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RESEARCH ARTICLES

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Participation of primary motor cortical neurons in a distributed network during maze solution: representation of spatial parameters and time-course comparison with parietal area 7a

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Abstract Traditionally, primary motor cortex (M1) has been thought to be involved solely in planning and generating movements. Recent evidence suggests that the arm area of M1 plays a role in other functions, such as the representation of serial order (Pellizzer et al. 1995, Science 269:702–705; Carpenter et al. 1999, Science 283:1752–1757) and spatial processing (Georgopoulos et al. 1989, Science 243:234–236). Previous studies of such cognitive processes have used tasks in which a directed arm movement was required, raising a question as to whether this brain area is involved in cognitive processing per se, or whether such cognitive signals may be gated into the arm area of M1 only when arm movements are required. To study this question, we developed a task that required a spatial analysis of a complex visual stimulus, but required no arm movement as a response. In this task, monkeys were shown an octagonal maze. After an imposed delay of 2 to 2.5 s, they indicated whether a path that emanated from the center of the maze exited at the perimeter (exit maze) or terminated within the maze (no-exit maze) by pressing a pedal with their left or right foot, respectively. We recorded from 785 cells from the arm area of M1 from two monkeys during the delay period of the maze task. We found that cell activity was influenced by both the exit status and the direction of the path, beginning soon after the maze was displayed. This activity was not related to the activation of arm muscles, suggesting that the directional signals observed represented abstract spatial aspects of maze processing. Finally, we compared maze-related activity of M1 neurons with those recorded from posterior parietal area 7a, reported previously (Crowe et al. 2004). Interestingly, cells from each area exhibited similar properties. Both the exit status and path direction were encoded by cells in M1 and 7a, although to different extents. An analysis of the time-course of the neural representation of these factors revealed that area 7a and M1 begin to encode these factors at the same time, suggesting these brain areas are part of a distributed system performing the spatial computations involved in maze solution.

Keywords Motor cortex · Spatial cognition · Area 7a · Maze solving

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Introduction

Many brain areas associated with sensorimotor function have also been linked to cognitive aspects of sensory-motor transformations. For example, signals related to working memory are found in both the principalis region of prefrontal cortex (Goldman-Rakic 1987) and in the lateral intraparietal area (LIP) (Gnadt and Andersen 1988), where cells respond to visual cue stimuli and discharge before, during, and after saccades (Barash et al. 1991). The posterior parietal cortex (Lynch et al. 1977; Robinson et al. 1978), the frontal eye fields (Moore and Fallah 2001), and the superior colliculus (Kustov and Robinson 1996) are sensorimotor areas thought to be involved in visual attention. Cognitive signals such as these, however, do not seem to be restricted to the middle of a sensory to motor hierarchy. For example, attentional effects are well documented in visual area V4 (Moran and Desimone 1985), and have also been shown to exist in premotor cortex (Lebedev and Wise 2001). Additionally, several motor areas are implicated in the production and learning

(Hikosaka et al. 1999; Tanji 2001) of movement sequences. Recently, even primary sensory and motor areas in the brain have been associated with cognitive processes, suggesting that cells involved in some aspects of cognition are distributed throughout the brain. For example, the activity of cells in V1 has been shown to relate to visual attention (Motter 1993; Roelfsema et al. 1998; Ito and Gilbert 1999). The primary motor cortex, too, has been shown to be involved in cognitive operations (Georgopoulos 2000). Cells in the arm area of M1 encode the serial order of potential movement targets in a memory-scanning task (Pellizzer et al. 1995; Carpenter et al. 1999). In addition, neurons in this area also reflect the spatial transformation involved in mental rotation (Georgopoulos et al. 1989; Lurito et al. 1991). Given the existence of cognitive and spatial signals seen in the arm area of M1, an interesting question is to what extent activity in this area would relate to such high-level signals in a task requiring no arm movements whatsoever. We studied this question using a visual maze task, the solution of which involved spatial processing without requiring a directed arm movement as a response. In this task, monkeys performed a covert analysis of a visual maze stimulus in order to determine whether a single path reached an exit or a blind-ending. In previous studies, we obtained evidence that humans and monkeys solved the task by covertly analyzing successive portions of the maze path from its start to its end, a time-consuming process that was systematically related to the length of the path processed and the number of turns it contained (Crowe et al. 2000; Chafee et al. 2002).

