grating and between KGO and KGP. Arrows indicate mean of distributions \((-2.23, 5.94, \text{and } 5.21^\circ\) in A, B, and C, respectively).
of kinetic grating selective cells declined from 44/324 (14%) cells for the representation of the central 10° in V4 to 8/158 (5%) for the parts of V4 representing the peripheral (beyond 10° in eccentricity) visual field. This change in the proportion of kinetic grating orientation selective neurons does not simply reflect a decrease in SI with eccentricity. For neither KGP, KGO, nor LG was there any significant correlation between SI and eccentricity (r of 0.14 or less). This lack of correlation is in sharp contrast with the effect of eccentricity on RF size: the correlation coefficient between square root of RF area and eccentricity equaled 0.93.

No such preference was observed among the cells selective for luminance defined gratings (Fig. 7B; χ² = 1.14; P < 0.76). Proportions were similar in the two eccentricity groups: 150/324 (46%) and 65/153 (42%) for the central and peripheral groups, respectively. The greater saliency of luminance stimuli may have contributed to a more selective response to luminance boundaries at higher eccentricities. A similar preference for more central eccentricities was seen among cells selective only for KGP (n = 118) gratings (χ² = 8.18; P < 0.04) but was not conspicuous among those selective solely for KGO (n = 128) gratings (χ² = 5.79; P < 0.121). This could be caused by the fact that KGO gratings contain an additional dynamic occlusion cue, thereby making the kinetic boundary more robust.

The decrease in the proportion of kinetic grating orientation selective neurons could simply reflect a decreased effectiveness of the carrier of the kinetic gratings, as pixel size was not adapted to eccentricity. To rule out this possibility, we analyzed the responses to uniform motion stimuli, made from the same pixels, as a function of eccentricity. There was no correlation between response to uniform motion stimuli and eccentricity (r = −0.03; P > 0.51). Neither was there any significant difference between the average responses to uniform motion stimuli of neurons with RFs within 10° from fixation point and those beyond (Mann-Whitney U test, not significant).

Properties of kinetic grating orientation selective neurons: responsiveness and selectivity

Table 1 and Fig. 8 compare the response levels of kinetic grating orientation selective cells to all other V4 neurons

![Diagram](https://via.placeholder.com/150)

**FIG. 7.** Eccentricity frequency histogram for cells displaying kinetic grating orientation selectivity or not (A) and luminance grating orientation selectivity or not (B). Dark columns indicate selective cells.

**different from zero (P > 0.12, t-test). These results clearly indicate that the selective cells largely retained their orientation preference whether the boundary is defined by luminance contrast or by relative motion, thus showing cue invariance in dorsal V4.**

**Properties of kinetic grating orientation selective neurons: eccentricity effects**

Figure 7A shows the frequency distribution of kinetic grating orientation selective and nonselective cells as a function of eccentricity of their RFs. The kinetic grating orientation selective group showed a significant (χ² = 8.00; P < 0.05) preference for the central 10° of the visual field. The proportion

