

Hugo Merchant · Alexandra Battaglia-Mayer ·
Apostolos P. Georgopoulos

Neural responses in motor cortex and area 7a to real and apparent motion

Received: 5 June 2003 / Accepted: 31 July 2003 / Published online: 25 October 2003
© Springer-Verlag 2003

Abstract The neural activity in area 7a and the arm area of motor cortex was recorded while real or path-guided apparent motion stimuli were presented to behaving monkeys in the absence of a motor response. A smooth stimulus motion was produced in the real motion condition, whereas in the apparent motion condition five stimuli were flashed successively at the vertices of a regular pentagon. The stimuli moved along a low contrast circular path with one of five speeds (180–540 deg/s). We found strong neural responses to real and apparent motion in area 7a and motor cortex. In the motor cortex, a substantial population of neurons showed a selective response to real moving stimuli in the absence of a motor response. This activity was modulated in some cases by the stimulus speed, and some of the neurons showed a response during a particular part of the circular trajectory of the stimulus; the preferred stimulus angular locations were evenly distributed across this neuronal ensemble. It is likely that these neural signals are continuously available to the motor cortex in order to generate responses that demand immediate action. In area 7a, two overlapping populations of neurons were observed. The first comprised cells the activity of which was tuned to the angular location of a

circularly moving stimulus in the real motion condition. These cells also responded to apparent motion at high stimulus speeds. A visual receptive field analysis showed that the angular tuning in most of the area 7a neurons did not depend on the spatial location of the stimulus in relation to their receptive field. The second population was selective to apparent moving stimuli and showed a periodic entrainment of activation with the period of the inter-stimulus interval of the flashing dots. Both the angular location and the inter-stimulus interval neural signals can be used to generate precise behavioral responses towards real or apparent moving stimuli.

Keywords Visual motion · Apparent motion · Motor cortex · Area 7a · Rhesus monkeys

Introduction

It is well known that a series of stationary visual stimuli, presented at the appropriate intervals in space and time, can elicit a strong perception of motion. This phenomenon is called apparent motion and has been very useful in the study of the critical features that elicit motion perception. When a curved gray path is flashed between two alternately displayed black dots, an illusion of a single dot moving back and forth over that path is induced. Under this condition, the inter-stimulus interval (ISI) necessary to produce an apparent motion illusion increased linearly with the length of the path (Shepard and Zare 1983). This illusion, called path-guided apparent motion, has been used in our laboratory in studies where human subjects and monkeys intercepted circularly moving targets (Port et al. 1996; Merchant et al. 2003a). These studies showed that human subjects and monkeys could intercept path-guided apparent moving stimuli, although the overall performance was less accurate than with real moving targets. In addition, it was demonstrated that the stimulus traveling time necessary for the decision to start an interception movement was longer in the apparent than in the real motion condition (Merchant et al. 2003a). These

H. Merchant · A. P. Georgopoulos
Brain Sciences Center, Veterans Affairs Medical Center,
Minneapolis, MN 55417, USA

H. Merchant · A. Battaglia-Mayer
Department of Neuroscience, University of Minnesota,
Minneapolis, MN 55455, USA

A. P. Georgopoulos
Departments of Neuroscience, Neurology and Psychiatry,
University of Minnesota,
Minneapolis, MN 55455, USA

H. Merchant (✉)
Brain Sciences Center (11B), Veterans Affairs Medical Center,
One Veterans Drive,
Minneapolis, MN 55417, USA
e-mail: merch006@umn.edu
Tel.: +1-612-7252282
Fax: +1-612-7252291

results suggested that subjects could perceive path-guided apparent moving stimuli with a circular trajectory, and that the motor system involved in the interception has better access to information that arises from real target motion than from the perceptually reconstructed motion, based on a sequence of stationary targets.

Visual motion information is processed in a large number of cortical areas, including V1, the middle temporal area (MT), the medial superior temporal area (MST), the superior temporal polysensory area (STP) and posterior parietal areas (PPC), such as area 7a. For example, MT cells respond selectively to the direction of visual motion, and, interestingly, this selectivity is maintained when apparent moving bars are flashed with the appropriate ISI and spatial separation (Mikami et al. 1986a; Newsome et al. 1986; Mikami 1991). However, there is a hierarchical organization of visual motion processing through this visual motion pathway. By the level of area 7a, cells respond selectively to the direction of motion of bars and random dots (Motter and Mountcastle 1981; Siegel and Read 1997), to optic flow stimuli (Siegel and Read 1997; Merchant et al. 2001, 2003b), to 2D and 3D rotatory stimuli (Sakata et al. 1986, 1994), and can combine visual motion signals with the angle of gaze (Read and Siegel 1997). However, to our knowledge, no studies have investigated whether area 7a is involved in apparent motion processing.

On the other hand, it is well established that the PPC and premotor and motor areas are directly involved in the integration of sensory information to prepare and control action towards stationary targets (Caminiti et al. 1998; Battaglia-Mayer et al. 2001). In fact, it has been demonstrated that besides its fundamental role in the preparation and execution of movement, the motor cortex also receives and processes visual information that can be used to drive behavior (Alexander and Crutcher 1990; Merchant et al. 2001; Port et al. 2001). Nevertheless, little is known about the neural mechanisms engaged in the visual motion processing, apparent motion perception, and the visuomotor transformations necessary to drive motor behavior towards moving objects.

In the present study we investigated the responses to real and path-guided apparent moving stimuli in area 7a and motor cortex of behaving monkeys. The comparison of the functional properties of these areas was important in order to understand the flux and transformation of visual motion information across the parieto-frontal system. Preliminary results have been published previously (Merchant et al. 1999).

Materials and methods

Animals

Two male monkeys (*Macaca mulatta*, 4 and 7 kg BW) were used in this study. Animal care conformed to the principles outlined in the Guide for Care and Use of Laboratory Animals (National Institutes for Health publication no. 85-23, revised 1985). The experimental

protocol was approved by the appropriate Institutional Review Boards.

Visual display

Stimuli were back-projected on a tangent screen using a LCD projector (NEC Multisync MT 820/1020) with a refresh rate of 60 Hz. The tangent screen was 69 × 69 cm and was placed 48.5 cm in front of the animal. The moving stimulus was a black circle of 1.44 cm (1.7 deg of visual angle [DVA]), and traveled on a low contrast circular annulus of 15.2 DVA outside diameter and 1.7 DVA width (Fig. 1). Five angular velocities were used in the two conditions below: 180, 300, 420, 480 and 540 deg/s. All the stimuli traveled counterclockwise.

There were two visual motion conditions, namely a “real” and an “apparent” one (Fig. 1). In the real motion condition the stimulus was displayed every 16.7 ms, resulting in a smooth motion which was indistinguishable from a continuously moving stimulus. In the apparent motion condition five stimuli were flashed successively for 16.7 ms at the vertices of a regular pentagon. The inter-stimulus interval (ISI) in this condition was 400, 240, 166.6, 150 and 133.4 ms for the speed of 180, 300, 420, 480 and 540 deg/s, respectively. Finally, the starting points were: 216, 198, 144, 126 and 108 deg for real moving stimuli, and 72, 36, 288, 288 and 0 deg, for apparent motion, corresponding to the speeds of 180, 300, 420, 480 and 540 deg/s, respectively.

Behavioral tasks

Visual task

The monkeys (monkey 1 and 2) were seated in a primate chair with the left arm restrained, and operated a semi-isometric joystick (Measurement Systems Inc., Model 467-G824, Norwalk CT, USA) with the right arm. This joystick was a vertical rod placed in front of the animal at midsagittal level and controlled a net force feedback cursor which was displayed in the monitor as a circle of 1.7 DVA in diameter. The feedback cursor was deflected constantly by 1.7 DVA upward to simulate a bias force of 0.108 N and reflected, at any given moment, the net force, i.e., the vector sum of this simulated force and the force exerted by the monkey on the joystick. At the beginning of the trial, the animal had to place the force feedback cursor within a red circle of 3.4 DVA in diameter (“center window”, located at the center of the screen) by exerting a minimum of 0.108 N force in the downward direction, and keep it there for a variable delay period (1–3 s). After the delay period, the stimulus began to move for 2 s. Monkeys received a liquid reward if the

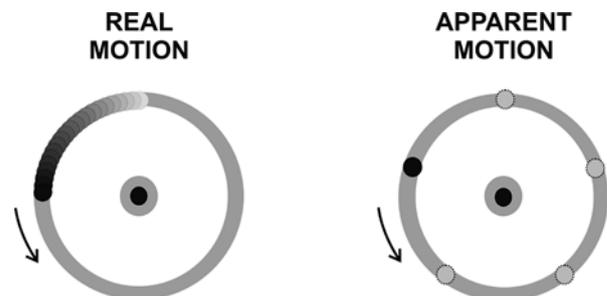


Fig. 1 Stimuli in the real and apparent motion conditions. A smooth real moving stimulus was produced in the real motion condition. In the apparent motion condition five stimuli were flashed at the vertices of a regular pentagon. All the stimuli traveled counterclockwise (CCW), through a circular low contrast path. The monkeys maintained eye fixation in the center of the circle, and kept a cursor in the center window by exerting a constant pulling force on a semi-isometric joystick with the right hand

cursor was maintained inside the center window throughout the entire duration of the trial. The monkeys were trained to fixate, within 2 DVA, a yellow dot (1 DVA in diameter) located in the center of the center window, for the duration of stimulus presentation. The X-Y eye position was monitored using an oculometer (Dr. Bouis, Karlsruhe, Germany). Both the eye and the joystick positions were sampled at 200 Hz; the tangential eye velocity was calculated by differentiating eye position.

The different combinations of stimulus velocities and motion conditions were interleaved and presented in a pseudorandom order. A repetition consisted of five trials in the real motion condition and of five trials in the apparent motion condition (with the same five stimulus velocities). At least five repetitions were collected.

Receptive field (RF) task

A detailed description of this task has been given elsewhere (Merchant et al. 2001). Briefly, a yellow spot of 0.32 DVA in diameter served as the fixation point (FP) and was presented in the center of the translucent tangent screen. The monkeys were trained to fixate this spot (within 2 DVA) for the duration of stimulus presentation. During that time, monkey 1 maintained the right hand in a relaxed position (monitored using a video camera) whereas monkey 2 maintained grasp of a vertical semi-isometric joystick with the right hand by exerting a constant pulling force on the joystick of ~ 0.22 N. First, the FP was turned on, which the monkeys fixated; following attainment of fixation, 100–500 ms were allowed for monkey 2 to grasp the joystick. Then, stimuli were presented on the screen for 400 ms. A juice reward was delivered randomly every 1.1–3.3 s while fixation was maintained; if fixation was broken, the trial was aborted. Stimuli were back-projected on a 71×71 DVA screen using an LCD projector, and were presented successively at 25 different positions or patches in a regular 5×5 grid. The small square patches of random dot stimuli were 16.2 deg of visual angle (DVA) on a side; stimuli were presented within such a patch for 400 ms, one patch at a time, with an inter-patch presentation interval of 150 ms. The stimuli were composed of 30 white dots moving within a square on a black background. Each dot was a circle of 0.35 DVA in diameter and moved for a maximum lifetime of 400 ms, after which it was assigned to a new random location within a square patch. If a moving dot traveled outside the patch displayed, it was relocated to a new random location within the square. The dots were relocated asynchronously, to avoid coherent flickering of the stimuli. This constant reshuffling essentially eliminated pattern and density artifacts, because the pattern of dots was changing constantly and each region within the square had approximately the same number of points at any time. The stimuli could move in eight different motion conditions: the four cardinal directions of translation (rightward, leftward, upward, downward), expansion, contraction, clockwise (CW) rotation and counterclockwise (CCW) rotation.