Materials and methods

Animals

Two male monkeys (*Macaca mulatta,* 5 and 7 kg bodyweight, designated KK and PP) were used. Animal care conformed to the principles outlined in the *Guide for Care and Use of Laboratory Animals* (US National Institutes for Health publication no. 85-23, revised 1985). The experiments were approved by the appropriate local ethics committees.

Maze task

A trial began when the monkey's eye position was within 1.5 degrees of visual angle (DVA) from a central fixation target. After a variable interval of 600 to 840 ms, an octagonal maze (Fig. 1) was displayed on a liquid crystal display projection screen at eye level directly in front of the monkey. The maze was composed of white lines (separated by 2.7 DVA) on a black background and subtended 30×30 DVA. It contained a central start box and a straight path extending outwards from the start box in one of eight radial directions. This path either extended to the perimeter of the maze (Fig. 1, 'exit' mazes) or terminated one path width (2.7 DVA) from the perimeter of the maze (Fig. 1, 'no-exit' mazes). Maze fragments in the remaining interior area of the maze were randomly generated. Since there was a gap in the perimeter of the maze for an exit path, two more such gaps (for a total of three) were added at random locations in the perimeter to ensure that the monkeys could not solve the maze based on the presence of a gap. In the case of a no-exit maze, three gaps were randomly added to the maze perimeter to keep the number of gaps constant across exit and no-exit mazes. After a 2–2.5 s variable delay, the fixation target dimmed ('go' signal), and the monkeys indicated whether or not the path exited the maze by pressing one of two pedals with their left or right foot, respectively. The monkey depressed the pedal for 300 ms, after which it was given a juice reward for a correct trial or white noise was sounded for an incorrect trial. If the monkey's eye position deviated 1.5 DVA or more from the fixation target from the time of initial fixation to reward, the trial was aborted. For each set of M1 cells recorded, monkey KK performed 240 correct trials, and monkey PP performed 160 correct trials. These trials were equally divided between exit and no-exit mazes (120 and 80 trials of each type for monkeys KK and PP, respectively), and also between the eight possible path directions (half exit, half no-exit). A new set of mazes was randomly generated before each day of neural recording. For each set of area 7a cells recorded, both monkeys performed 160 correct trials, divided as above. The order of presentation of mazes with different directions and exit statuses was random.

Experimental setup

Eye position was monitored using the scleral search coil (CNC Engineering, Seattle, WA, USA) technique in monkey KK (Fuchs and Robinson 1966), and an infrared eye tracking system (ISCAN, Burlington, MA, USA) in monkey PP. The horizontal and vertical components of the eye position were recorded at a sampling rate of 200 Hz (eye coil) or 60 Hz (infrared eye tracking system) simultaneously with neural recordings. We recorded the extracellular signals of neuronal activity using seven (monkey KK) and 16 (monkey PP) independently-driven microelectrodes (Mountcastle et al. 1991; Lee et al. 1998) (Uwe Thomas Recording, Marburg, Germany). Electromyographic (EMG) activity was recorded while the monkeys performed the maze task, separately from neural recordings. The monkeys were first sedated with ketamine. Then, Teflon-coated, multi-stranded stainless steel wire pairs were inserted approximately 1 cm apart into each muscle recorded. The electrical