**TABLE 1. Response properties of V4 neurons to grating set of stimuli**

<table>
<thead>
<tr>
<th>Stimuli</th>
<th>Population</th>
<th>Median-Response (quartiles)</th>
<th>Median SI (quartiles)</th>
<th>Mean Latency</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>KGP</td>
<td>All cells</td>
<td>6.75 (2.48 14.26)</td>
<td>0.2 (0.1–0.3)</td>
<td>105 ± 4.9</td>
<td>353</td>
</tr>
<tr>
<td></td>
<td>KG–Sel</td>
<td>10.29 (5.4 20.2)</td>
<td>0.29 (0.19–0.37)</td>
<td>104 ± 3.9</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>KG–Nonsel</td>
<td>5.2 (2.4 14.06)</td>
<td>0.17 (0.09–0.25)</td>
<td>105 ± 5.1</td>
<td>301</td>
</tr>
<tr>
<td>KGO</td>
<td>All cells</td>
<td>6.87 (2.34 14.21)</td>
<td>0.2 (0.1–0.3)</td>
<td>104 ± 5.2</td>
<td>351</td>
</tr>
<tr>
<td></td>
<td>KG–Sel</td>
<td>13.1 (7.53 24.91)</td>
<td>0.29 (0.17–0.39)</td>
<td>103 ± 3.4</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td>KG–Nonsel</td>
<td>5.65 (2.03 14.19)</td>
<td>0.16 (0.09–0.26)</td>
<td>104 ± 5.5</td>
<td>299</td>
</tr>
<tr>
<td>Transp</td>
<td>All cells</td>
<td>3.76 (1.12 11.0)</td>
<td>0.16 (0.09–0.22)</td>
<td>106 ± 5.1</td>
<td>376</td>
</tr>
<tr>
<td></td>
<td>KG–Sel</td>
<td>6.25 (3.06 15.3)</td>
<td>0.16 (0.1–0.21)</td>
<td>106 ± 5.2</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>KG–Nonsel</td>
<td>3.63 (1.05 10.49)</td>
<td>0.17 (0.09–0.22)</td>
<td>106 ± 5.4</td>
<td>335</td>
</tr>
<tr>
<td>Uni</td>
<td>All cells</td>
<td>5.27 (1.37 12.82)</td>
<td>0.14/0.15 (0.09–0.21/0.1–0.22)</td>
<td>103 ± 6</td>
<td>380</td>
</tr>
<tr>
<td></td>
<td>KG–Sel</td>
<td>7.22 (3.43 17.58)</td>
<td>0.14/0.15 (0.09–0.21/0.1–0.29)</td>
<td>104 ± 4.1</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>KG–Nonsel</td>
<td>4.7 (1.16 12.43)</td>
<td>0.14/0.14 (0.09–0.21/0.06–0.22)</td>
<td>103 ± 6</td>
<td>334</td>
</tr>
<tr>
<td>LG</td>
<td>All cells</td>
<td>11.37 (4.6 24.44)</td>
<td>0.22 (0.12–0.34)</td>
<td>72 ± 5.1</td>
<td>423</td>
</tr>
<tr>
<td></td>
<td>KG–Sel</td>
<td>21.32 (8.6 34.28)</td>
<td>0.27 (0.11–0.44)</td>
<td>73 ± 4.1</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td>KG–Nonsel</td>
<td>11.1 (4.45 21.97)</td>
<td>0.2 (0.12–0.32)</td>
<td>72 ± 5.3</td>
<td>374</td>
</tr>
</tbody>
</table>

Latency values are mean ± SE and are expressed in milliseconds. Numbers in parenthesis indicate the n for each group. For median responses number of cells (n) for All cells = 482; KG–sel = 52; KG–Nonsel = 430. SI values for Uni stimuli are seperately indicated for forward/backward directions of motion.

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grouped together in a nonselective group. Kinetic grating selective cells responded more vigorously than the nonselective group of cells did, not only for the kinetic grating stimuli, as one would expect, but also for the luminance gratings and control stimuli. These differences between responses of kinetic grating selective and nonselective cells were all significant (repeated-measures ANOVA). More interestingly, while all V4 neurons responded better to kinetic grating than to the control stimuli \( (P < 0.00001; \text{Wilcoxon matched pair test; for KGP vs. transparent and for KGP vs. uniform motion stimuli}) \), this difference was greater for the kinetic grating selective cells than for the other cells \( (P < 0.00001 \text{ and } P < 0.026, \text{interaction between group and stimulus in ANOVA, for transparent or uniform motion, respectively}) \).

**FIG. 8.** Frequency distribution of average net firing rates (A–C) and of selectivity index (SI) (D–F) for KGP stimuli (A and D), KGO stimuli (B and E), and luminance gratings (C and F). Cells selective for kinetic grating orientation are indicated by dark gray bars; those nonselective by white bars. Arrows indicate medians.
Overall orientation selectivity was relatively low in dorsal V4 for our grating stimuli as indicated by the low SI indices in (Table 1; Fig. 8). Median SIs of 0.22, 0.20, and 0.20 were observed for luminance grating, KGP, and KGO, respectively. Selectivity was even lower for the axis of uniform motion stimulus, with a median SI of 0.15. Direction selectivity indices were 0.14 and 0.15 for the forward and the backward directions, respectively.

Properties of kinetic grating orientation selective neurons: response latencies

Selectivity for the orientation of the kinetic grating began at the same time as the response onset among the selective neurons. This can be seen when we superimpose the responses of these selective neurons to preferred and nonpreferred orientations. As shown in Fig. 9A, plotting the population PSTHs, there was no apparent difference in the onset timing of preferred and nonpreferred orientation, but average responses diverged as soon as they started. This was also true for the luminance defined gratings as shown in the figure (Fig. 9A).

