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Dynamics of Parietal Neural Activity during Spatial Cognitive Processing

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Summary

Dynamic neural processing unrelated to changes in sensory input or motor output is likely to be a hallmark of cognitive operations. Here we show that neural representations of space in parietal cortex are dynamic while monkeys perform a spatial cognitive operation on a static visual stimulus. We recorded neural activity in area 7a during a visual maze task in which monkeys mentally followed a path without moving their eyes. We found that the direction of the followed path could be recovered from neuronal population activity. When the monkeys covertly processed a path that turned, the population representation of path direction shifted in the direction of the turn. This neural population dynamic took place during a period of unchanging visual input and showed characteristics of both serial and parallel processing. The data suggest that the dynamic evolution of parietal neuronal activity is associated with the progression of spatial cognitive operations.

Introduction

Cognitive processing is likely to involve a progression of activity states in cortical networks that can be decoupled from sensory or motor processing. Our objective in this study was to determine whether changes in neural representations of space in parietal cortex could be related to a specific spatial cognitive operation as it unfolded in time. For this purpose, we developed a visual maze task. In this task, subjects had to follow a path through a visual maze stimulus to find the path's endpoint. This task recruits a covert spatial cognitive process that operates on the path that is followed. The length of time required by a subject to process a path is a linear function of its length and the number of turns it contains, whether eye movements are allowed to track the path (Crowe et al., 2000) or not (Chafee et al., 2002). Processing time therefore bears a parametric relation to the path being analyzed in the absence of movement—evidence that this cognitive process is dynamic and can be decoupled from saccade planning and execution. In this way, spatial processing in maze solving appears similar to that recruited in covert curve tracing as studied in other behavioral paradigms (Houtkamp et al., 2003; Jolicoeur et al., 1986; McCormick and Jolicoeur, 1991) and cortical areas (Roelfsema et al., 1998; Roelfsema et al., 2000). In the maze task, the dependency of the processing time on path parameters provided a means to recruit and control a dynamic spatial cognitive operation with a temporal evolution we could then relate to changes in neural population activity in the posterior parietal cortex.

We reported previously that neural activity in area 7a of monkeys is systematically tuned to the direction of the path covertly followed through the maze (Crowe et al., 2004). This spatial tuning was not correlated with either the visual receptive field location in area 7a or the direction of planned but unexecuted saccades. Also, path tuning was not present while physically identical mazes were attended to without being solved. If path tuning is a correlate of a spatial cognitive process that works to track a path through the maze, then the direction coded by the population of parietal neurons should change if the path that is mentally followed turns, even without any physical change in the visual stimulus or any change in motor output. We provide evidence of this in the present report. As monkeys mentally tracked a path that contained an orthogonal turn (Figure 1, one-turn mazes), we found that the direction coded by a population of posterior parietal neurons shifted in the direction of that turn. The neural mechanism of this shift in the population signal exhibited aspects of both serial and parallel processing. Evidence for a serial component of the process was provided by the fact that the neural representation changed progressively to reflect parts of the path farther from the start point as the cognitive process progressed in time. A parallel component of the process was indicated by the fact that later in the processing time, multiple parts of the path were represented by the concurrent activation of neurons with different directional preferences.

Results

Neural Database

The analyses presented in this report are based on data from 280 neurons whose activity was significantly tuned to path direction, which are part of a database that has been described previously (Crowe et al., 2004). An example of the activity of a single neuron tuned for path direction during the maze task is shown (Figure 2). This neuronal sample was obtained from area 7a in the posterior parietal cortex.

Population Vector Encoding of Path Direction

We performed a series of population vector analyses. First, we analyzed mazes with straight main paths

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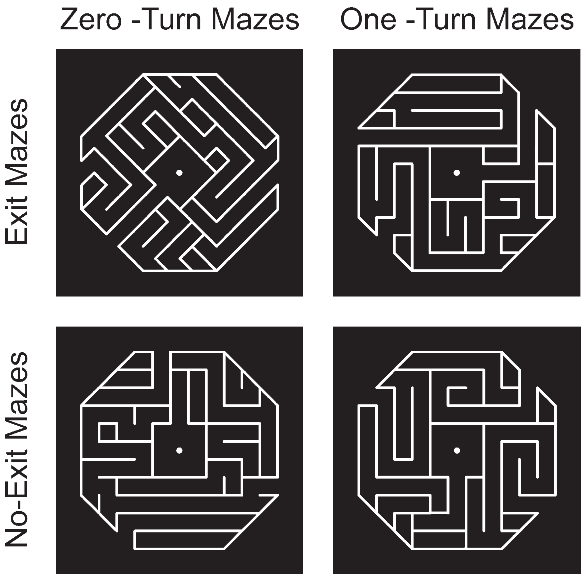