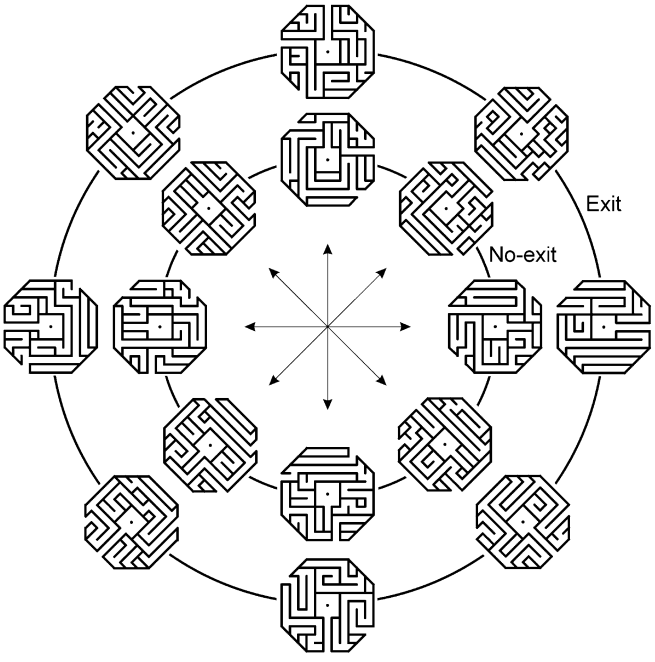

Fig. 1 Examples of mazes used during neural recordings. Maze paths could be in one of eight directions, and could be either an exit maze (*outer circle*) or a no-exit maze (*inner circle*). One maze was shown at a time. The monkeys maintained fixation throughout the trial at the fixation spot in the center of the maze

signal was amplified, filtered, and rectified using a Neurodata Acquisition System 12 (Grass Instrument Co., Quincy, MA, USA) and collected at 200 Hz with a DAS8 analog-to-digital conversion board (RMS Instruments, Mississauga, ON, Canada). From monkey KK we recorded the activity of four muscles contralateral to the recording chambers, including latissimus dorsi, triceps, medial deltoid, and pectoralis. We recorded the EMG activity of seven muscles from monkey PP, including biceps, triceps, forearm flexor, forearm extensor, pectoralis, trapezius, and medial deltoid. Monkey KK solved 480 mazes (60 of each direction, half exit, half no-exit) during EMG recording. Monkey PP solved 240 mazes (30 of each direction, half exit, half no-exit).

Recording locations

Area 7a and M1 recording locations were initially verified by magnetic resonance imaging after chamber implantation (Fig. 2). Chamber placements in the arm area of motor cortex were confirmed with microstimulation. We stimulated with one electrode at a time, using a train of 200-μs biphasic pulses at 330 Hz for 60 ms generated from a BAK stimulator (BAK, Germantown, MD, USA). Figure 3 shows the locations of stimulation sites and the muscles activated. All muscles were activated using current strength between 5 and 40 μA. Finally, the recording locations were confirmed after the monkeys were killed and the brains removed. The recording locations of cells in area 7a have been described previously (Crowe et al. 2004).

Results

We recorded the impulse activity of 785 cells from the arm area of the motor cortex and 1200 cells from area 7a in two monkeys during the delay period of the maze task. We recorded activity from all active cells encountered, with no pre-selection. Figure 4 shows rasters of a cell recorded from monkey KK. The direction of the maze path is indicated by the arrows in the center of the figure, pointing to each raster. Interestingly, the discharge rate varied as a function of both the direction and exit status of the path (only no-exit mazes are shown). To test whether cells in the arm area of motor cortex were significantly related to these aspects of the maze stimulus, we performed a factorial analysis of covariance (ANCOVA) using the activity of each cell during the delay as the dependent variable. Path direction (k=8 directions), path exit status (exit or no-exit, k=2) were the factors. We used the time of recording and the pretrial cell activity as covariates to account for possible time trends and changes in baseline firing, respectively. The level of statistical significance was set at α=0.05. We found that cell activity during the delay period was influenced both by the direction of the main path and by the exit status of the path, as follows: 105/785 (13%) showed a significant main effect of direction, 345/785 (44%) showed a significant main effect of exit status, and 81/785 (10%) showed a significant direction-by-exit interaction. This same analysis has been carried out on the activity of 1200 cells recorded from area 7a of the posterior parietal cortex during maze solution (Crowe et al. 2004). A comparison of the results of this analysis for M1 and area 7a is shown in Table 1.