Marcar et al. (2000) had shown in their V2 study that response latencies for their kinetic edge selective neurons were longer than in their nonselective group. This was the main argument supporting their speculation that the kinetic edge responses originated at a higher cortical area, probably V4. Figure 8B shows the population PSTHs for the kinetic grating selective cells in V4 to luminance grating, kinetic grating, and uniform motion stimuli compared similar histograms for nonselective cells. The differences in onset times of the population responses were matched by the mean differences in response latencies of single neurons, calculated using the Poisson spike train analysis (see METHODS). Luminance stimuli elicited the earliest responses (mean latency, 73 ± 4.1 ms; Table 1). Kinetic grating responses followed luminance responses with mean latencies of 104 ± 3.9 and 103 ± 3.4 ms for KGP and KGO, respectively (Table 1). There were no differences in the average onset response latencies of kinetic grating orientation selective cells and nonselective cells (Table 1), in contrast to
what has been observed in V2 (Marcar et al. 2000). Interestingly, neither was there any difference between the onsets of responses to kinetic grating and uniform motion stimuli.

**Shape stimuli**

Two hundred ninety-five dorsal V4 neurons were subjected to the shape test. Most of these neurons (n = 256) were also tested in the grating test. Of the 295 cells tested, 223 (76%), 229 (78%), 266 (90%), and 251 (85%) elicited significant responses to KSV, KSH, LSB, and LSW, respectively.

**Shape selectivity in V4**

Of the cells responsive to our shape stimuli, 63 were found to be selective for both types of kinetic shape stimuli (KSV and KSH), as determined by a significant effect of shape in ANOVA, and were therefore classified as kinetic shape selective neurons. These 63 neurons were also selective for both polarities of luminance-defined shapes (LSB and LSW) as assessed by an ANOVA. Of the 256 neurons tested both with grating and shape stimuli 254 were not selective for the orientation of kinetic gratings. This might have been a result of our effort to find selectivity for kinetic patterns, which prompted us to discontinue the grating test after fewer runs with the neurons that appeared nonselective during the testing than with those appearing selective. Thus the small percentage of neurons selective for grating orientation among the neurons tested in both tests simply reflects our experimental strategy, not the true proportion among V4 neurons. The remaining two neurons, although selective for the orientation of kinetic gratings, were not among the 63 shape selective neurons. Thus no neurons in the present sample were shown to be selective for both kinetic grating orientation and kinetic shapes.

Figure 10A shows the PSTHs of an example cell illustrating selective responses to the shape stimuli. This cell was considered kinetic and luminance shape selective, because it not only elicited significant responses (P < 1.0 × 10^{-6} response significance, ANOVA) to all types of shape stimuli, but shape was also a significant factor (ANOVA, P < 1.0 × 10^{-6}) for each of these shape types. Figure 10B shows the average net responses of the same cell (2 types of kinetic and 2 types of luminance shapes averaged), and Fig. 10C depicts a second cell that also retained its shape selectivity across luminance and kinetic stimulus types.

For a cell to qualify as selective for shape defined by relative motion, its shape selectivity should be invariant for motion direction. Hence we would expect such a cell to show a high degree of correlation between its responses to the two types of kinetic shapes: KSV and KSH. Figure 11 displays frequency histogram of the correlation coefficients for the responses to these two types of kinetic shape stimuli for all 63 cells shown to be selective for shapes by ANOVA. All but two cells had positive correlation coefficients, and the mean (0.551) of the distribution was statistically different from 0 (t-test; P < 0.000001).

**Cue invariance of kinetic shape selective V4 neurons**

To study the cue invariance of the shape selectivity of the kinetic shape selective neurons we compared the shape preference for the luminance and kinetic shapes, using the same procedure as Sary et al. (1993). We ranked the responses of each cell to LSB stimuli from its strongest to weakest and applied the same ranking to the responses for the other types of shape stimuli. For each cell, we normalized the net responses by expressing them as a fraction of the maximal net response for the LSB shape.