Figure 1. Examples of Maze Stimuli

All maze stimuli were centered on the fixation dot, which appeared always at the center of the display. Each maze contained a "start box" (square region at the center of the maze surrounding the fixation dot), and a "main path," which was the single maze path that was continuous with the start box. Maze stimuli were of two types, exit or no-exit (top and bottom rows, respectively), with main paths containing zero turns or one turn (left and right columns, respectively). Exit mazes were those in which the main path led continuously from the start box to an exit in the maze perimeter. No-exit mazes were those in which the main path led to a blind ending.

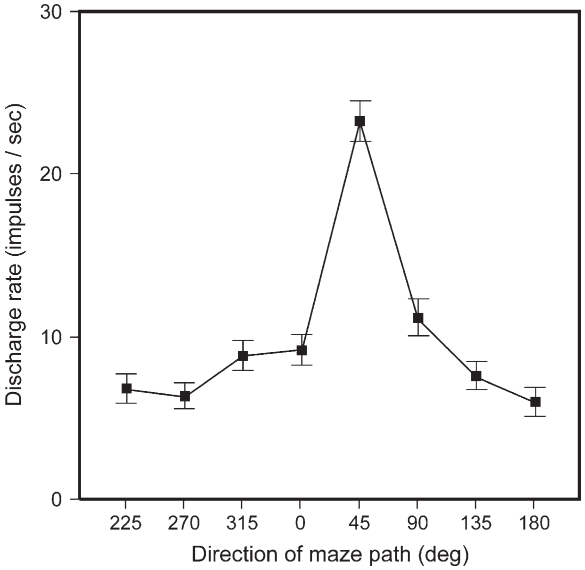

Figure 2. Activity of a Tuned Cell in Response to Mazes of Eight Path Directions

Values are the mean firing rate of the cell during the delay period of the task during the solution of mazes with paths in eight directions. Error bars indicate the mean ± SEM.

(zero-turn mazes; Figure 1), using the average cell discharge rate during the delay period. This analysis revealed that the direction of the population vector was very close to the direction of the maze path. The mean ± SEM signed difference between the two directions was 0.2 ± 1.9 deg (N = 8 directions) and the absolute difference was 11.5 ± 4.5 deg. In addition, the direction of the time-varying population vector, calculated every 10 ms, also pointed in the direction of the path (Figure 3).

Sequential Activation of Populations with Different Preferred Directions

We found that, during the solution of mazes with an orthogonal turn, different populations of cells in area 7a were sequentially activated. Cells with preferred directions aligned with the initial path segment (Figures 4A and 4B, blue line) were activated first. Those with preferred directions offset by 45 degrees in the direction of the turn became active at a later time (Figures 4A and 4B, red line) and at a lower level. Cells with preferred directions offset by 90 degrees (black line) were not activated. We also tested cells with preferred directions aligned 45 degrees away from the direction of the turn. This population was slightly activated, with an onset between cells with preferred directions at 0 and 45 degrees. The level of activation of each population at 450 ms remained constant throughout the rest of the delay period (up to 2500 ms). We calculated the average time of activity onset for each population of cells (see Experimental Procedures) and found that cells with preferred directions aligned with the initial path segment were activated significantly earlier than those with preferred directions aligned 45 degrees in the direction of the turn (221 ms for 0 degrees and 290 ms for 45 degrees; F = 15.8, p = 0.011). Cells aligned at −45 degrees were activated at an intermediate time (266 ms). The difference between this value and that for cells at 0 degrees (221 ms) approached significance (F = 8.4, p = 0.056). A cumulative sum of the activations of these populations is shown in Figure 4C.

Shift of the Neural Population Vector Tracking a Path with an Orthogonal Turn

We performed the time-based population vector analysis described above on data acquired during the solution of one-turn mazes. Figure 5 illustrates the direction of the population vector calculated in 10 ms time bins in this case. The direction of the vector is expressed relative to the direction of the initial section of the main path connected with the start box. Positive values along the y axis indicate angles in the direction of the turn in the main path (for an example of a one-turn maze, see Figure 1, right). Negative values indicate angles away from the direction of the turn in the path. At 200 ms after maze display (when the population vector abruptly grew in length), the population vector began to rotate in the direction of the turn in the path. This supports the hypothesis that mazes are solved by a progressive visual analysis extending from the center of the maze outward and that this is reflected in neural activity in area 7a.