The eight different motion conditions were interleaved and presented in a pseudorandom order. The 25 different patch locations were nested within each stimulus motion condition and were also presented pseudorandomly. A complete run consisted of the presentation of all conditions in three repetitions.

Center out motor task

In this task the monkeys produced semi-isometric force pulses on the joystick in eight radial directions, in response to the presentation of a peripheral target on an imaginary circle of 0.89 N force radius. A force feedback cursor on the screen indicated the current net force exerted on the joystick; a constant upward bias of 0.108 N was applied, corresponding to a deflection of the cursor of 0.85 DVA. A trial began with the appearance of a light spot at the center of the screen which prompted the monkey to exert a downward force of 0.108 N on the joystick to align the force feedback cursor to the center spot within a circular force window of 0.217 N radius. Then,

after a variable delay of 1,000–3,000 ms, a light spot appeared in one of eight locations, separated by 45 deg and with an eccentricity of 6.8 DVA, which prompted the monkey to apply a force pulse (>0.89 N) on the joystick such that the force feedback cursor would move in the direction of the peripheral stimulus for the monkey to obtain a liquid reward. Five repetitions of this task were performed in a randomized block design.

Neural recordings

Impulse activity of single neurons was recorded extracellularly from area 7a and the proximal arm area of the motor cortex (left hemisphere) during the three tasks (see Merchant et al. 2001 for details). All isolated neuronal potentials were recorded regardless of their activity during the task, and the recording sites changed from session to session. The presentation of the visual stimuli, behavioral control and data collection was controlled by a personal computer. Online raster displays were generated on a computer monitor.

Electromyographic (EMG) activity

The EMG was recorded in the same two monkeys in separate sessions from the neural recordings using intramuscular, multi-stranded, Teflon-coated wire electrodes (Schwartz et al. 1988). EMG activity of the following muscles was recorded in monkey 1, contralateral to the recording side: rhomboideus major, trapezius, deltoideus (anterior, middle and posterior), pectoralis major, triceps brachii, biceps brachii, extensor digitorum communis and forearm flexor (unspecified). The same muscles were recorded from in the second monkey, with the addition of supraspinatus, infraspinatus and latissimus dorsi. The EMG signal was amplified, rectified, filtered and sampled at 200 Hz.

Data analysis

General

An analysis of covariance (ANCOVA) was performed for each neuron, using the frequency of discharge (based on spike counts) during the visual stimulation period (2 s) as the dependent variable, the motion Condition and stimulus Speed were fixed factors, and the discharge rate during the last 500 ms of the control-holding period was a covariate. The spike counts were square-root transformed to stabilize the variance (Cox and Lewis 1966; Snedecor and Cochran 1989; Tukey 1977). The program 2 V of the BMDP/Dynamic statistical package (BMDP Statistical Software Inc., Los Angeles, 1992) was used to execute the ANCOVA. In addition, for those neurons that did not show statistically significant effects in the ANCOVA, we performed a one-way analysis of variance (ANOVA) between the discharge rate during the control and visual stimulation periods, to identify the cells that showed general changes in their activity during the presentation of visual stimuli. The level of statistical significance to reject the null hypothesis for all statistical analyses was set at $\alpha = 0.05$. The results of the ANCOVA and the ANOVA were consistent between monkeys and were combined. Cells were included in the analysis if they were recorded for at least four task repetitions and had a mean firing rate larger than 0.6 impulses/s during the visual stimulation period. Of a total of 936 cells recorded in area 7a, 780 fulfilled the criteria above. In motor cortex 1,122 cells were recorded and 903 fulfilled the criteria.

Spike density function

The spike trains for each trial in the task were converted to time-varying spike density functions using the fixed kernel method with a

Gaussian pulse of 20 ms (Richmond and Optican 1987). The average population spike density function (PSDF) was calculated for each stimulus speed and motion condition for different populations of neurons. The onset time of increase in activity for the cell populations was defined as the earliest time when the PSDF exceeded the mean+2SD of the control spike density function, during the 500 ms immediately preceding stimulus onset.

Calculation of the preferred stimulus angular location of cells

The preferred stimulus angular location (PSAL) of each cell was computed as follows. First, an angle was assigned to each action potential during the visual stimulation period. This angle corresponded to the actual (real motion) or the perceptual (apparent motion) stimulus location in the circular path when the action potential occurred. Figure 2 illustrates the conversion of conventional rasters (Fig. 2A) to spatio-temporal circular rasters (Fig. 2B). The stimulus position is displayed at the bottom of Fig. 2A; notice that the activity of this cell increased when the stimulus was between 0 and 90 deg. This becomes obvious in the circular raster of Fig. 2B.

The second step was to compute the mean direction and the circular standard deviation (Mardia 1972), using the angles assigned to each action potential (Fig. 2C). For this purpose, only the first stimulus revolution was used, starting at 240 deg for the following stimulus speeds: 300, 420, 480 and 540 deg/s. This starting position allowed us to skip at least the first 250 ms of visual stimulation, and then to eliminate the initial, phasic responses to stimulus onset. The slowest speed (180 deg/s) was not used, because there were not enough data to calculate the mean direction and the circular standard deviation. We used a bootstrapping technique to determine whether the cells were significantly tuned to the stimulus location (Lurito et al. 1991). For that purpose, the length of the mean resultant (R) was calculated first using the data of the five repetitions collected (Fig. 2C). Then a bootstrap sample was generated by assigning randomly a new angle (with replacement) to each action potential recorded during the analyzed stimulus revolution, and its mean resultant R^* calculated. A cell was considered to be significantly tuned to the stimulus location if the discharge rate during first revolution was larger than 10 spikes/s and the length of R was greater than 99% of the lengths of R^* ($k = 5,000$ bootstrap samples). This corresponded to a chance probability of $p < 0.01$. In this case, the direction of R was the preferred stimulus location of the cell.

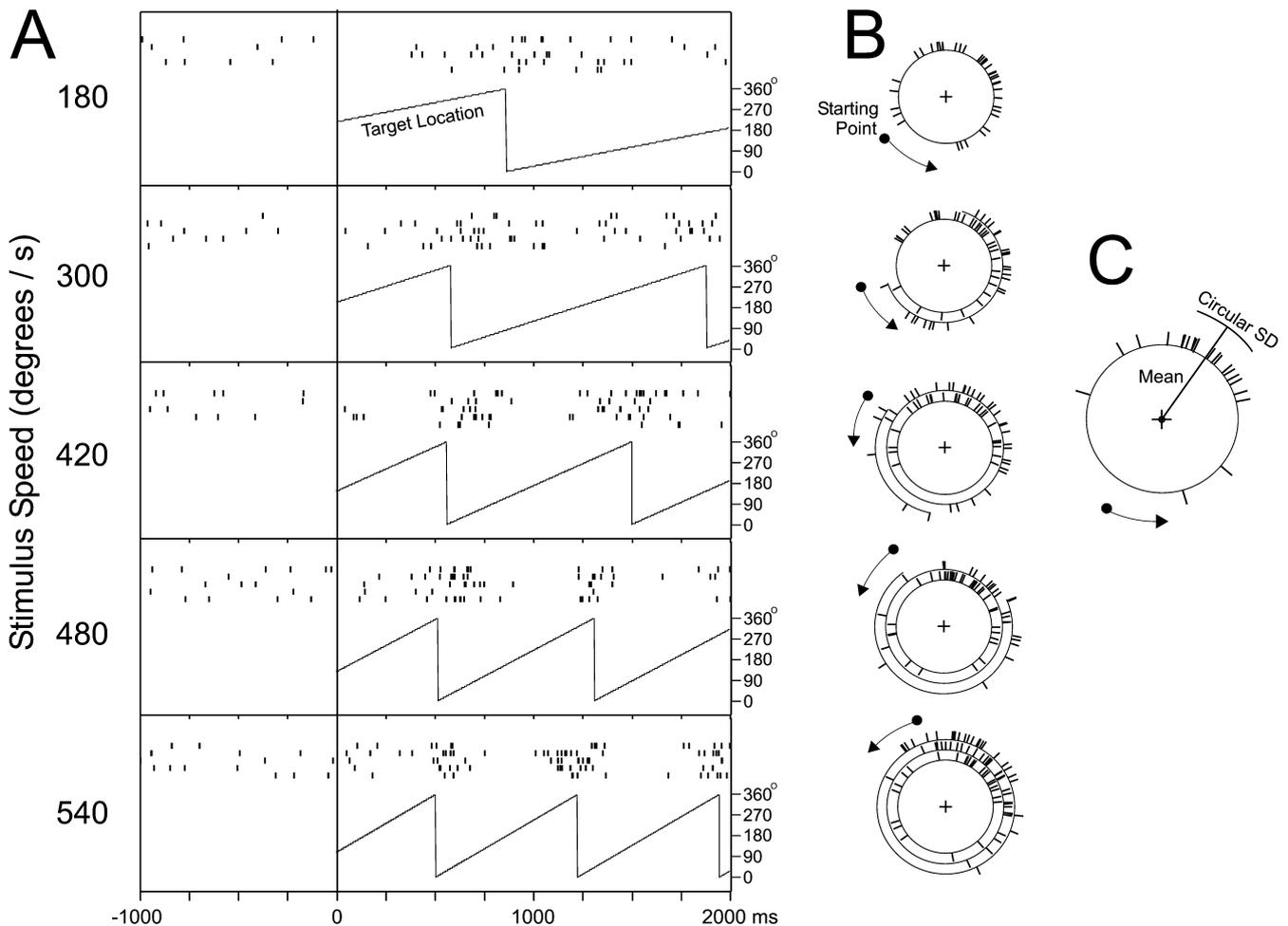


Fig. 2A–C Calculation of the preferred stimulus angular location (PSAL). **A** Rasters of an area 7a neuron during the task, aligned to the stimulus onset (0 ms on the time scale in the ordinate). For each stimulus speed, the raster (top) and stimulus location (bottom) are depicted. **B** Circular raster of the activity in **A**. An angle was assigned to each action potential during the visual stimulation period. This angle corresponded to the actual stimulus location in the circular path when the action potential was recorded. The *inner circle* represents the first stimulus revolution, the *intermediate circle*

the second revolution and the *outer circle* the third stimulus revolution. The *small filled circle* in the periphery indicates the stimulus starting location. **C** Mean direction and circular standard deviation using the angles assigned to each action potential. Only the first stimulus revolution was used, starting at 240 deg. This starting position allowed to skip at least the first 250 ms of visual stimulation, and then to eliminate the initial responses to the stimulus onset

Finally the circular standard deviation was calculated (Mardia 1972).

Periodic neural activation

The neural representation of the ISI in the apparent motion condition was characterized using harmonic analysis (Fast Fourier transform, FFT). The mean SDF for each stimulus speed, during the 2 s of stimulus presentation, was analyzed separately in order to construct specific periodograms and spectral densities for the different ISIs. The sampling frequency was 1 kHz, the resolution was 0.5 Hz and the range was 0.5–500 Hz. The data were padded, centered on the mean, and then tapered using split-cosine-bell transformation in 20% of the data, in order to reduce the frequency leakage in the periodogram (Bloomfield 2000). In addition, the Shimshoni test ($p < 0.01$) was used to determine whether the four largest harmonic ordinates were significantly larger than those expected from a white noise distribution (Shimshoni 1971). This analysis was performed on neurons that presented a significant increase in cell activity during apparent motion (but not during the real motion) with respect to the control period (ANOVA, $p < 0.05$).