Figure 12A shows the averaged normalized responses to kinetic and luminance shape stimuli for all 63 cells. The curves show a similar monotonic decrease for kinetic shape (P < 0.001 for KSV stimuli, P < 0.002 for KSH stimuli, repeated-measures ANOVA) and luminance shape (P < 0.0001 for LSB stimuli, repeated-measures ANOVA), indicating that the selective neurons were cue invariant, that is, preferred a similar
shape, regardless of how the shape boundaries were generated. The figure rank curve for luminance shape stimuli is, however, steeper than the curve for kinetic shape stimuli, indicating that either the invariance might be incomplete at the single cell level or that the shape selectivity is not as strong for the relative motion cue compared with the luminance cue.

At the single neuron level, the degree of selectivity to shapes can be quantified by calculating the depth of selectivity index (DOS) (Rainer and Miller 2000; Rainer et al. 1998). This measure, which takes all eight shapes into account, is given by

\[
\text{DOS} = \frac{n - \sum_{i=1}^{n} \lambda_i / \lambda_{\text{max}}}{n - 1}
\]

where \( n \) is the number of shapes (8), \( \lambda_i \) is the response to \( i \)th shape, and \( \lambda_{\text{max}} \) is the response to the best or preferred shape. DOS varies from 0 to 1, where higher values indicate stronger selectivity. We calculated the DOS for our kinetic shape selective neurons separately for each of the cue types. The result shows that the mean DOSes for kinetic and luminance shape responses were similar and that their distribution was not statistically different (means 0.49 and 0.51 kinetic and luminance shapes, respectively; Wilcoxon matched pair test, not significant). Ranking responses of the shape selective neurons separately for kinetic and luminance shape stimuli shows the high degree of similarity in the selectivity for shapes generated by these two cues. Figure 12B shows such a plot averaged across all the selective neurons. Figure rank curves are similar for both luminance and kinetic shapes with both dropping to \( \sim 30\% \) of the maximum value. Thus shape selectivity is similar for the two cues, but the cue invariance of this selectivity is incomplete at the single cell level.

**Properties of kinetic shape selective V4 neurons**

As for kinetic grating selective neurons, kinetic shape selective neurons tended to be more prevalent in the central representation (58/257, 22% in the central 10°) than in more peripheral parts (5/38, 13%). However, this difference did not reach statistical significance (\( \chi^2 = 1.96 \), not significant).

In our sample, a majority of the neurons responded significantly to kinetic and luminance-defined shape stimuli. As with gratings, luminance shape responses were, on average, stronger than kinetic shape responses (means, 20.9 ± 4.4 and 13.1 ± 4.0 spikes/s for LS and KS, respectively). This difference was slightly smaller for kinetic shape selective cells than for nonselective cells (Table 2), a difference that was statistically significant (\( P < 0.025 \); interaction, repeated-measures ANOVA). As in the case of grating responses, kinetic shape stimuli elicited significantly stronger responses than their transparent controls (\( P < 1.0 \times 10^{-6} \)), as did luminance shape stimuli compared with their controls (Table 2). More interestingly, these effects were clearly stronger for kinetic shape selective cells than for nonselective cells (both interactions, \( P < 0.00001 \), ANOVA).

**FIG. 11.** Frequency histogram of correlation coefficients between responses to KSV and KSH for kinetic shape selective neurons (\( n = 63 \)). Arrow indicates mean correlation (0.551), which was significantly different from 0.

**FIG. 12.** A: average normalized response of kinetic shape selective cells (\( n = 63 \)) to luminance shape (LSB: gray solid line, LSW: gray dashed line) and kinetic shape (KSH: black solid line, KSV: black dashed line) plotted as a function of the figure rank. Figure rank was based on responses to LSB. Vertical bars indicate SE. B: similar figure rank plot (\( n = 63 \)) showing average normalized responses to luminance (LSB: gray full line, LSW: gray dashed line) and kinetic shape (KSH: black full line, KSV: black dashed line). However, ranking was based separately on responses to each of the 4 stimulus types. Vertical bars indicate SE.
As was the case for the grating selectivity, shape selectivity was present from the onset of the response, as attested by the population PSTHs (Fig. 9C). Furthermore, responses to luminance shape stimuli had a shorter latency than responses to kinetic shape (Fig. 9D). The latencies of these kinetic shape responses did not differ whether measured in kinetic shape selective or nonselective cells, exactly as we observed for kinetic grating selective and nonselective cells (Fig. 9B).