Although the population vector finished rotating by approximately 450 ms, it still pointed in the direction of

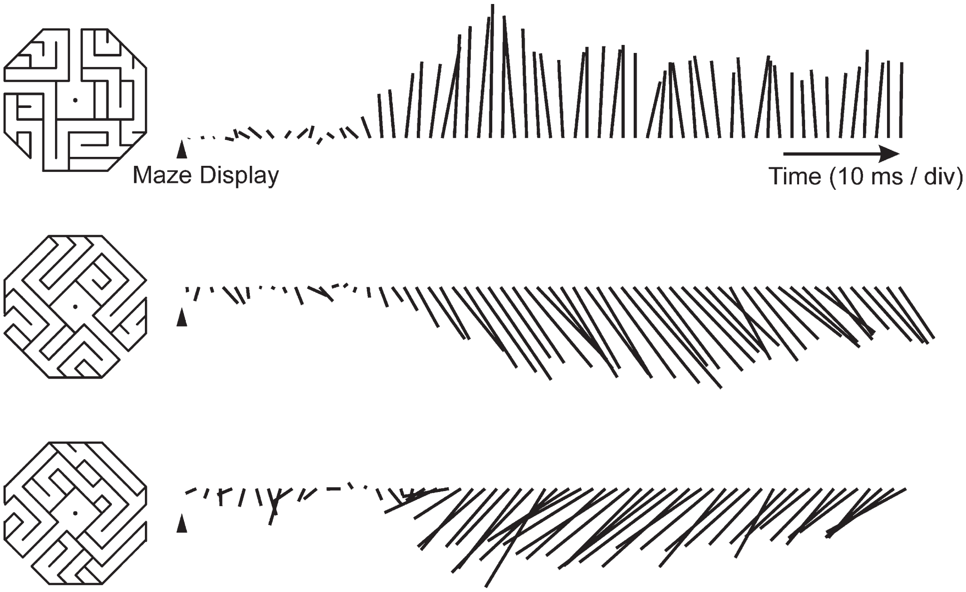

Figure 3. The Population Vector Calculated Every 10 ms for Zero-Turn Mazes

Time after maze onset proceeds from left to right. Each line represents the length and direction of the population vector calculated from neural activity in the corresponding time bin (bin width, 10 ms). Data from three representative path directions are shown.

the turn throughout the delay period (2000–2500 ms). The length of the population vector peaked at about 300 ms and then fell to approximately half of its peak value at about 800 ms, where it remained for the duration of the delay period.

Discussion

Cognitive operations are dynamic and can unfold in time in a manner that is decoupled from concurrent sensory or motor output. Neural correlates of cognitive operations should exhibit these same characteristics. The link between neural and spatial cognitive processing in the temporal domain has been studied in the context of movement planning in both the motor (Georgopoulos et al., 1989) and prefrontal (Takeda and Funahashi, 2004) cortices. Studies of this relationship may ultimately provide a neural account for the temporally dynamic aspect of cognitive function. We studied the dynamics of neural population activity in posterior parietal cortex as a specific spatial cognitive operation was underway. We provide evidence that neural representations of space in posterior parietal cortex evolve during this time interval and that the nature of this evolution is logically related to the cognitive operation being performed.

Dynamics of the Population Vector

In prior neurophysiological experiments, we found that single neurons in area 7a were systematically tuned to the direction of a maze path being covertly followed (Crowe et al., 2004). This tuning did not reflect a known sensorimotor property of posterior parietal neurons because preferred directions were not related to the locations of visual receptive or saccadic movement fields. In that study, we found that path tuning was not evident when a naive monkey attended to the same visual maze stimuli without solving them. These behavioral and neurophysiological data led to the following prediction: If a subject used a dynamic cognitive operation to process the maze by following the path through it, and if this cognitive process were reflected in the temporal evolution of activity in spatially tuned parietal neurons, then the spatial coordinate represented by population activity should shift when the subject (monkey) mentally processed a path that turned. We tested that prediction in the present report and describe a dynamic change in neural population activity that took place while the monkey processed a path that turned through the maze. We found that the direction represented by neural population activity rotated in the direction of that turn during the processing time (Figure 5). During this process, population activity changed in a manner consistent with a model in which the neural population first represented the portion of the path nearest to the fixation target, and then, as time progressed, evolved to include representation of the second segment. The progressive center-outward process (see also Figure 3 for straight paths) suggested by this neural dynamic is consistent with prior behavioral data in humans (Crowe et al., 2000). The observation that population activity coding space is dynamic while the spatial attributes of sensory input and motor output are held constant is consistent with the hypothesis that activity reflects the progression of a cognitive process recruited to analyze the maze.