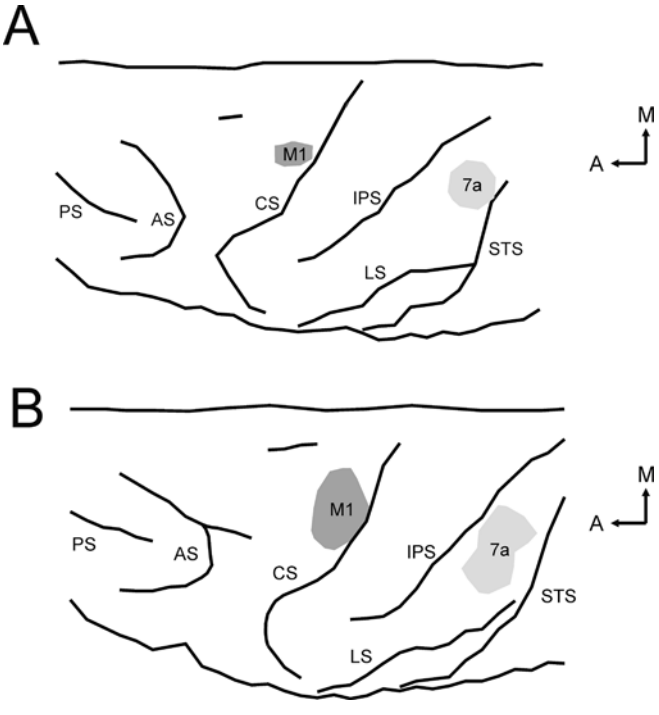

Fig. 2A, B Recording locations in M1 (*dark gray*) and area 7a (*light gray*) from monkey KK (**A**) and monkey PP (**B**). *PS* Principal sulcus, *AS* arcuate sulcus, *CS* central sulcus, *IPS* intraparietal sulcus, *LS* lateral sulcus, *STS* superior temporal sulcus

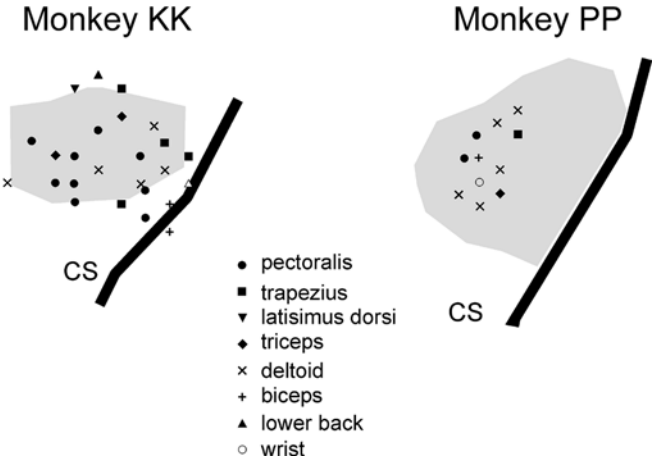

Fig. 3 Microstimulation sites in primary motor cortex (M1) of the two monkeys. *CS* Central sulcus

Table 1 Comparison of cell activity for M1 and area 7a during the delay period in the maze task. Factorial ANCOVA was performed using the activity of each cell during the delay as the dependent variable. The factors were path direction (eight directions), and path exit status (exit or no-exit)

Factors	Significant cells	
	M1	Area 7a
Direction	13% (105/785)	44% (529/1200)
Exit	44% (345/785)	22% (262/1200)
Direction × exit	10% (81/785)	29% (345/1200)