### Clustering of kinetic boundary selective neurons

Kinetic boundary selective neurons were not uniformly distributed within the central 10° of dorsal V4. During the recording sessions, we noted that kinetic grating orientation or kinetic shape selective cells tended to be grouped together. To substantiate this impression, Fig. 13 plots the position in the recording chamber of all penetrations made in the two monkeys and indicates those daily penetrations in which at least one kinetic shape or/and kinetic orientation selective neuron was recorded (positive penetrations). Penetrations in which neurons were recorded that, although not selective for kinetic grating orientation, still responded significantly (Wilcoxon’s matched pair test) more to KGP than to transparent motion stimuli are also labeled. Notice that given the duration of the tests performed per neuron, only a few neurons could be tested per penetration. A few penetrations were made into the banks of the lunate or superior temporal sulci, as indicated by a continuous stretch of gray matter to a depth of 5 mm from the surface. The kinetic grating orientation selective cells recorded in these penetrations were localized within 2 mm from the surface and hence the penetrations could safely be included in the figure. In both monkeys, most penetrations with kinetic selective (for orientation or shape) neurons were located in three relatively small regions of dorsal V4. In monkey I, 30 of the 34 positive penetrations were located in three patches representing 5.2 mm² of the 22.1 mm² explored in total. In monkey V, 27/30 positive penetrations were also located in three patches occupying 2.9 mm² of the total of 18.5 mm² explored. Thus in both monkeys, about 90% of the kinetic selective or strongly responsive neurons were concentrated in 20% of the cortical surface explored. These patches also contained the vast majority of the penetrations with neurons more responsive to kinetic gratings than transparent control (70% in monkey I and 73% in monkey V). To evaluate the significance of this clustering, we subdivided the recording area into nine equal parts and evaluated the observed compared with expected frequencies keeping only those parts in which at least five penetrations were made. We tested both the distributions of penetrations in which kinetic selective neurons were recorded and those in which cells significantly more responsive to KGP than transparent were recorded. In monkey I (Fig. 13A), both distributions deviated significantly from uniform

### TABLE 2. Average net responses to shape stimuli

<table>
<thead>
<tr>
<th>Stimuli</th>
<th>Population</th>
<th>Median Response (Quartiles)</th>
</tr>
</thead>
<tbody>
<tr>
<td>KS</td>
<td>All cells</td>
<td>6.14 (1.9 18.21)</td>
</tr>
<tr>
<td></td>
<td>KS-sel</td>
<td>13.25 (6.93 25.62)</td>
</tr>
<tr>
<td></td>
<td>KS-nonsel</td>
<td>5.16 (1.05 13.89)</td>
</tr>
<tr>
<td>Transp</td>
<td>All cells</td>
<td>1.16 (0.9 5.2)</td>
</tr>
<tr>
<td></td>
<td>KS-sel</td>
<td>1.74 (1.2 6.1)</td>
</tr>
<tr>
<td></td>
<td>KS-nonsel</td>
<td>1.16 (0.87 5.2)</td>
</tr>
<tr>
<td>LS</td>
<td>All cells</td>
<td>12.63 (5.18 27.48)</td>
</tr>
<tr>
<td></td>
<td>KS-sel</td>
<td>17.93 (9.82 31.27)</td>
</tr>
<tr>
<td></td>
<td>KS-nonsel</td>
<td>10.98 (4.33 26.12)</td>
</tr>
<tr>
<td>Avg.Lum</td>
<td>All cells</td>
<td>3.33 (0.19 4.1)</td>
</tr>
<tr>
<td></td>
<td>KS-sel</td>
<td>4.41 (0.5 12.26)</td>
</tr>
<tr>
<td></td>
<td>KS-nonsel</td>
<td>3.16 (0.08 9.18)</td>
</tr>
</tbody>
</table>

Number of cells for All = 295; KS = 63; NKS = 232.

As was the case for the grating selectivity, shape selectivity was present from the onset of the response, as attested by the population PSTHs (Fig. 9C). Furthermore, responses to luminance shape stimuli had a shorter latency than responses to kinetic shape (Fig. 9D). The latencies of these kinetic shape responses did not differ whether measured in kinetic shape selective or nonselective cells, exactly as we observed for kinetic grating selective and nonselective cells (Fig. 9B).