Results

General

We analyzed the activity of 903 cells in motor cortex (511 in monkey 1 and 392 in monkey 2) and 780 cells in area 7a (418 in monkey 1 and 362 in monkey 2) that fulfilled the criteria for number of trials and strength of responses during the task. The total number of cells with a statistically significant effect of visual stimulation was 453 (453/903, 50.2%) in the motor cortex and 467 (467/780, 59.9%) in area 7a. In motor cortex, 215/903 (23.8%) cells showed significant effects of motion condition and/or stimulus speed in the ANCOVA, and 238/903 (26.4%) showed statistically significant differences between the control and visual stimulation periods. In area 7a, 214/780 (27.4%) cells showed significant effects of motion condition and/or stimulus speed in the ANCOVA, and 253/780 (32.4%) showed statistically significant differences between the control and visual stimulation periods.

Selective neural responses to real and apparent motion

The number of neurons with statistically significant effects of motion condition, stimulus speed and/or motion condition \times stimulus speed interaction is listed in Table 1. It is clear from these results that motion condition was more effective than stimulus speed in modulating neuronal activity in motor cortex and area 7a. Figure 3 illustrates the PSDF for cells with a significant motion condition effect in area 7a and motor cortex. Both cortical areas showed a population of cells with a selective activation during real motion stimulation (Fig. 3A, motor cortex [$N = 87$]; Fig. 3C, area 7a [$N = 110$]). However, the temporal profile of activation of these cells differed between the two areas. The population onset latency of

response for real motion selective cells was significantly longer in the motor cortex (193 ± 27 ms; mean \pm SEM) than in area 7a (90 ± 9.3 ms; t -test, $p < 0.001$). In addition, area 7a showed a group of cells with selective responses to apparent motion stimuli (Fig. 3D, $N = 52$), with a population response latency of 95.2 ± 9.2 ms. These cells were almost the mirror counterpart of the real motion selective cells. However, in motor cortex the same type of cells showed a decrease in discharge rate during real motion stimulation instead of an increase during apparent motion stimulation (Fig. 3B, $N = 64$). Therefore, these results indicated that partially overlapping neuronal ensembles are engaged in processing real and apparent moving stimuli in area 7a. Furthermore, an ensemble of motor cortical cells showed a selective activation during real motion, but few neurons in this area showed a selective increase in activity during apparent motion.

Parametric relations to stimulus speed

As can be seen in Table 1, the stimulus speed per se affected a small group of cells in either one of the areas studied. However, we were interested to investigate the quantitative relations between neural activity and stimulus speed in those cases which showed a significant effect in the ANCOVA. For that purpose, we used a linear regression analysis which yielded the following results. In the motor cortex a total of 82 cells showed a significant effect of stimulus speed in the ANCOVA (see above) and, of those, 35 (42.7%) showed a linear dependence on the stimulus speed in the regression analysis (25 for real motion only, 5 for apparent motion only, and 5 for both real and apparent motion, F test, $p < 0.05$). In area 7a, 70 cells showed a significant effect of stimulus speed in the ANCOVA, and 44 (62.9%) of them showed a linear dependence on the stimulus speed in the regression analysis (17 for real motion only, 13 for apparent motion only, and 14 for both real and apparent motion, F test, $p < 0.05$). The slope of the relation could be positive or negative. Figure 5 plots mean discharge rate (\pm SEM) against stimulus speed for these groups of cells in motor cortex (Fig. 4A, B) and area 7a (Fig. 4C, D). The magnitude of the slopes was similar in both areas and between real and apparent motion conditions, although in the latter condition the intercept tended to be smaller in both areas.

Table 1 Numbers and percentages of neurons with the noted effects in the ANCOVA

Effect	Motor cortex	Area 7a
Motion condition only	124 (57.7%)	136 (63.6%)
Stimulus speed only	34 (15.8%)	27 (12.6%)
Motion \times speed interaction	57 (26.5%)	51 (23.8%)
Total	215 (100%)	214 (100%)

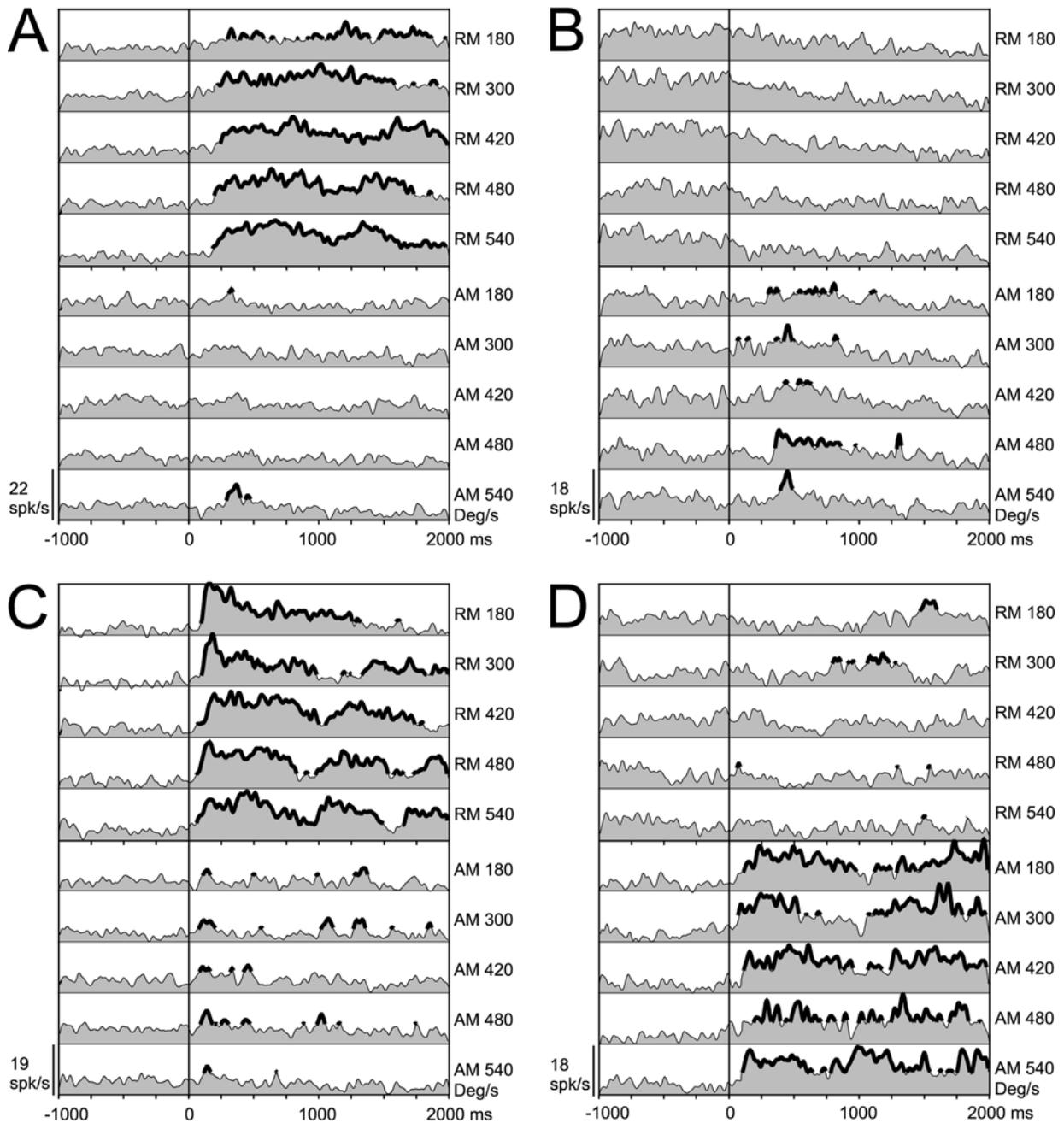


Fig. 3A–D Average population spike density functions (PSDF) of neurons with significant effects in motion condition. **A** Motor cortical cells ($N = 87$) with selective responses to real moving stimuli. **B** Neurons in the motor cortex ($N = 64$) with a decrease in activity during the apparent motion condition. **C** Area 7a neurons (N

$= 110$) with selective responses in the real motion condition. **D** Selective activity during the apparent motion condition in area 7a neurons ($N = 52$). The PSDF are aligned to the beginning of the stimulus period (0 ms in the ordinate time scale)

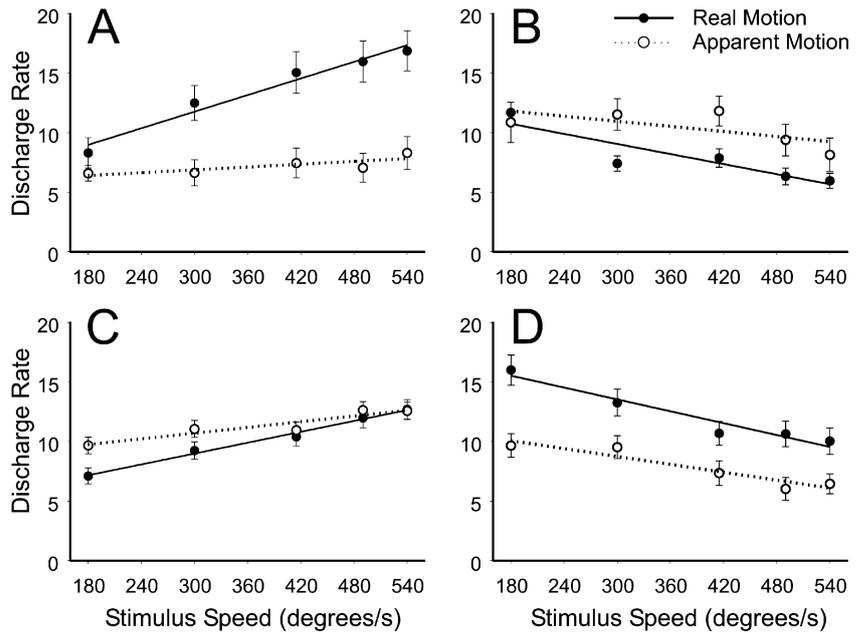
Cell responses to stimulus angular location

We noticed that a group of cells in both areas showed a cyclic activation. The period of this activation varied for different stimulus speeds and, when the spike rasters were represented as in Fig. 2B such that each action potential was aligned with respect to the stimulus position in time, a clear relationship between the cell activity and the stimulus position was revealed (Fig. 5). We quantified this relation by calculating the preferred stimulus angular

location (PSAL) of each cell and testing its statistical significance (see “Materials and methods”). An example of a motor cortical cell with PSAL for different stimulus speeds in the real motion condition is shown in Fig. 5A, and of a cell in area 7a with PSAL in all stimulus speed and motion conditions is shown in Fig. 5B.