Mechanism of Vector Rotation

We found that the spatial cognitive process represented by these features of dynamic neural activity exhibited both serial and parallel characteristics. The ro-

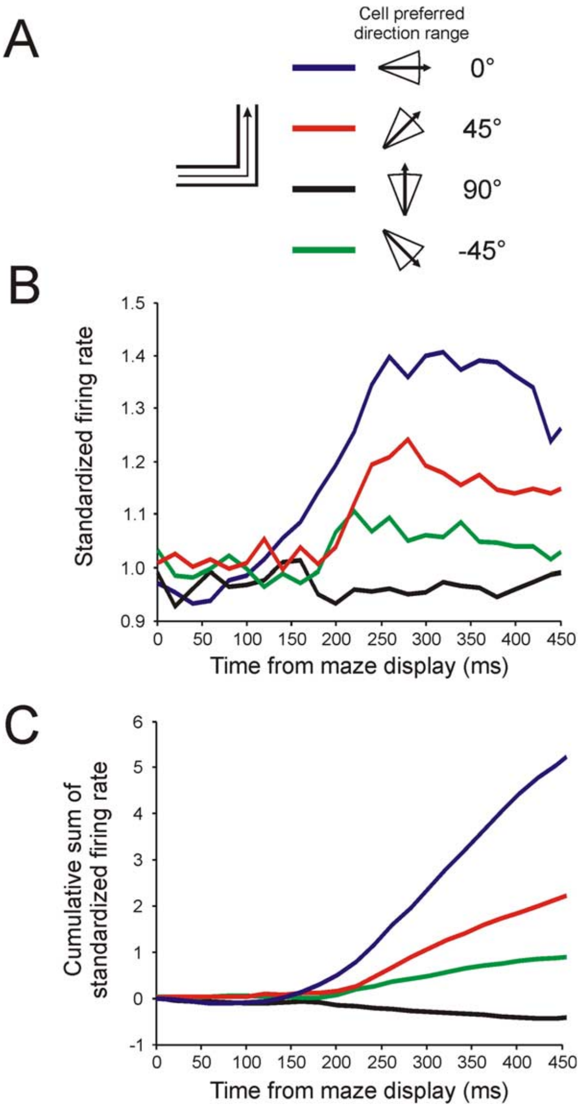

Figure 4. Time Course of Activity for Different Populations of Cells during One-Turn Maze Solution

(A) Cells were grouped by the relationship of their preferred direction to the maze path. Each line in (B) and (C) represents the standardized activity time course of a population of cells with preferred direction ranges centered on 0, 45, 90, and −45 degrees away from the initial path segment, in the direction of the turn. (B) Standardized firing rate of each of these groups during maze solution. (C) Cumulative sum of lines in (B) after subtraction of average baseline activity.

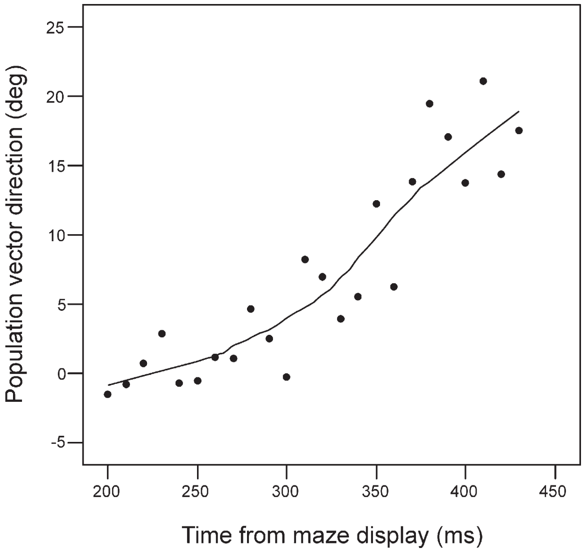

Figure 5. Average Direction of the Population Vector across All One-Turn Mazes

The direction of the vector is expressed relative to the direction of the initial section of the main path in all mazes. Positive values along the y axis indicate angles in the direction of the turn in all mazes. Negative values indicate angles away from the direction of the turn in the path. The line is a loess fit (Epanechnikov kernel, fitting 50% of points).