**FIG. 13.** Positions of penetrations in the recording chamber for monkey I (A) and monkey V (B). Dorso-ventral distance from the center of chamber is plotted as a function of antero-posterior distance from center. Negative ordinate and abscissa values indicate ventral and posterior directions. Red crosses indicate positions of sulci: superior temporal sulcus in *right top corner* and lunate sulcus on *left*. Green squares, blue dots, and red triangles: penetrations in which kinetic grating selective cells, kinetic shape selective cells, and both cells selective to kinetic grating and kinetic shape were recorded, respectively. Light blue dots indicate penetrations in which neurons were recorded that responded more strongly to KGP than to transparent motion stimuli. Blue and green stars indicate penetrations into banks of sulci in which kinetic shape or orientation selective neurons were recorded. Black dots and triangles indicate negative penetrations (no kinetic selective neurons encountered) into the gyrus and sulci, respectively. Black and blue hatched rectangles indicate regions explored and regions rich in kinetic selective cells, respectively.
distributions ($\chi^2 = 29.04, P < 0.0001$ for selective neurons and $\chi^2 = 11.44, P < 0.02$ for responsive neurons). In monkey V, the deviation did not reach significance ($\chi^2 = 7.34$, not significant and $\chi^2 = 8.42$, not significant, respectively).

**DISCUSSION**

We explored dorsal V4 to study the response properties of neurons in that cortical area to kinetic patterns. Our results show that a moderately high proportion (115/521, 22%) of dorsal V4 neurons are selective for form features defined by relative motion, specifically grating orientation or shape. Most neurons selective for the kinetic patterns were cue-invariant in their stimulus preference and tended to have their RF within the central 10° of the visual field. Selective neurons had the same response latencies as nonselective neurons, unlike what has been reported in a previous study of V2 (Marcar et al. 2000). Responses to kinetic patterns were much stronger than the uniform and transparent motion controls used in previous fMRI experiments. Furthermore, the selective neurons tended to be clustered, even those within the central 10° representation in dorsal V4.

**Eccentricity of stimulus and neuronal selectivity**

The proportion of kinetic boundary selective neurons in V4 decreases with eccentricity in the visual field, and for the representation of the central 10° ranges between 14 and 22%, depending on whether gratings or shapes were used. This change with eccentricity is not caused by decreased effectiveness of the stimulus carrier at larger eccentricities, because the responses to uniform motion stimuli, made from the same pixels as the kinetic gratings, did not depend on eccentricity. A similar lack of eccentricity effect was observed in a psychophysical study of motion perception using similar stimuli (van de Grind et al. 1983). There is some psychophysical evidence that kinetic boundaries are processed more efficiently in the central part of the visual field. Human psychophysical experiments have shown that log detection thresholds for detecting relative motion boundaries is proportional to eccentricity, even when stimulus size is adapted (Regan 2000; Regan and Beverley 1984). In the monkey, Lauwers et al. (2000) provided evidence that orientation discrimination with kinetic gratings degrades with increasing eccentricity. As in this study, these authors used both KGP and KGO for behavioral testing. At an eccentricity of 12.5°, only orientation differences of 45° or more could be reliably discriminated with kinetic gratings, whereas much smaller differences could be discriminated with luminance-defined stimuli. These behavioral data match the decrease in proportion of V4 neurons selective for kinetic grating orientation beyond 10° eccentricity and the differential effect of eccentricity on proportions of V4 neurons selective for kinetic and luminance defined orientation (Fig. 7).

**Cue invariant form processing in dorsal V4**

The cells considered as orientation selective for static kinetic patterns in this study meet stringent criteria ensuring that their response depends on the orientation of kinetic boundaries and not on the local motion present in the kinetic stimuli. Such control tests were not performed in previous studies of either V4 or the V3 complex (Logothetis 1994; Zeki et al. 2003). Although a previous study using anesthetized monkeys reported cue invariant orientation selectivity of V3/V3a neurons including for motion-defined bars (Zeki et al. 2003), the stimuli used in that study were fundamentally different from the stimuli we used. They tested V3/V3a neurons using moving kinetic boundaries as opposed to the static albeit relative motion-defined boundaries that we used to test the dorsal V4 neurons. The texture-defined bar in the study of Zeki et al. (2003) moved orthogonally to the long axis of the bar, against a static, random texture background, and passed through the RF of the neuron. Because this type of pixel movement contains an additional dynamic occlusion cue (Sary et al. 1994), it is hard to know which of the four cues, occlusion, kinetic boundary orientation, local motion, or boundary motion direction, contributed to the selective responses of the V3/V3a neurons. By comparing the orientation selectivity for KGO and KGP, we were able to isolate kinetic boundary orientation as the cue eliciting the V4 neuron selective responses. Furthermore, the overwhelming majority of kinetic selective cells in our study was found to be cue invariant, either by having similar orientation preference for the grating stimuli or by retaining shape preference to the shape stimuli. Importantly, this invariance for luminance and motion-defined stimuli was independent of the direction of relative motion with respect to the boundary (Fig. 6).