The significant PSALs for different motion conditions and stimulus speeds are shown in Fig. 6 for both areas. In the motor cortex (Fig. 6A), 146 cells showed at least one significant PSAL for a total of 245 significant cases (a case

Fig. 4A–D Discharge rate (mean \pm SEM) of neurons that showed a significant linear relation with the stimulus speed in the real and apparent motion conditions. Neurons with a discharge rate that increased as a function of the stimulus speed are shown in **A** for the motor cortex (real motion $N = 18$; apparent motion $N = 6$) and in **C** for area 7a (real motion $N = 18$; apparent motion $N = 14$). The discharge rate of neurons with a decrease in activity as a function of the stimulus speed is shown in **B** for the motor cortex (real motion $N = 12$; apparent motion $N = 3$) and in **D** for area 7a (real motion $N = 13$; apparent motion $N = 13$)



corresponds to one stimulus speed and one motion condition), and in area 7a (Fig. 6B) 283 cells showed at least one significant PSAL for a total of 627 significant cases. The distribution of the preferred PSALs on the unit circle did not differ significantly from a uniform one (Rayleigh test, $p > 0.05$) in all motion conditions and stimulus speeds in area 7a and motor cortex. With respect to the spread of the stimulus locations associated with single spikes, the circular standard deviation was significantly larger in the motor cortex (67.9 ± 0.7 deg, mean \pm SEM) than in area 7a (61.9 ± 0.5 deg; t -test, $p < 0.0001$). Finally, in area 7a there was an increase of cells with significant PSALs as a function of the stimulus speed in the apparent motion condition.

We compared the PSALs across stimulus speeds in the real and apparent motion condition using the Watson-Williams test ($p < 0.01$). The results of this analysis are shown in Table 2, where it is evident that the majority of neurons did not show significant differences in their PSALs across stimulus speeds. In order to perform a valid Watson-Williams test, the neurons included in the analysis showed a minimum of 30 spikes per condition and a mean resultant larger than 0.4. No motor cortical neurons in the apparent motion condition fulfilled these constraints.

More cells were significantly tuned to the stimulus location in the real than in the apparent motion condition, particularly in motor cortex (motor cortex: 197 cases real and 46 apparent motion; area 7a: 393 cases real and 234

Fig. 5A, B Circular raster of neurons with a significant preferred stimulus angular location (PSAL). **A** Motor cortical cell with a significant PSAL in the upper left quadrant of the stimulus trajectory, or all stimulus speeds in the real motion condition. **B** Neuron in area 7a with a significant PSAL for all stimulus speeds in the real and apparent motion conditions. The vector from the center cross to the circular raster represents the significant PSAL

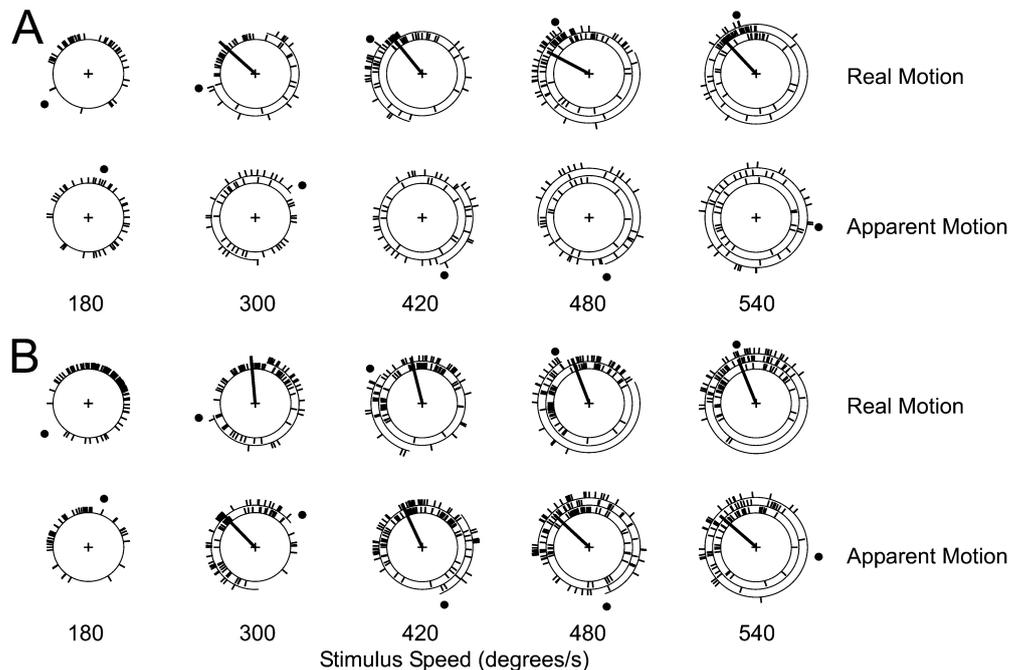


Fig. 6 Distribution of the significant preferred stimulus angular locations of motor cortical neurons (**A**) and neurons in area 7a (**B**). The number of significant cases was larger in the real than in the apparent motion conditions, particularly in the motor cortex

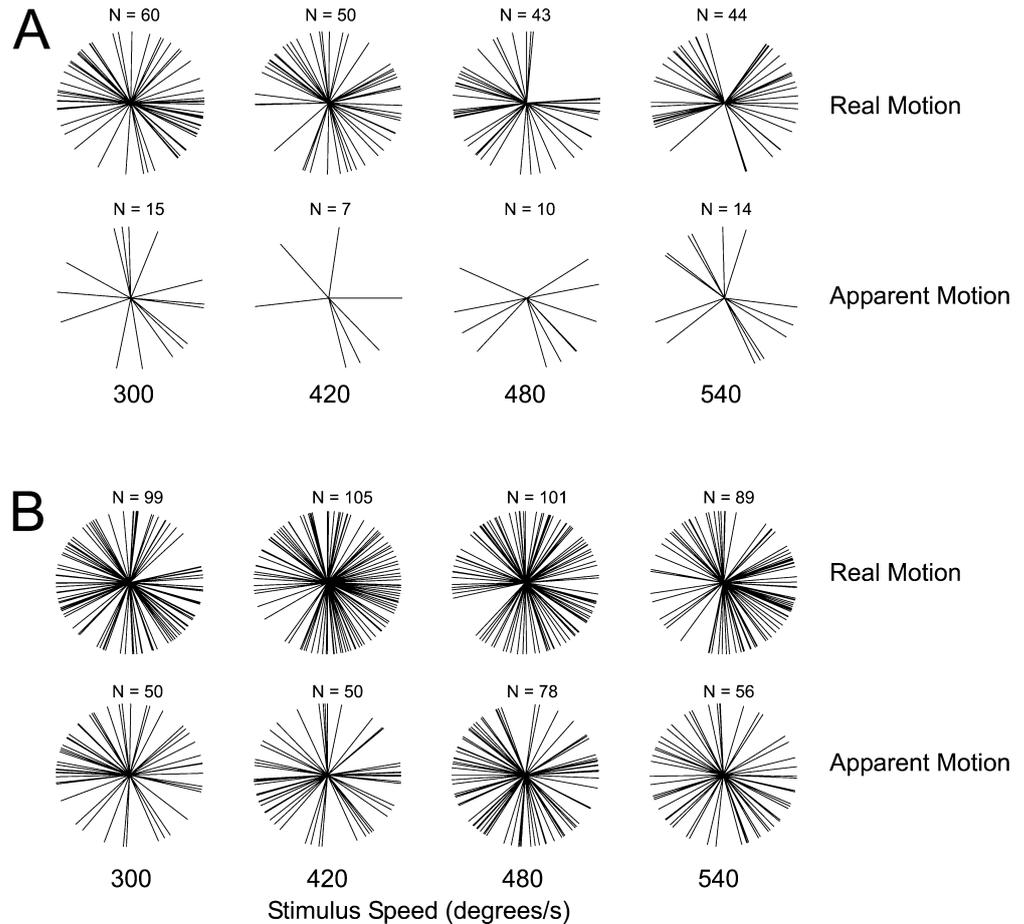


Table 2 Numbers and percentages of neurons with significant or non-significant differences in the preferred stimulus angular location for different stimulus speeds in the Watson-Williams test

Motion condition	Watson-Williams test	Motor cortex	Area 7a
Real	Significant	5 (18.5%)	17 (19.3%)
	Non-significant	22 (81.5%)	71 (80.7%)
	Total	27 (100%)	88 (100%)
Apparent	Significant	-	17 (37.8%)
	Non-significant	-	28 (62.2%)
	Total	0	45 (100%)

apparent motion). In fact, all the motor cortical cells with at least two significant PSALs in the real motion ($N = 54$) showed also selective responses to real moving stimuli in the ANCOVA, which indicates that most of the motor cortical neurons with selective responses in the real motion condition were tuned to the stimulus angle.

In area 7a, however, the picture is more complex, since the neurons with PSALs could not only present selective responses to the motion condition but also they show sensitivity to the stimulus speed. We analyzed 143 neurons in area 7a that showed at least two significant PSALs in the real motion and/or apparent motion conditions. Of these, 71 neurons showed PSALs in both motion conditions, 58 in the real motion only and 14 in apparent motion condition only. Consequently, these findings

indicated the existence of two main cell populations that responded during a particular portion of the stimulus trajectory, one that was selective to real moving stimulus and another that responded in both motion conditions.

Speed sensitivity of PSAL in area 7a during apparent motion

The visual inspection of circular rasters indicated that the neurons in area 7a with PSALs in both motion conditions showed a monotonic increase in firing rate as a function of the stimulus speed in the apparent motion condition but presented a similar response in the real motion condition for all stimulus speeds. In order to quantify this observation, we determined first the discharge rate, for each motion condition and stimulus speed, during the intervals where the SDF was above the control period mean + 2SD. This analysis allowed the identification of activation periods related to the stimulus location. Then an ANOVA was performed using the discharge rate during the activation periods as the dependent variable and the stimulus speed as a factor in the real and apparent motion conditions separately. The results indicated that 48 (48/71, 67.6%) neurons with PSALs in both motion conditions showed a significant effect on stimulus speed in the apparent motion condition but not in the real motion

condition (ANOVA, $p < 0.05$). Figure 7A illustrates an example of a cell in area 7a that showed a similar PSAL and discharge rate as a function of the stimulus speed in the real motion condition, and presented an increase in discharge rate in the apparent motion condition. The discharge rate of these 48 cells is plotted against the stimulus speed in Fig. 7B, where it is clear that the population cell activity increases as a function of the speed in the apparent motion, reaching the firing rate observed in real motion in the highest stimulus speeds. In addition, most of these cells (40/48, 83.3%) showed a significant PSAL at stimulus speeds larger than or equal to 420 deg/s. Therefore, this group of cells showed a location specific response to the apparent moving stimulus when the stimulus speed and the ISI reached a certain value. This value correspond to 420 deg/s, since at this speed the population discharge rate in the apparent motion condition reached the cell activity observed in the real motion condition (Fig. 7B).