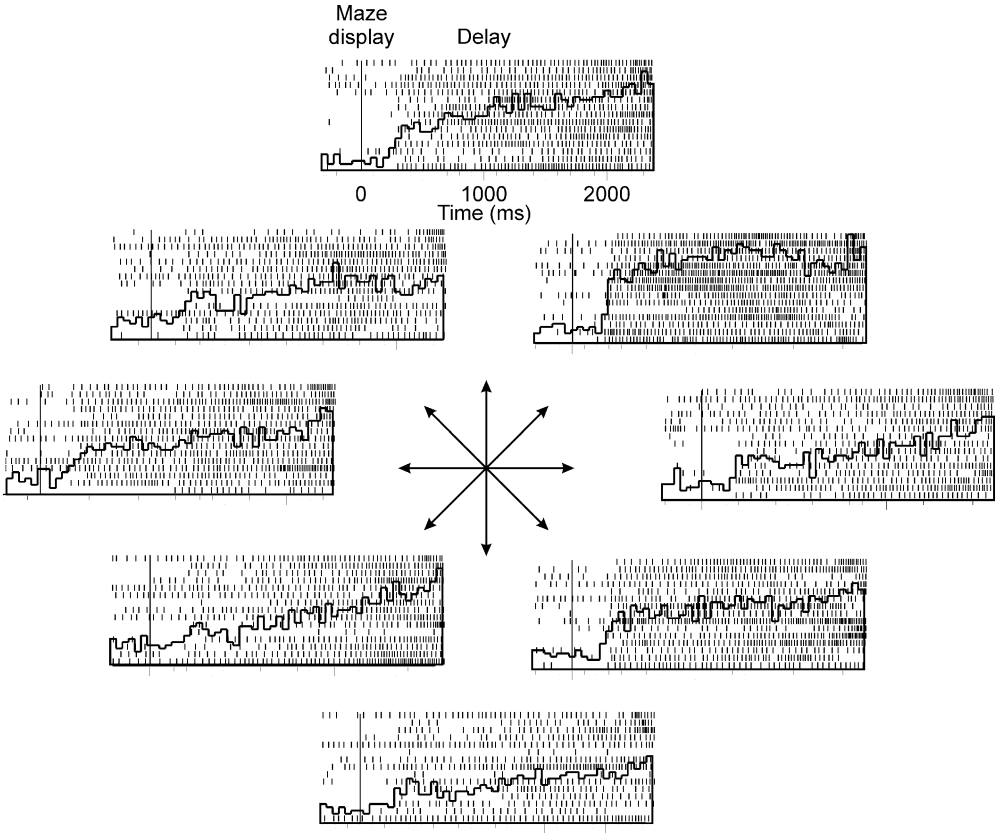

Fig. 4 Example of M1 neuron from monkey KK (no-exit mazes). Rasters and histograms are aligned to maze onset, indicated by the vertical bar at time zero. The eight directions of *center arrows* denote the direction of the maze path

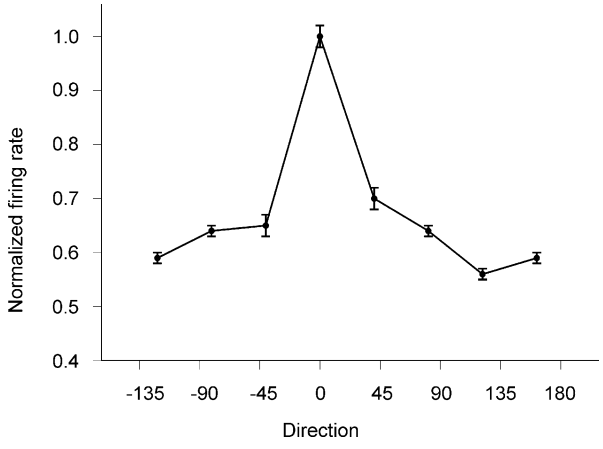

Fig. 5 Population tuning of M1 neurons for maze path direction. First, each cell's tuning curve (mean rate at each of the eight path directions) was normalized to its maximum rate. Then, all tuning curves were realigned to each cell's preferred direction, and were averaged across cells to produce the population curve shown. The population included all neurons whose activity was significantly tuned to path direction. Data points are means ±SEM (N=43)

To determine whether the directional signal shown above could be explained by muscle activity, we recorded EMG activity from arm muscles during the delay period of the maze task. The monkeys made no visible arm movements during any part of the task, and the EMG traces rarely showed any activation during the delay period. A *t*-test performed on this activity showed that no muscle recorded varied significantly from baseline during the delay period. However, in case muscle activity was somehow modulated in an orderly fashion up and down from baseline with maze parameters, we performed the above ANCOVA on EMG activity of the delay period, using twice as many trials as in the case of the neural recording to increase the test's sensitivity. This analysis revealed no significant effect of direction on the activity of any muscle recorded. Two muscles were significant for exit status: the right pectoralis muscle of monkey KK was active more for no-exit mazes, and the right latissimus dorsi of monkey KK was more active for exit mazes. Given that the maze task required no arm movements, that monkeys' response was a mono-directional foot-press, and the results of the EMG controls, we believe that the directional signals in M1 during the delay period represent a spatial process applied to the maze in its solution.