While the cue invariance of kinetic shape selective V4 neurons, in terms of preferred stimulus, was not always complete at the single cell level, it was quite invariant at the population level (Figs. 6 and 11). Thus most of the invariance of the shape selectivity observed in the earlier study in IT (Sary et al. 1993) is already present within theafferent input from V4.

**Selectivity for kinetic patterns**

This is the fifth visual area explored with (static) kinetic patterns, following the studies of IT, MT/V5, V1, and V2 (Marcar et al. 1995, 2000; Sary et al. 1993, 1995). These results differ considerably from those obtained in MT/V5 (Marcar et al. 1995). When V4 neurons were tested with gratings generated by parallel and orthogonal motion, the preferred orientation for each of the two stimuli differed by $<40°$ in two-thirds of the sample (59/87) in which the factor orientation had shown a significant effect for both of these grating stimuli. No MT/V5 neuron exhibited such a small difference between the preferred orientations for KGO and KGP (Marcar et al. 1995), indicating that MT/V5 neurons do not encode kinetic orientation. While V4 neurons differed markedly from those in dorsal area MT/V5 in the way they responded to the kinetic gratings, rather consistent trends were noticeable in the sequence of the three ventral areas explored: V1, V2, (Marcar et al. 2000), and V4 (this study). The fraction of neurons for which the factor “orientation” was significant for both kinetic grating types steadily decreased from 47% in V1 to 30% in V2 and 18% in V4 (50/122 in V1, 34/127 in V2, and 87/482 in V4). One should keep in mind that not all neurons for which the factor “orientation” was significant for both kinetic gratings types turned out to be selective for the orientation of kinetic gratings, because this requires in addition that the preferred orientations for the two types match (Fig. 6).

On the other hand, the ratio of neurons tuned to the direction of
local motion compared with those tuned to orientation of kinetic boundary also consistently decreased from 4/1 in V1 to 1/1 in V2 and 1/5 in V4 (14/4 in V1, 15/13 in V2, and 11/52 in V4). These proportions indicate that as we continue along the ventral pathway the proportion of neurons selective for local motion decreases steadily. This sharply contrasts with MT/V5 in which nearly all neurons are selective for local motion direction (Marcar et al. 1995).

When selectivity for shapes in V4 is compared with that obtained in IT using very similar stimuli (Sary et al. 1993; Vogels and Orban 1996), it is clear that the ranking curves were steeper in IT than in V4 (cf. curves in Fig. 11 with those in Fig. 6 of Vogels and Orban 1996). A lower selectivity for shapes in V4 compared with IT is in agreement with the results of Kobatake and Tanaka (1994) and with the evidence provided by Pasupathy and Connor (2001, 2002), indicating that V4 neurons are more selective for components of shape than for shape itself.

Do V4 neurons extract kinetic contours?