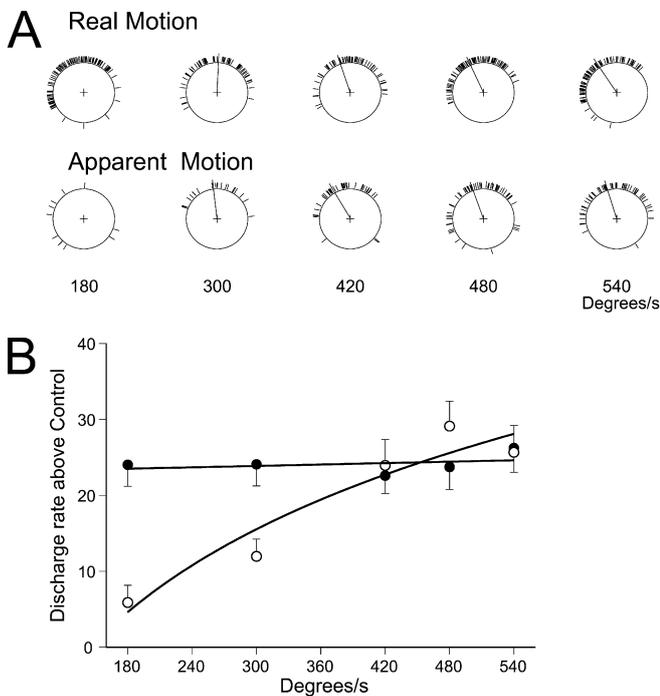


Fig. 7 **A** Circular raster of a cell in area 7a with a significant increase in discharge rate during the apparent motion condition (ANOVA, $p < 0.05$). The PSAL of this cell is similar for different stimulus speeds and motion conditions. **B** Discharge rate (mean \pm SEM) of the population of cells in area 7a ($N = 48$) that showed significant increase in neural activity as a function of the stimulus speed during apparent motion (*open circles*) but not during the real motion condition (*filled circles*). A gradual increase in discharge rate is observed as a function of the stimulus speed in the apparent motion condition, until it reaches values that were similar to ones observed in the real motion condition in the fastest stimulus speeds

Relations between the visual receptive field position and the neural responses during real and apparent motion stimulation in area 7a

The stimulus position tuning in area 7a could be due to the possibility that only part of the stimulus trajectory might have been inside the receptive field of the cells, producing an activation of the cells in a particular portion of the stimulus trajectory. Thus it was important to determine the position of visual receptive field of the cells to test this possibility. For that purpose, visual receptive fields were mapped using the RF task, in which moving visual stimuli were presented to the monkeys, while they fixated their eyes and did not move their arm (see “[Materials and methods](#)”). In area 7a, 728 cells were studied in the visual motion and the RF tasks, and of these, 281/728 (38.6%) showed a significant PSAL in at least one stimulus speed and motion condition: 216/728 (29.7%) in the real and 148/728 (20.3%) in the apparent motion. In addition, 461/728 (63.3%) cells also showed significant receptive fields to at least one of the eight stimulus conditions used in the RF task. The number of neurons with a significant PSAL and a significant receptive field was 188/728 (25.8%; 148 neurons in real motion, and 99 neurons in apparent motion).

A quantitative analysis of the overlap between the PSAL and the receptive field was performed as follows. First, the half-height areas of the receptive fields, defined as 50% of the maximum response in the significant Gaussian regressions with a positive depth of the tuning, were calculated. Second, the arc defined by the angular confidence interval ($PSAL \pm CSD$) was calculated as a measure of stimulus location spread. Then the overlap between this arc and the receptive field was calculated. This was performed for real and apparent motion separately. The results of this analysis showed that the PSAL arc and the receptive field overlapped in 70/728

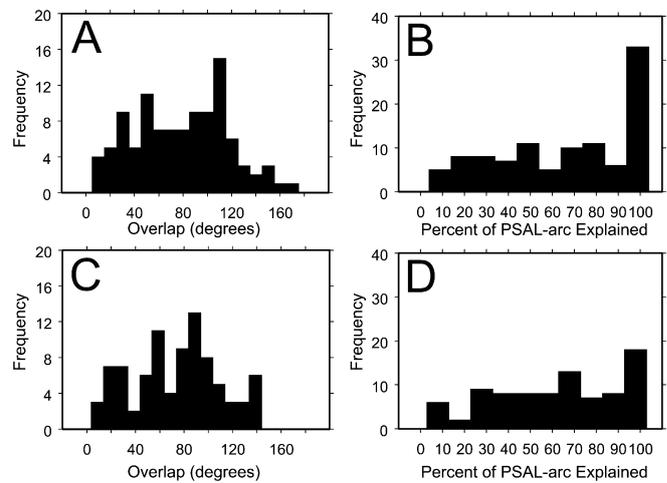


Fig. 8 Histograms showing the amount of overlap (in deg) between the receptive field and the PSAL arc in area 7a neurons, for the real (**A**) and apparent motion condition (**C**). The histograms in **B** and **C** show the percent of the PSAL explained by the receptive field position, for the same neurons, in the real and apparent motion, respectively

(9.6%; 104 cases) cells in the real motion condition, whereas 52/728 (7.1%; 87 cases) neurons showed an overlap in the apparent motion condition. Figure 8 illustrates the overlap arc length (Fig. 8A real motion, Fig. 8C apparent motion) and the percentage of PSAL arc explained by the receptive field position (Fig. 8B real motion, Fig. 8D apparent motion). These results indicate that the relation between the PSAL and the receptive field position varies across the population of neurons, ranging from close alignment between the two measures in a group of cells (Fig. 9A), to cells that showed poor or no overlap between the PSAL and the receptive field (Fig. 10A, B). Finally, 54 neurons (54/728, 7.4%; 79 cases) in the real motion condition and 33 neurons (33/728, 4.5%; 46 cases) in the apparent motion condition showed a receptive field that included all the stimulus trajectory in the visual task (Fig. 9B).

Neural activity entrainment to stimulus timing in the apparent motion condition

An analysis was performed to determine whether the selective neural responses to the apparent motion condi-

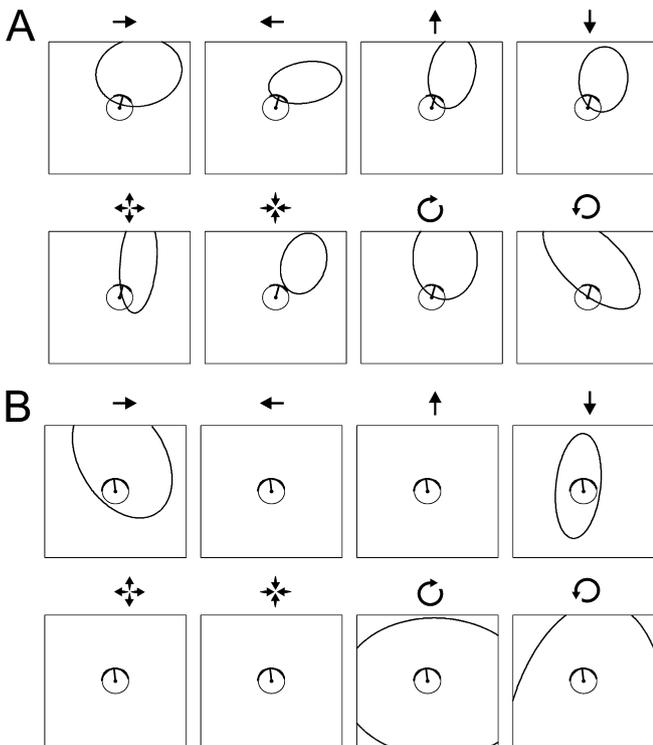


Fig. 9A, B Location of the visual receptive field (*black ellipse, half-height area*) for the eight different kinds of motion in the RF task, and the extent of the PSAL arc (*gray arc*) in the visual task. The *central circle* represents the trajectory of the stimulus in the visual task and the vector from the center to the periphery of this circle specifies the PSAL. **A** Area 7a neuron with a perfect overlap between the RF and the PSAL arc. **B** Neuron in area 7a that showed a RF in the rightward, downward, and the CW and CCW rotations that included a large proportion of the trajectory of the visual field mapped, including the complete stimulus trajectory in the visual task. The square side is 71 DVA

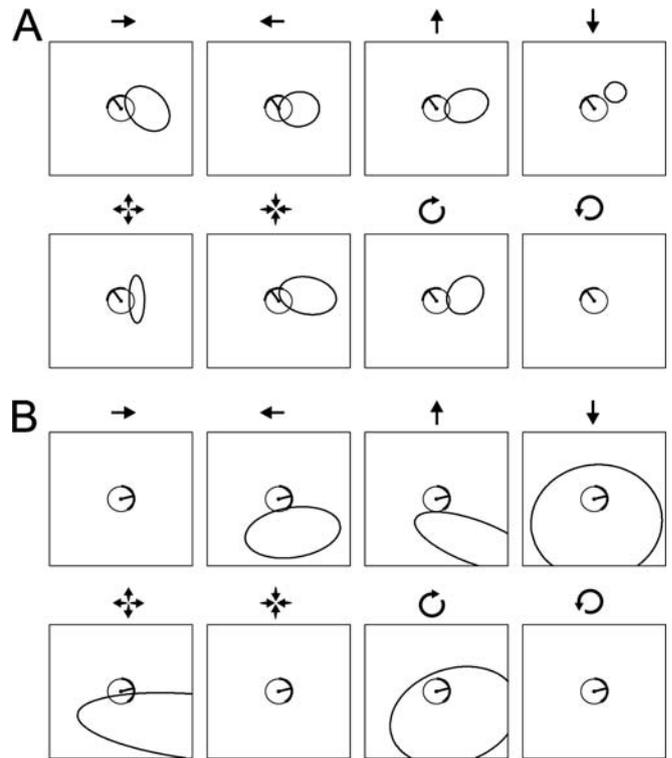


Fig. 10 Example of two neurons (**A, B**) with a receptive field (*black ellipse*) in the RF task that did not overlap with the PSAL arc (*gray arc*) in the visual task. Same conventions used as in Fig. 9

tion were due to activity induced by the successive flashing of dots at the vertices of a regular pentagon. For this purpose, spectral analysis was used to characterize the periodic profile of neural activation associated with the stimulus flashing. This analysis was performed on neurons in motor cortex and area 7a that showed a significant increase in discharge rate during the stimulus presentation in the apparent motion condition only. The results indicated that 66 neurons in area 7a showed a periodogram with significant power levels (Shimshoni test, $p < 0.01$) in the frequencies at which the apparent moving stimuli were presented. Figure 11A illustrates an area 7a neuron with an activation profile that follows the presentation of the apparent moving stimuli represented as red circles. In addition, the population spectral density demonstrated that this group of cells showed a periodic entrainment of activation with the same period of the ISI in the apparent motion condition, illustrated as a red vertical line in Fig. 11B, C. These 66 neurons showed a significant periodogram in at least two of five stimulus speeds tested, and the number of significant cells was: 41, 32, 37, 33 and 24 for the speeds of 180, 300, 420, 480 and 540 deg/s, respectively. These results demonstrated that there is a strong representation of inter-stimulus intervals in area 7a. This time interval neural representation seems to be running in parallel to the neural responses associated with the circular motion illusion. Fourteen out of the 66 (14/66, 21.2%) neurons with significant harmonics at the ISI

frequencies also showed a significant PSAL at those stimulus speeds. Finally, only five motor cortical cells showed a significant harmonic in the periodogram at the ISI frequency.

mental conditions; different results could have been obtained if, for example, the interception movement were to follow (or be instructed by) a stimulus moving in the same direction.