Next, we tested whether changes in cell activity varied in an orderly fashion with path direction by performing a tuning analysis on those cells that showed a significant main effect of direction in the above ANCOVA. To do this, we regressed the delay period activity against the x–y components of the direction of the maze path, as described previously for the direction of movement (Georgopoulos et al. 1982). Of the 105 cells with significant main effect of direction in the ANCOVA, 43 (41%) were significantly tuned (α=0.05). The cell displayed in Fig. 4 is an example of a tuned cell. We constructed a population tuning curve by first standardizing individual cell-tuning curves to their maximum rate, and then aligning their peaks and averaging them. The average population-tuning curve for

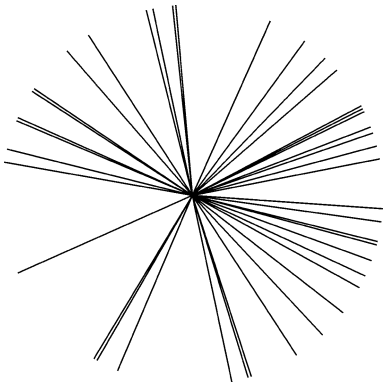

Fig. 6 Preferred directions of 43 motor cortical cells tuned to path direction. Each *radial line* represents a tuned cell, pointing in the cell's preferred direction

these cells is shown in Fig. 5. Cell's preferred directions were distributed throughout all 360 degrees (Fig. 6), and were marginally skewed toward the left (mean resultant 26°, $p \approx 0.06$, bootstrap test, see Lurito et al. 1991). These tuning results demonstrate the orderly involvement of the arm area of motor cortex in the maze task. By comparison, 53% (280/529) of directionally significant area 7a cells were significantly tuned (Crowe et al. 2004).

In a final series of analyses, we examined the time-course of neural activity of cells in both M1 and in parietal area 7a, whose relationship to maze parameters has been described previously (Crowe et al. 2004). Figure 7 (*solid line*) shows the population time-course of all 105 directionally selective M1 cells, recorded on trials with maze paths in each cell's preferred direction (of the eight radial path directions). Activity increased immediately after maze display, peaking at approximately 300 ms. By about 600–700 ms, the activity returned to baseline. This time-course of activity is nearly identical to that of directionally selective cells in area 7a of parietal cortex (Fig. 7, *dashed line*). Finally, we wished to determine the time-course of the neural representation of path direction and exit status, hypothesizing that the direction would be encoded first, and then, after the spatial analysis had reached the maze perimeter, the exit status would be encoded. To test this hypothesis, we performed the above ANCOVA in consecutive 50-ms bins, starting at maze onset, through 600 ms of the delay. We then plotted the percentage of significant cells in each bin as a function of time (Fig. 8, *dashed lines*). We found that the effects of path direction and exit were temporally dissociated: the directional effect appeared first (Fig. 8A), shortly after maze onset, and the exit effect appeared later (Fig. 8B). Interestingly, these path parameters began to be encoded at about the same time in M1 and area 7a.

Discussion

Recent experiments have shown the arm area of primary motor cortex to be involved in cognitive processing in tasks requiring a directed arm movement. We sought to test whether this brain area is involved in such processing in a task that required no arm movements whatsoever. Indeed, we found that neural activity in M1 varied with specific spatial aspects of the maze stimulus, in the absence of movement. The maze-related properties of cells with such activity were similar to those of cells in parietal area 7a.