The latencies reported in this study provide some indication that kinetic contours might be extracted locally in V4. It is difficult to compare absolute latencies of responses to the stimuli in this study with the latencies reported by the Marcar et al. (2000), because of differences in the contrast of the luminance-defined stimuli and the anesthesia used in the earlier study. However, the relative latencies for selective and nonselective cells in the two studies would likely not be influenced by such factors and could provide meaningful insights into processing of relative motion boundary signals. In V2, the longer latencies of responses to kinetic gratings for selective compared with nonselective cells was interpreted as reflecting a feedback loop from a higher order area, giving rise to the kinetic selectivity in V2. The shorter latencies of nonselective neurons were interpreted as arising from direction selective cells in which the response depended only on the local processing within V2. The latencies of the selective neurons for luminance patterns would be the same as that of nonselective cells because the response of the selective neurons as that of nonselective neurons depended on the feedforward signals. Within this framework, the simplest interpretation of these results is that the selectivity for kinetic patterns is produced by local processing in V4. It is not difficult to devise simple combinations of the direction selective V2 input that could generate selectivity for kinetic boundary orientation in V4 (Orban and Gulyas 1988). A scheme similar to that proposed by Hubel and Wiesel (1962) for orientation selectivity for luminance edges in V1, and probably supplemented by local processing (Douglas and Martin 2004 for review), can be applied. The fact that the latency is the same for both kinetic grating and uniform motion supports this interpretation because this motion signal would also reflect local processing of V2 input within V4, just as the kinetic responses of selective cells do. These latency data provide only very indirect evidence concerning the possible cortical origin of kinetic responses. Inactivation studies would be needed to provide confirmation of this hypothesis.

Responses of V4 neurons to transparent motion

Which are the RF features that could explain the differences in the responses of V4 neurons to the three types of dynamic stimuli: kinetic gratings, uniform, and transparent motion? On average, V4 neurons gave significantly stronger responses to kinetic gratings than to uniform or transparent motion. This was true of all neurons, but the difference was much greater for kinetic selective neurons (Table 1). Previous reports have shown that opponent motion, which is present in both transparent motion and in kinetic gratings, when presented within the RF of the MT/V5 neurons, suppress their responses to their preferred directions (Qian and Andersen 1994; Snowden et al. 1991). This suppression is caused by the inhibition evoked by local motion in the nonpreferred direction elicited from the RF. Except for the few strongly direction selective neurons, such a suppressive mechanism seems unlikely to operate in the general V4 population, because these neurons respond best to the kinetic gratings that also includes opponent motion, albeit spatially segregated.

The fact that average responses to kinetic gratings is larger than that to transparent (and uniform) motion in the nonselective group of neurons suggest that these neurons probably responded to the relative motion component of the kinetic grating stimulus, without being orientation selective. This might reflect either an interaction within the excitatory RF or the presence of an antagonistic surround, which is well documented in V4 for static stimuli (Desimone and Schein 1987). The latter interpretation implies first that the surround also operates for dynamic stimuli and second that it extends into the excitatory RF, as it does in MT/V5 neurons (Raiguel et al. 1995). It is supported, however, by the results of the shape test. V4 neuronal responses to transparent controls used in the shape test were much weaker compared with the same controls used in the grating test (Tables 1 and 2). Because the transparent motion extends over the entire background (37.2° diam) in the shape test compared with an average extent of only 3.72° diam in the grating test, the weaker responses are most likely caused by stronger surround suppression. The fact that the selective group of V4 neurons responded much more strongly to the kinetic grating than to the uniform or transparent motion than nonselective cells no doubt reflects the specific response of these neurons to the boundary defined by the relative motion arising from the excitatory RF, in addition to a suppressive effect of the antagonistic surround on the transparent motion response, common to the “average” V4 neuron.

Previous functional imaging studies experiments (Dupont et al. 1997; Orban et al. 1995; Tootell and Hadjikhani 2001; Van Ostendorf et al. 1997; Zeki et al. 2003) have indicated that a region in human cortex, referred to as KO and located in a position similar to monkey V4 dorsal with respect to V3A and MT/V5, was activated more strongly by kinetic patterns than by uniform and transparent motion controls. These single cell experiments showing that cells in dorsal V4 fire more strongly in response to kinetic patterns than to transparent (or uniform) motion controls predict somewhat stronger MR signals in V4 for kinetic gratings than for transparent (or uniform) motion. It should be pointed out that, all V4 neurons, including those not selective for kinetic patterns, are similar in responding more strongly to the kinetic pattern than to the controls, although the difference between the responses is significantly greater for the
selective than for the nonselective neurons. Thus it is difficult to infer selectivity for kinetic patterns from fMRI results that simply compare response levels to kinetic patterns and transparent control patterns in any straightforward manner (Logothetis 2000). This experiment has shown, however, that the kinetic pattern selective neurons are more prevalent in the central than in the peripheral representation of V4 and that these neurons may be clustered within this central representation, observations that can be tested in the fMRI in the monkey, even though it may require increased resolution above that presently available in the awake monkey experiments (Denys et al. 2004; Koyama et al. 2004).

REFERENCES