Comparison of the neural responses during the visual and center→out tasks in motor cortex

It is possible that the PSAL observed in motor cortex was associated with planning a movement towards the moving stimulus in a particular direction. Thus, in order to explore this possibility we analyzed the neural activity of 753 motor cortical neurons studied during both the visual and the center→out tasks. We found that 330 (330/753, 43.8%) neurons were tuned during the center→out task (Bootstrap, $p < 0.05$, Lurito et al. 1991), and 127 (127/753, 16.9%) neurons showed significant PSAL. However, only 77 (77/753, 10.2%) neurons showed both a preferred direction in the center→out and a significant PSAL in the visual task. The angular difference between these two measures is shown in Fig. 12, where it is clear that the PSAL of most of the motor cortical cells was not correlated to their preferred direction in the center→out task. Therefore, it is likely that the cells with PSAL in the motor cortex were engaged in processing visual motion information, instead of being associated with motor planning. Of course, this holds for the present experi-

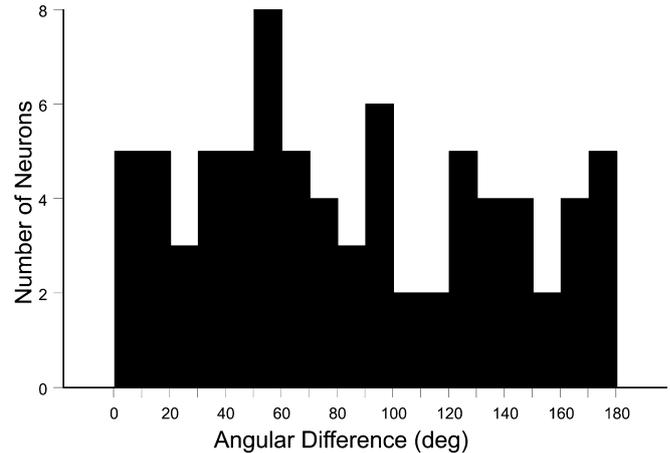


Fig. 12 Angular difference between the preferred direction in the center→out task and the PSAL in the visual task of 77 motor cortical cells

Fig. 11A–C Periodic neural activation in area 7a. **A** Neuron in area 7a that showed a clear periodic response to the flashed stimuli (represented as *red dots*) in the apparent motion condition. **B** Mean spectral densities of 66 neurons for each stimulus speed in the apparent motion condition. The Daniell window with a span of 3 was used. The *red vertical line* represents the inter-stimulus interval (ISI) of the apparent moving stimuli. **C** Contour plot of the mean spectral power of the 66 neurons in area 7a. The ISI is plotted in the *abscissa*, and the period of the spectra in the *ordinate*. The color code goes from *dark blue* to *red*

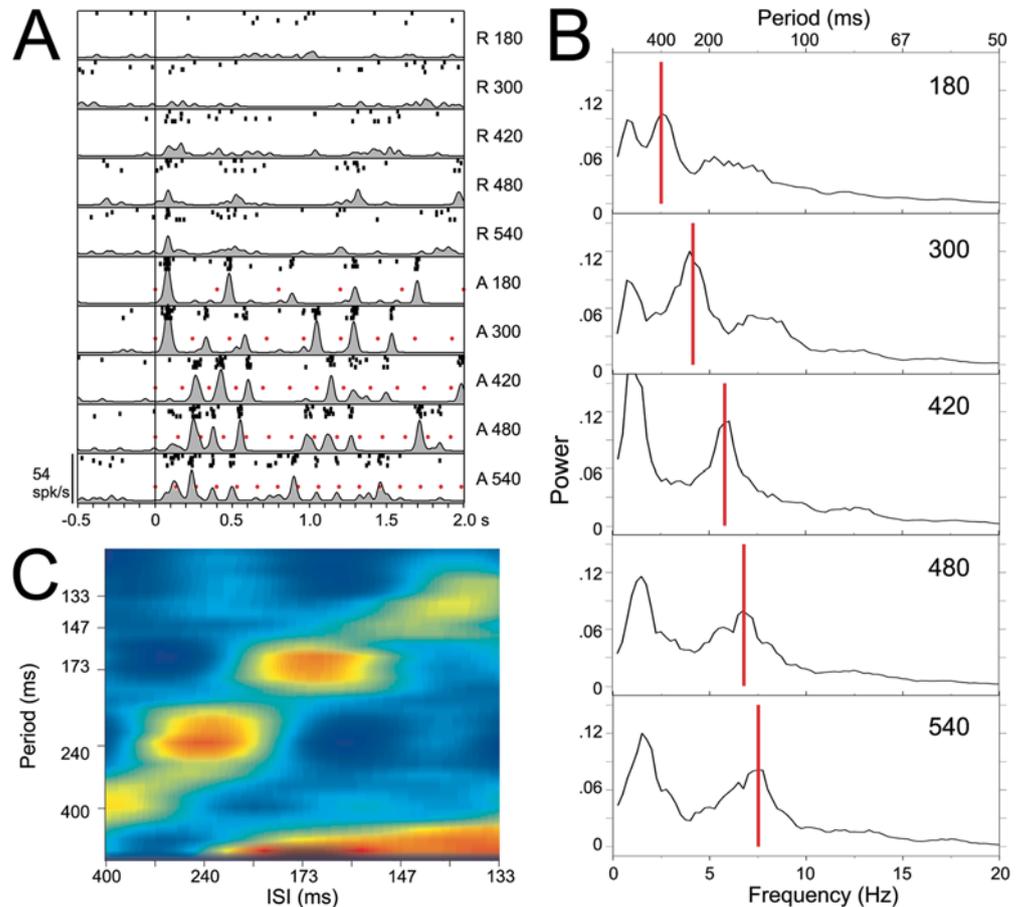
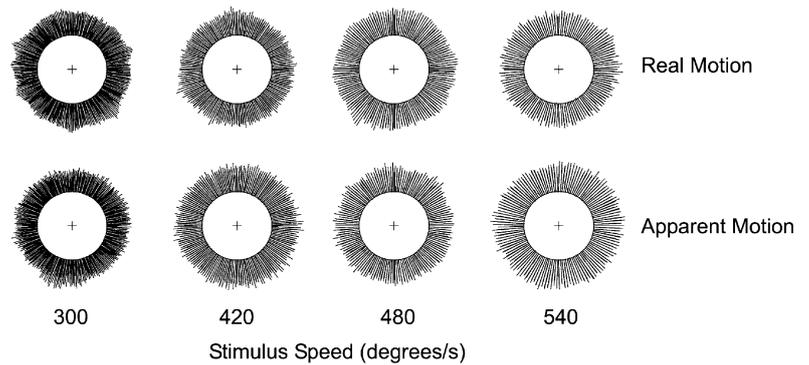


Fig. 13 Circular histogram of the normalized magnitude of the EMG of the biceps brachii of monkey 1 during the visual task for different motion conditions and stimulus speeds



EMG activity

An ANCOVA was performed on the mean EMG activity during the stimulus presentation in 13 shoulder, upper and forearm muscles, using the motion condition and stimulus speed as factors, and the mean EMG activity during the control period as the covariate. The results showed that there were no significant effects in the stimulus motion condition, the stimulus speed or the condition \times speed interaction on muscular activity in any of the muscles studied. In addition, the ANOVA comparing the muscular activity during the control and stimulus presentation indicated that only one muscle (romboideus) in one monkey showed a significant difference between these two task periods; however, the same muscle did not show any effect in the other monkey. This lack of a significant EMG change, as compared to the significant cell responses, could be due to a possible high variability in the EMG signal. However, this was not the case, for the EMG variability was small, as evidenced by the fact that the geometric mean of the coefficient of variation for the EMG of all the muscles studied in both monkeys was only 3.9%. Finally, the PSAL of each muscle was computed using the normalized magnitude of the EMG activity, and was statistically validated using the same bootstrap technique performed in the neural activity (see “[Materials and methods](#)”). A representative example is illustrated in Fig. 13. Only the pectoralis of monkey 2 showed a significant PSAL at a stimulus speed of 540 deg/s in the real motion condition; however, the same muscle did not show any effect in the other monkey. Overall, these analyses indicated that the EMG activity of shoulder, upper and forearm muscles during the task performance did not show the selective activation observed in a large group of cells in the motor cortex and area 7a in relation to motion condition, stimulus speed and stimulus angle position.

Discussion

The results of the present study documented strong neural responses to real and/or apparent motion in area 7a and motor cortex. Neurons in these two areas were modulated by the stimulus speed, the motion condition and some of them showed a preference to a particular part of the

circular trajectory of the stimulus. Nevertheless, as expected by their connectivity and functional properties, clear differences were observed between these areas, including weak responses to apparent motion in motor cortex, and the parallel location-time representation of the stimulus in area 7a. These issues and their functional implications will be discussed separately after some methodological considerations are reviewed.

Methodological considerations

The recording of neural activity in the present study was performed for all the isolated cells without customizing the stimulus parameters for the preferred speed, direction or receptive field position of each cell. This experimental strategy, therefore, is well suited to determine the role of neurons with different visual profiles in the representation of a particular stimulus in a more natural context. However, the exclusive use of CCW direction of travel of the stimuli precluded the possibility of studying the directional selectivity in neuronal discharge.

Real motion responses in motor cortex

The main finding in the motor cortex was that cells responded to real moving stimuli in the absence of a motor response. Previous studies have described motor cortical responses to stimuli moving passively across the visual field (Wannier et al. 1989; Merchant et al. 2001; Port et al. 2001). However, in those experiments rectilinear (Port et al. 2001; Wannier et al. 1989) or optic flow stimuli (Merchant et al. 2001) were used. To our knowledge, this is the first report of neural responses to circularly moving stimuli in the motor cortex.

We found that the motor cortical responses were modulated by the stimulus speed. In fact, we observed a group of cells that increased or decreased their firing rate as a function of the angular speed of the stimulus. In a preceding paper, it was found that the initial response of motor cortical neurons to a rectilinear moving target during an interception task was graded according to the initial target velocity (Lee et al. 2001). Therefore, the motor cortex can encode specific parameters of moving stimuli such as the stimulus speed. In addition, we found

that another parameter was represented in the activity of motor cortical cells, namely the stimulus angular position, to which neuronal activity was frequently tuned in the real motion condition.

An intriguing observation was the relatively few neuronal responses to apparent moving stimuli in the motor cortex. We assumed that in this condition there was a perceptual “reconstruction” of motion based on a sequence of stationary targets. In separate psychophysical experiments performed in nine human subjects, we observed that the detection threshold for apparent motion was 314 deg/s (ISI 223.3 ms; Merchant et al., unpublished observations). Taking into consideration the similarities in visual processing between human subjects and monkeys, it was possible that at speeds above 314 deg/s the monkeys perceived apparent motion. Be that as it may, the present findings suggest that the motor cortex had a limited access to static flashing dots information, at least in the absence of a motor response.