Representation of exit status

We found that a large number of cells discharged differentially for exit versus no-exit mazes. Predominantly, these cells fired more for no-exit mazes, which required a right foot (contralateral to the recording site) pedal press. M1 cells begin to represent this variable early in the delay period (Fig. 8B, *dashed line*). Because the exit status was confounded with the foot used in the response (i.e., the right foot was always used for no-exit mazes), it is difficult to say whether this signal is related to some process involved in the exit/no-exit decision or simply reflects the

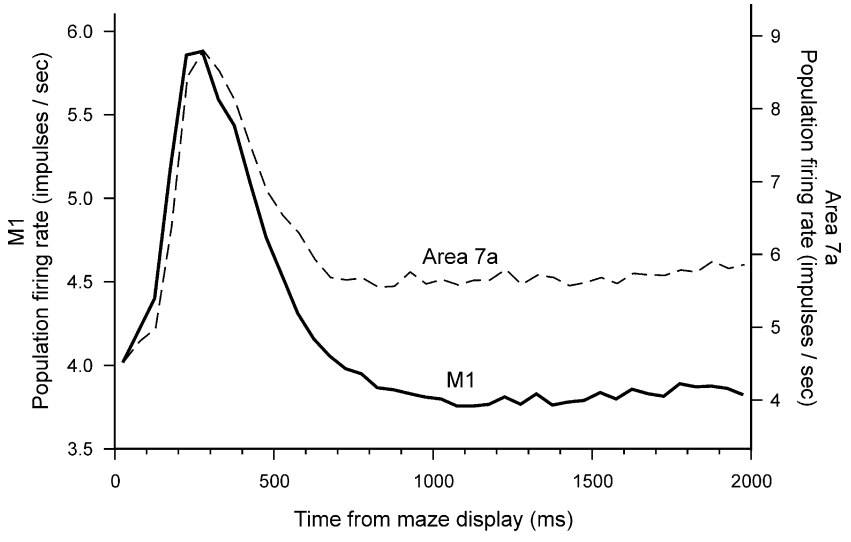

Fig. 7 Time-course of activity in M1 (*solid line*) and area 7a (*dashed line*) during the delay period of the maze task. Data for the population activity comes from neuronal responses to cells' preferred maze direction

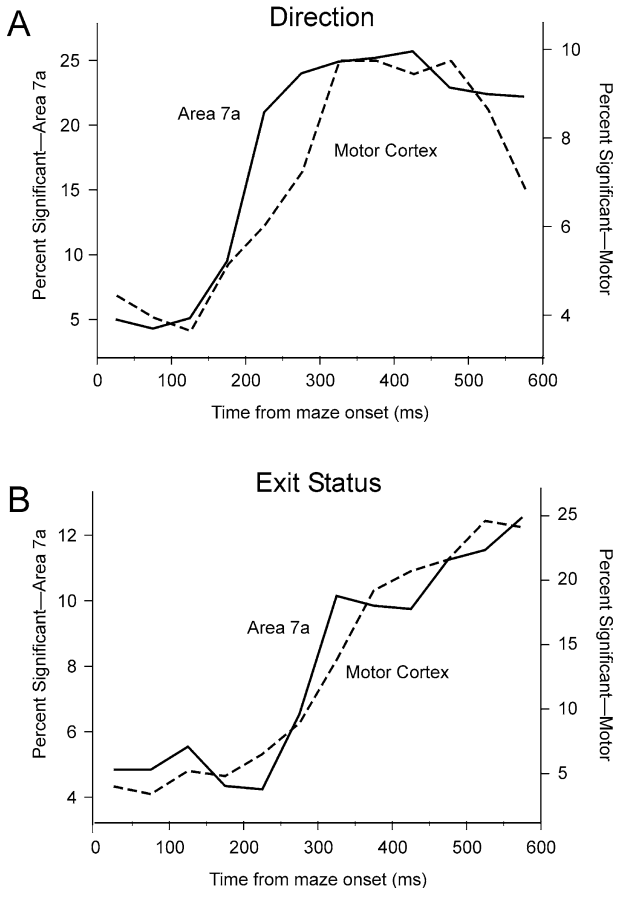

Fig. 8A, B Time-course of the representation of direction (**A**) and exit status (**B**) among M1 (*dashed line*) and area 7a (*solid line*) cells. *Lines* are the percentage of recorded cells showing a significant effect of the factor in each 50-ms time bin