tation in the population vector was mediated by the staggered recruitment of neurons with different preferred directions and by changes in their relative levels of activity as processing progressed (Figure 4). The dynamic nature of this neural representation was consistent with a serial process in which the path section closest to the fixation target dominated the spatial representation early in the process, whereas the path section that was farther away exerted an increasing influence on processing as time progressed. This progression is in some way consistent with spotlight or zoom lens models of visual attention that are serial in nature (McCormick and Jolicoeur, 1991; Posner et al., 1980). Models of this type are characterized by a singular region of limited spatial extent, where visual processing resources are concentrated, that can be moved independently from the angle of gaze. The neurophysiological correlate of the spotlight of attention has often been a change in the sensitivity of cortical neurons to visual stimuli when their receptive fields fell within the scope of the spotlight (Bushnell et al., 1981; Moran and Desimone, 1985; Steinmetz et al., 1994).

During maze solution, neural activity exhibited serial characteristics, but did not strictly conform to the serial model as outlined above. For example, the preferred directions of parietal neurons did not correspond to the locations of their visual receptive fields mapped with more simple stimuli (Crowe et al., 2004), suggesting the possibility that neural activity during maze solution was cast in a task-dependent reference frame. In addition, by the end of processing, neurons with different preferred directions were simultaneously active, suggesting that near and far sections of the path were represented in parallel and not strictly in series. This parallel representation of different path directions by population activity could simply result from variation in processing time across trials and neurons, with a consequent blurring of the associated phasic neural signals at the population level. However, this was unlikely since the activity of individual neurons began between 221 and 290 ms after maze onset and activity was tonic, lasting throughout the entire 2000–2500 ms delay period.

It was interesting that neurons with preferred directions offset by 90 degrees from the initial path direction (i.e., those coding the final path section) were never activated. This provides evidence that neural activity did not code the orientation of the far section of the path explicitly. Instead, neurons with preferred directions aligned with the initial path section and others with preferred directions 45 degrees offset in the direction of the turn did become active. This suggests that activity represented a vector, with an origin that remained anchored at the fovea and a tip pointed toward the current locus of spatial processing as this progressed from near to far sections of the path. Interestingly, the different populations of cells were activated to different degrees, with cells tuned to the initial path direction having the highest activity. This may stem from a bias of the monkeys to represent straight paths, as this was by far the most common maze type. Alternatively, it may reflect the fact that the initial path segment is closer to the point of fixation.

The degree of vector rotation may provide some insight into how the direction of the maze path is represented at the neural population level. We found that the direction of the population vector rotated, on average by about 20 degrees, across all one-turn mazes, which represented a small degree of rotation relative to the 90 degree turn in the path. This degree of rotation was determined by the fact that, once activated, neurons coding the initial path section (the 0 degree population) remained active throughout the processing time, contributing to the population vector (indicative of a parallel representation) and retarding its further rotation.

Behavioral Significance

In previous studies, neural activity in parietal cortex has been functionally related to spatial attention (Bisley and Goldberg, 2003; Gottlieb et al., 1998; Mountcastle et al., 1981; Steinmetz et al., 1994), spatial working memory (Chafee and Goldman-Rakic, 1998; Gnadt and Andersen, 1988; Gottlieb and Goldberg, 1999), motor intention (Bracewell et al., 1996; Mazzoni et al., 1996; Snyder et al., 1997, 1998), and decision processing (Platt and Glimcher, 1999; Shadlen and Newsome, 2001; Sugrue et al., 2004). In the present study, the primary behavioral correlate of neural activity was a spatial cognitive operation that appeared to be involved in maze processing.

This relationship between neural activity and maze solution does not exclude additional relationships between parietal neural activity and spatial parameters, such as those that have been well characterized by previous studies. For example, it may be that neural activity during maze solution reflects the deployment of covert spatial attention. In another behavioral context, we have observed that neural activity and visual attention are related during spatial cognitive processing, even in the case where neural activity codes an abstract spatial parameter and not the position of an attended visual stimulus (Chafee et al., 2005). A similar relationship may also hold during maze processing. Likewise, the spatial coordinate coded by neurons during maze solution could play a role in oculomotor function, for example, in saccade endpoint selection when saccade metrics are not dictated directly by the location of a visual target. This potential role is supported by anatomical data that showed that area 7a and the lateral intraparietal area (LIP) are directly and reciprocally connected (Andersen et al., 1990; Cavada and Goldman-Rakic, 1989) and by physiological evidence that area LIP provides directional control for saccades (Snyder et al., 1998), although to what extent neural activity in LIP directly specifies saccade metrics or the deployment of attention that accompanies eye movements is debated (Bisley and Goldberg, 2003).