The motor cortex has been considered the main node in the generation and control of cortical motor output. A wealth of information supports this notion, including lesion studies in patients and nonhuman primates, as well as electrical stimulation and neurophysiological experiments (for reviews see Asanuma 1989; Porter and Lemon 1993). A current view postulates that the motor cortical activity is associated with static motor parameters, such as isometric force and limb position, under static behavioral situations, and to dynamic variables, such as change of force and limb velocity, under dynamic conditions (for review see Georgopoulos 1999). In this paper, we suggest that the motor cortex not only represents different motor parameters depending on context, but it can also process sensory information according to the behavioral value of this information. Kalaska and Crammond (1995) indicated that neurons in dorsal premotor cortex responded during the preparation and execution of movements towards stationary visual stimuli, but did not respond when the stimuli were presented passively in the absence of a motor response. In addition, it has been reported that motor cortical neurons respond to the direction of a stationary stimulus, but only when it is used as reaching target (Alexander and Crutcher 1990; Shen and Alexander 1997). In contrast, the present findings documented motor cortical responses to passive but moving visual stimuli. Thus it seems that the motor cortex has a differential access to visual information depending whether the stimulus is stationary or it is moving. We argue that the motor cortex has continuous access to visual motion information because of its ecological value (Gibson 1979). Moving objects with respect to a subject can potentially demand an immediate action towards them, in circumstances such as collision avoidance or interception (Lee 1976). It is possible that the moving stimuli in the current experiment might have triggered neural events in the motor cortex in preparation of an interceptive motor response, since both monkeys were also trained in the interception task (Merchant et al. 2003c). However, we believe that this is unlikely, since the neurons in motor

cortex responded during the real motion condition, and encoded the angular position and speed of the stimuli. In addition, only a small percentage of cells was tuned to both the direction of movement in the center→out task and the angular position of the real moving stimuli, and the angular difference between these two measures was not correlated in most of these cells. Finally, the analysis of EMG signal showed that the activity of various shoulder, upper and forearm muscles did not vary in relation to the motion condition, stimulus speed or stimulus angular position.

In conclusion, the location and speed of a moving target are important variables that need to be taken into account during diverse behavioral conditions, such as interception, catching and avoidance of moving objects. The present results suggest that these stimulus parameters may be represented in the activity of motor cortical ensembles during different behavioral contexts, even in the absence of a motor response towards the stimuli. It is likely that these neural signals are continuously available to the motor cortex in order to generate responses that demand immediate action.

Circular motion and area 7a

Area 7a forms part of the inferior parietal lobule and has been considered an association structure, in which sensory signals are integrated and sensorimotor transformations are taking place (Mountcastle 1995). This area contains several classes of neurons with diverse functional properties, including cells with visual responses (Mountcastle et al. 1975; Robinson et al. 1978; Motter et al. 1987). The results of the present study demonstrated that neurons in area 7a are activated by circularly moving stimuli, and that the activity of these neurons was modulated by the angular position and speed of real and apparent moving stimuli.

Visual neurons in area 7a respond to complex stimuli such as optic flow (Siegel and Read 1997; Merchant et al. 2001, 2003b), have large receptive fields, and are modulated by the attentional load of the visual stimuli (Mountcastle et al. 1981; Constantinidis and Steinmetz 2001a, 2001b). Thus, these properties indicate that a high degree of convergence and integration of visual motion information is taking place in this area. Indeed, due to its connectivity and physiology area 7a has been considered at the top level of the dorsal stream (Andersen et al. 1990; Felleman and Van Essen 1991). An example of the visual integrative properties of this area was characterized by Sakata and collaborators (Sakata et al. 1986, 1994). These authors recorded neurons in area 7a that responded to rotatory stimuli that moved in depth or in the frontoparallel plane. Most of these rotation-sensitive neurons had large receptive fields and showed an increase in discharge rate as a function of the stimulus angular speed. The present results confirm qualitatively these previous observations. We found neurons that showed a slight linear increase or decrease in their firing rate as a function of the angular speed. Similar observations have been reported for

rectilinear stimuli (Motter et al. 1987). In addition, it has been shown that area 7a neurons possess speed selectivity for optic flow (Phinney and Siegel 2000). Therefore, the parameter speed is represented in the activity of area 7a neurons, and can be used in conjunction with distance information to avoid collisions or intercept objects. Nevertheless, it is important to notice that the modulation in the cell responses by the stimulus speed in the present study is far weaker than the one observed in MT and MST (Lagae et al. 1994), although the range of speeds used here was limited.

The direction of moving stimuli is another parameter that is represented in the activity of area 7a neurons (Robinson et al. 1978; Motter and Mountcastle 1981; Siegel and Read 1997), including the direction of rotatory stimuli (Sakata et al. 1986, 1994). In this paper, we used only stimuli moving CCW, and consequently we could not test the directionality of the cells. However, within the CCW domain, we found that the angular position of the stimulus was another important parameter that influenced neural activity in area 7a. Although the PSALs were computed based on stimulus position, the possibility cannot be ruled out that the positional tuning observed might not have been due to a directional selectivity to rectilinear stimulus motion. Be that as it may, the distributed selectivity of the cells to a particular portion of the circular trajectory of the stimulus, in combination with the modulation of neuronal activity by the stimulus speed, would be sufficient for the specification of the position of the stimulus over time, i.e., the stimulus trajectory. This could be achieved, for example, using a population vector code. This information could then be used in intercepting or avoiding circularly moving stimuli (Merchant et al. 2003c).

Receptive fields in area 7a

There is a gradual increase in the receptive field (RF) size from V1 through V5 (for review see Zeki 1993). At the highest levels of the dorsal stream hierarchy, such as area 7a, the receptive fields are quite large and often bilateral (Robinson et al. 1978; Motter and Mountcastle 1981; Andersen et al. 1990). The initial idea was that the receptive field structure was based entirely on the anatomical inputs, and the increase in receptive field size was the result of convergent inputs from increasingly larger receptive fields. However, it has been demonstrated that the receptive field structure is profoundly affected by the spatial and temporal context in which a stimulus is presented, even in V1 (Maffei and Fiorentini 1976; Hammond and McKay 1975; Gulyás et al. 1987; Worgotter and Eysel 2000). In area 7a the size and structure of RFs are clearly determined by the attentional state of the monkey (Mountcastle et al. 1981) and the angle of gaze (Andersen and Mountcastle 1983), questioning the value of the RF concept as a “passive” property of the cells in an association area. Furthermore, the structure and location of the RFs in area 7a depend on the

parameters and the temporal succession of the stimuli used to map them (Motter and Mountcastle 1981; Motter et al. 1987). We found that the RFs could change in size and location depending on the optic flow stimuli used during the mapping task (see also Merchant et al. 2001). In addition, the relation between PSAL and RF position varied across the population of neurons in area 7a, ranging from a perfect overlap between the two measures to cells that showed no overlap, or in which the RF included all the circular trajectory of the stimulus. Therefore, even though it is possible that some of the PSAL depend on the relation in position between the RF and stimulus, it is likely that the PSAL is the result of the dynamic structure of neural responses in area 7a to the spatial characteristic of the stimulus. The mechanism underlying this new type of cell tuning may depend on feed-forward inhibition generated locally within the parietal cortex, as observed in opponent vector organization (Motter et al. 1987). This feed-forward inhibition, characterized using testing stimuli with different trajectory lengths, preceded the stimulus for 10–20 DVA, lasted for hundreds of milliseconds, and was relatively independent of the receptive field and stimulus speed (Motter et al. 1987). As we discuss in the next section, inhibition is also responsible for direction and speed selectivity, strengthening our hypothesis. Further experiments using conditioning-test paradigms are needed to determine whether this dynamic inhibitory process is shaping the angular position selectivity during the circular trajectory of the stimulus.

Neural mechanism of path-guided apparent motion in area 7a

In a series of pioneering studies, Wurtz and collaborators established the relation between the spatial and temporal intervals of stroboscopic stimuli and the directional selectivity of MT neurons (Mikami et al. 1986a, 1986b; Newsome et al. 1986). The most common mechanism of direction selectivity was a large suppression of discharge when successive stimuli were presented in the null direction of the cells, with low spatial and temporal interflash intervals. In addition, an inhibitory mechanism contributed to the speed tuning in this area. Nevertheless, a key observation was that given a constant speed the minimum spatial interval necessary to produce direction selective responses was very close to the psychophysical threshold to detect apparent motion in human subjects under the same experimental conditions (Newsome et al. 1986). These findings have been partially confirmed using random dot displays in a recent study (Churchland and Lisberger 2001).

It may be emphasized that in the present paper we utilized path-guided apparent motion, an illusion characterized by Shepard and Zare (1983). They demonstrated that the minimum interstimulus interval needed to perceive apparent motion increases as a function of the length of a low contrast path connecting the flashing dots. A major finding in the present results was that a group of area 7a

neurons responded similarly to both real and path-guided apparent circular motion. The neurons were selective to the angular position of the stimulus in both motion conditions. Nevertheless, this neural population was quite sensitive to the stimulus speed in the apparent motion condition, in that all reached similar responses to the real motion condition only in the fastest speeds of the apparent moving situation. In fact, 420 deg/s (ISI: 173 ms) was the minimum stimulus speed necessary for a similar population response in the apparent motion condition. In addition, the number of neurons tuned to angular position also increased as a function of the stimulus speed. In psychophysical experiments performed in nine human subjects, we observed that the detection threshold for apparent motion was 314 deg/s (ISI 223.3 ms; Merchant et al., unpublished observations). These values are similar to those obtained from the neural results above.

Although this is the first report of a single cell neural correlate of path-guided apparent motion in the posterior parietal cortex, recent studies have emphasized the role of the posterior parietal cortex in apparent motion perception. For example, using functional MRI it was found that not only the occipitotemporal junction (hMT+/V5), but also the superior and inferior parietal cortex are activated during perception of circular motion in the “spinning wheel illusion” (Sterzer et al. 2002). In addition, it was reported recently that the lateral intraparietal area in the PPC showed responses that are tightly linked to the perception of apparent motion (Williams et al. 2003). Furthermore, it was demonstrated that lesions in the right parietal cortex of human patients produce a bilateral deficit for apparent motion perception, as well as an hemilateral neglect with marked problems in visuospatial and attentional processes (Batelli et al. 2001). Since these lesions do not produce impairments in the direction discrimination of visual motion, it was suggested that the perception of apparent moving stimuli depends on a high-level system that includes the parietal cortex and depends on attention mechanisms (Batelli et al. 2001). Indeed, psychophysical experiments indicated that a low-level motion system is independent of a high-level system mediated by attention (Cavanagh 1992). The low level system is passive, effortless, is based on speed changes, and probably depends on early visual cortices including MT, whereas the high level system is based on position signals (Seiffert and Cavanagh 1998; Lu and Sperling 2001). Thus, it is highly justified to suggest that the position-selective responses in area 7a are part of a high level neural mechanism underlying (1) the rapid deployment of transient attention to the discrete sequential flashes of the stimuli, and (2) the integration of this information for the perception of path-guided apparent motion.

Time intervals and area 7a

We found a population of area 7a neurons with selective activity during the apparent motion condition that responded periodically to the flashing dots. These neurons

showed significant harmonics at the ISI frequencies in the spectral analysis. The nature of these responses may be linked to the speed sensitivity of neurons to develop directional or angular location specific responses, and then may be the result of a simple passive visual property of neurons in this area. For instance, the directional responses in MT neurons to apparent motion depend on the spatial separation of the stimuli, the ISI and the preferred speed of the cells (Mikami et al. 1986a; Churchland and Lisberger 2001). MT neurons with high preferred speeds develop directional selective responses at a stimulus spatial and temporal separations that are higher than those observed in neurons with low preferred speeds (Churchland and Lisberger 2001). Thus it can be hypothesized that the neurons in area 7a with responses to the flashing dots might have been selective to stimulus speeds lower than those used in the present study, and consequently their responses were fragmented. However, this is not very likely, since area 7a neurons were just slightly modulated by the stimulus speed. In addition, these neurons showed periodic activity during apparent motion, but did not respond during real motion. Alternatively, it is possible that the periodic neurons may be involved in time perception and behavioral operations that are time-dependent. In fact, the successive onset and offset of nearby flashes not only induce the illusion of apparent motion, but also create a temporal framework where time intervals can be perceived and used to drive the subject behavior (Merchant et al. 2003c). This is particularly true in the present experiment for the following reasons: (1) the ISIs used were in the range of intervals that can be resolved in time by human subjects (100–1,000 ms; Wing and Kristofferson 1973; Getty 1975; Ivry and Hazeltine 1995), and probably also by monkeys; (2) the ISI varied across speeds, but the space between the flashing dots and the length of the low contrast path were constant; and (3) in a previous paper we demonstrated that during interception of path-guided apparent motion stimuli, the variable that was better represented in the activation profile of area 7a neurons was the time-to-contact, not the target position (Merchant et al. 2003c).