outcome of such a process with regard to which side of the body will be making the subsequent response. However, a representation of a perceptual decision has been seen in at least one other motor area (Gold and Shadlen 2000), and the activity of some primary motor cortical cells has been shown to represent the category of a sensory stimulus (Salinas and Romo 1998). It is interesting to note that there is an increase in the number of M1 cells that represent exit status at about 200 ms after maze display (Fig. 8B, *dashed line*). After recording from area 7a cells during the same task (Fig. 8B, *solid line*), we found that these parietal neurons begin processing the exit status at the same time. Thus, these signals exist in the motor cortex at the same time as they appear in a brain area less likely to be directly involved in the motor response. Irrespective of whether these brain regions are involved directly in the computations related to determining the exit status of the path, both M1 and area 7a encode this variable soon after the maze is displayed.

Representation of direction

It is remarkable that cells in the arm area of primary motor cortex were modulated by the path direction during the solution of visual mazes. It is even more remarkable that the signals occurred during the delay period, in which no motor responses were made, and in a task that required no arm movements whatsoever. Many previous studies in this area have shown activity during a delay period. However, all of them—even those showing a relation of the arm area of M1 to cognitive function—included a directional arm movement. For example, in the study of mental rotation (Georgopoulos et al. 1989; Lurito et al. 1991), monkeys were trained to make a directional arm movement 90° away from a stimulus. In a context-recall task (Pellizzer et al. 1995; Carpenter et al. 1999), monkeys moved their arm to the target displayed in a sequence after the target that changed color. Directional arm movements were also made in experiments which showed that M1 cells encode the direction of a stimulus, where movement trajectories were dissociated from the targets (Alexander and Crutcher 1990; Shen and Alexander 1997). In the present experiment, no directional arm movements were made, and the final response of the monkeys was a foot-press, suggesting that the signals we observed represent a form of abstract spatial processing.

As above with the exit status, we calculated the time-course of significant effects of direction in both M1 and in area 7a. Although area 7a had a larger percentage of cells that were significant for direction (Crowe et al. 2004), both populations began to increase early after maze display (~100 ms). The concurrent representation of both the exit status and the direction in M1 and area 7a suggests that both these brain areas participate in a distributed network involved in the solution of mazes.

Our data suggest that some cells in primary motor cortex encode abstract spatial aspects of the maze, specifically, path direction. This activity did not represent the direction of arm movements the monkey made during the task. We never observed any movement of the monkeys' arms during maze solution, nor were the monkeys ever trained to make arm movements in any other task. Additionally, we recorded EMG activity while the monkeys performed the task and found that no muscle was significantly activated during the delay period, and that none of the muscles' activity varied as a function of path direction. Another possibility is that changes in cell activity may reflect simulated, or imagined, movements by the monkey. It has been shown in humans that imagined movements (Beisteiner et al. 1995; Lang et al. 1996; Lotze et al. 1999) activate the primary motor cortex and that observation of movements activates premotor cortex (Buccino et al. 2001). Thus, it is possible that neural activity in M1 could reflect the monkey's imagining of movements. Because the monkeys were never trained to make arm movements, either in response to the maze or in any other task, this seems an unlikely explanation. Rather, there is evidence that motor cortical neurons code spatial attributes of visual stimuli (Alexander and Crutcher 1990; Hocherman and Wise 1991; Riehle 1991; Shen and Alexander 1997; Johnson et al. 1999; Merchant et al. 2001). These data, along with the present results, suggest that motor cortex codes spatial variables in addition to arm

movement direction. It may be that signals coding abstract spatial variables derived from the visual input in motor cortex serve to influence motor processing, and that representation of these non-motor variables may be linked to both to motor execution and motor imagery or simulation.

Finally, an interesting question that arises from the existence of abstract spatial processing in the arm area of motor cortex is why it is there at all. This part of the brain requires spatial information in order to direct the arm to its proper target, but our results and others indicate that it may be involved in spatial processing when no arm movement is made. It is possible that because so many of the primates' visuospatial judgments lead to directional arm movements, the motor cortex, and the arm area specifically, has evolved to be a part of a distributed system performing these spatial computations.

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