Altogether, our results demonstrated the presence of two overlapping populations of neurons in area 7a. One population is modulated by the angular location of a circularly moving stimulus and also responded in the apparent motion situation at stimulus speeds that produce a compelling motion percept in humans. The second population was selective for apparent motion stimuli and showed a periodic entrainment of activation with the same period of the ISI of the flashing dots.

Acknowledgements This work was supported by United States Public Health Service grant PSMH48185, the United States Department of Veterans Affairs, and the American Legion Brain Sciences Chair.

References

- Alexander GE, Crutcher MD (1990) Neural representations of the target (goal) of visually guided arm movements in three motor areas of the monkey. *J Neurophysiol* 64:164–178
- Andersen RA, Mountcastle VB (1983) The influence of the angle of gaze upon the excitability of the light-sensitive neurons of the posterior parietal cortex. *J Neurosci* 3:532–548
- Andersen RA, Asanuma C, Essick G, Siegel RM (1990) Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. *J Comp Neurol* 296:65–113
- Asanuma H (1989) *The motor cortex*. Raven Press, New York
- Battaglia-Mayer A, Ferraina S, Genovesio A, Marconi B, Squatrito S, Molinari M, Lacquaniti F, Caminiti R (2001) Eye-hand coordination during reaching. II. An analysis of the relationships between visuomanual signals in parietal cortex and parieto-frontal association projections. *Cereb Cortex* 11:528–544
- Battelli L, Cavanagh P, Intriligator J, Tramo MJ, Henaff MA, Michel F, Barton JJ (2001) Unilateral right parietal damage leads to bilateral deficit for high-level motion. *Neuron* 32:985–995
- Bloomfield P (2000) *Fourier analysis of time series: an introduction*. John Wiley & Sons, New York
- Caminiti R, Ferraina S, Mayer AB (1998) Visuomotor transformations: early cortical mechanisms of reaching. *Curr Opin Neurobiol* 8:753–761
- Cavanagh P (1992) Attention-based motion perception. *Science* 257:1563–1565
- Churchland MM, Lisberger SG (2001) Shifts in the population response in the middle temporal visual area parallel perceptual and motor illusions produced by apparent motion. *J Neurosci* 21:9387–9402
- Constantinidis C, Steinmetz MA (2001a) Neuronal responses in area 7a to multiple stimulus displays: II. Responses are suppressed at the cued location. *Cereb Cortex* 11:592–597
- Constantinidis C, Steinmetz MA (2001b) Neuronal responses in area 7a to multiple-stimulus displays: I. Neurons encode the location of the salient stimulus. *Cereb Cortex* 11:581–591
- Cox DR, Lewis PAW (1978) *The statistical analysis of series of events—monographs on applied probability and statistics*. Chapman and Hall, London
- Felleman DJ, Van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cereb Cortex* 1:1–47
- Georgopoulos AP (1999) News in motor cortical physiology. *News Physiol Sci* 14:64–68
- Getty DJ (1975) Discrimination of short temporal intervals: a comparison of two models. *Percept Psychophys* 18:1–8
- Gibson JJ (1979) *The ecological approach to visual perception*. Houghton Mifflin, Boston
- Gulyás B, Orban GA, Duysens J, Maes H (1987) The suppressive influence of moving textured backgrounds on responses of cat striate neurons to moving bars. *J Neurophysiol* 57:1767–1791
- Hammond P, McKay DM (1975) Differential responses of cat visual cortical cells to textured stimuli. *Exp Brain Res* 22:427–430
- Ivry RB, Hazeltine RE (1995) Perception and production of temporal intervals across a range of durations: evidence for a common timing mechanism. *J Exp Psychol Hum Percept Perform* 21:3–18
- Kalaska JF, Crammond DJ (1995) Deciding not to GO: neuronal correlates of response selection in a GO/NOGO task in primate premotor and parietal cortex. *Cereb Cortex* 5:410–428
- Lagae L, Maes H, Raiguel S, Xiao DK, Orban GA (1994) Responses of macaque STS neurons to optic flow components: a comparison of areas MT and MST. *J Neurophysiol* 71:1597–1626
- Lee DN (1976) A theory of visual control of braking based on information about time-to-collision. *Perception* 5:437–459
- Lee D, Port NL, Kruse W, Georgopoulos AP (2001) Neuronal clusters in the primate motor cortex during interception of moving targets. *J Cogn Neurosci* 13:319–331
- Lu ZL, Sperling G (2001) Three-systems theory of human visual motion perception: review and update. *J Opt Soc Am A Opt Image Sci Vis* 18:2331–2370
- Lurito JT, Georgakopoulos T, Georgopoulos AP (1991) Cognitive spatial-motor processes. 7. The making of movements at an angle from a stimulus direction: studies of motor cortical activity at the single cell and population levels. *Exp Brain Res* 87:562–580
- Maffei L, Fiorentini A (1976) The unresponsive regions of visual cortical receptive fields. *Vision Res* 16:1131–1139
- Mardia KV (1972) *Statistics of directional data*. Academic, London
- Merchant H, Battaglia-Mayer A, Georgopoulos AP (1999) Interception of real and path-guided apparent moving targets: neural mechanisms in parietal cortex. *Soc Neurosci Abs* 25:380
- Merchant H, Battaglia-Mayer A, Georgopoulos AP (2001) Effects of optic flow in motor cortex and area 7a. *J Neurophysiol* 86:1937–1954
- Merchant H, Battaglia-Mayer A, Georgopoulos AP (2003a) Interception of real and apparent motion targets: psychophysics in humans and monkeys. *Exp Brain Res* (in press)
- Merchant H, Battaglia-Mayer A, Georgopoulos AP (2003b) Functional organization of parietal neuronal responses to optic flow stimuli. *J Neurophysiol* 90:675–682
- Merchant H, Battaglia-Mayer A, Georgopoulos AP (2003c) Neural responses during interception of real and apparent circularly moving targets in motor cortex and area 7a. *Cereb Cortex* (in press)
- Mikami A (1991) Direction selective neurons respond to short-range and long-range apparent motion stimuli in macaque visual area MT. *Int J Neurosci* 61:101–112
- Mikami A, Newsome WT, Wurtz RH (1986a) Motion selectivity in macaque visual cortex. II. Spatiotemporal range of directional interactions in MT and V1. *J Neurophysiol* 55:1328–1339
- Mikami A, Newsome WT, Wurtz RH (1986b) Motion selectivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. *J Neurophysiol* 55:1308–1327
- Motter BC, Mountcastle VB (1981) The functional properties of the light-sensitive neurons of the posterior parietal cortex studied in waking monkeys: foveal sparing and opponent vector organization. *J Neurosci* 1:3–26
- Motter BC, Steinmetz MA, Duffy CJ, Mountcastle VB (1987) Functional properties of parietal visual neurons: mechanisms of directionality along a single axis. *J Neurosci* 7:154–176
- Mountcastle VB (1995) The parietal system and some higher brain functions. *Cereb Cortex* 5:377–390
- Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C (1975) Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *J Neurophysiol* 38:871–908
- Mountcastle VB, Andersen RA, Motter BC (1981) The influence of attentive fixation upon the excitability of the light-sensitive neurons of the posterior parietal cortex. *J Neurosci* 1:1218–1225
- Newsome WT, Mikami A, Wurtz RH (1986) Motion selectivity in macaque visual cortex. III. Psychophysics and physiology of apparent motion. *J Neurophysiol* 55:1340–1351
- Phinney RE, Siegel RM (2000) Speed selectivity for optic flow in area 7a of the behaving macaque. *Cereb Cortex* 10:413–421
- Port NL, Pellizzer G, Georgopoulos AP (1996) Intercepting real and path-guided apparent motion targets. *Exp Brain Res* 110:298–307
- Port NL, Kruse W, Lee D, Georgopoulos AP (2001) Motor cortical activity during interception of moving targets. *J Cogn Neurosci* 13:306–318
- Porter R, Lemon R (1993) *Corticospinal function and voluntary movement*. Clarendon Press, Oxford
- Read HL, Siegel RM (1997) Modulation of responses to optic flow in area 7a by retinotopic and oculomotor cues in monkey. *Cereb Cortex* 7:647–661

- Richmond BJ, Optican LM (1987) Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex. II. Quantification of response waveform. *J Neurophysiol* 57:147–161
- Robinson DL, Goldberg ME, Stanton GB (1978) Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. *J Neurophysiol* 41:910–932
- Sakata H, Shibutani H, Ito Y, Tsurugai K (1986) Parietal cortical neurons responding to rotary movement of visual stimulus in space. *Exp Brain Res* 61:658–663
- Sakata H, Shibutani H, Ito Y, Tsurugai K, Mine S, Kusunoki M (1994) Functional properties of rotation-sensitive neurons in the posterior parietal association cortex of the monkey. *Exp Brain Res* 101:183–202
- Schwartz AB, Kettner RE, Georgopoulos AP (1988) Primate motor cortex and free arm movements to visual targets in three-dimensional space. I. Relations between single cell discharge and direction of movement. *J Neurosci* 8:2913–2927
- Seiffert AE, Cavanagh P (1998) Position displacement, not velocity, is the cue to motion detection of second-order stimuli. *Vision Res* 38:3569–3582
- Shen L, Alexander GE (1997) Neural correlates of a spatial sensory-to-motor transformation in primary motor cortex. *J Neurophysiol* 77:1171–1194
- Shepard RN, Zare SL (1983) Path-guided apparent motion. *Science* 220:632–634
- Shimshoni M (1971) On Fisher's test of significance in harmonic analysis. *Geophys J R Astr Soc* 23:373–377
- Siegel RM, Read HL (1997) Analysis of optic flow in the monkey parietal area 7a. *Cereb Cortex* 7:327–346
- Snedecor GW, Cochran WG (1989) *Statistical methods*. The Iowa State University Press, Ames
- Sterzer P, Russ MO, Preibisch C, Kleinschmidt A (2002) Neural correlates of spontaneous direction reversals in ambiguous apparent visual motion. *Neuroimage* 15:908–916
- Tukey JW (1977) *Exploratory data analysis*. Addison Wesley, Reading
- Wannier TM, Maier MA, Hepp-Reymond MC (1989) Responses of motor cortex neurons to visual stimulation in the alert monkey. *Neurosci Lett* 98:63–68
- Williams ZM, Elfar JC, Eskandar EN, Toth LJ, Assad JA (2003) Parietal activity and the perceived direction of ambiguous apparent motion. *Nat Neurosci* 6:616–623
- Wing AM, Kristofferson AB (1973) Response delays and the timing of discrete motor responses. *Percept Psychophys* 14:5–12
- Worgotter F, Eysel UT (2000) Context, state and the receptive fields of striatal cortex cells. *Trends Neurosci* 23:497–503
- Zeki S (1993) *Vision of the brain*. Blackwell Science, London