An important aspect of the present results is that they show that the spatial representation supported by neural activity in area 7a evolves in a manner that is consistent with the temporal progression of spatial problem solving. Specifically, the rotation of the population vector in the direction of the turn in the path appears to reflect a progressive mental analysis of the structure of the maze, as suggested by behavioral data (Chafee et al., 2002; Crowe et al., 2000). The dynamics of this process were not driven by concurrent changes in visual input, nor did they appear to reflect motor planning; rather, the evolution of neural activity was most closely related to the progress of a mental operation.

Experimental Procedures

Subjects

Two monkeys (*Macaca mulatta*; BW, 5–7 kg) were trained to solve visual mazes while maintaining eye fixation at the center of the display. Care and treatment of the animals conformed to the Principles of Laboratory Animal Care of the NIH (NIH publication no. 86-23, revised 1995). The Internal Animal Care and Use Committees of the University of Minnesota and the Minneapolis Veterans Affairs Medical Center approved all experimental protocols.

Maze Task

Each trial began with ocular fixation of a small fixation target presented at the center of a screen. After a variable interval (600–840 ms), a maze stimulus was presented (Figure 1). Each maze was 30 degrees in diameter and consisted of a set of paths delineated by orthogonal line segments. Each maze contained a central “start box” surrounding the fixation target. A single path (the “main path”) began at the start box and progressed outward through the maze toward its perimeter. In some cases, the path was straight (Figure 1, left); in other cases, it contained a single 90 degree turn (Figure 1, right). In addition, mazes were segregated into two classes according to whether the main path reached an open exit in the maze perimeter (Figure 1, top: exit mazes) or reached a terminus within the maze instead (Figure 1, bottom: no-exit mazes). The monkey’s task was to respond on the basis of the exit status of the main path, pressing one of two foot pedals to signify an exit maze and the other pedal to signify a no-exit maze. A delay period was enforced to separate in time processing of the maze stimulus from execution of the motor response. Monkeys were required to maintain fixation of the central target for a variable delay period after maze onset (2000 to 2500 ms; the maze was visible throughout the delay). Following this, the dimming of the fixation target served as a go signal, and the monkey was rewarded with a drop of juice for pressing the correct pedal. Eye position was monitored using the scleral search coil technique in one monkey (Fuchs and Robinson, 1966) (CNC Engineering, Seattle, WA) and an infrared eye tracking system in the other (ISCAN, Burlington, MA). Monkeys were required to maintain fixation within 1.5 degrees of the fixation target throughout the trial.

Neural data were recorded during two sets of trials. In the first set, all mazes contained main paths that were straight. This set consisted of 160 trials, equally divided between exit and no-exit mazes (80 trials of each type) and also between the eight possible path directions (20 trials of each direction, half using exit and the other half, no-exit mazes). The directions of straight main paths were separated by 45 degrees. Monkeys were required to successfully solve each maze in the set (mazes for which the monkeys responded incorrectly were repeated later in the set). In the second set, all mazes contained main paths that included a single turn. In this case, the initial section of the main path (connected to the start box) was oriented in one of the four cardinal directions, and the main path could turn either to the left or the right relative to the initial segment. This produced eight types of one-turn mazes. There were 20 repetitions of each of these types (160 trials total), equally divided between exit and no-exit mazes. New sets of zero- and one-turn mazes were randomly generated before each day of neural recording.

Neural and Behavioral Data Acquisition

The electrical signals of neural impulse activity were recorded extracellularly using seven independently driven microelectrodes in one monkey and sixteen microelectrodes in the other (Mountcastle et al., 1991) (Thomas Recording, Marburg, Germany). These signals were discriminated into the action potentials of single units. We recorded all cells encountered and analyzed all cells with spontaneous activity without any preselection. Titanium recording chambers (7 mm i.d.) were placed on the skull overlying area 7a in the left cerebral hemisphere, using stereotaxic information from magnetic resonance imaging (MRI) data obtained in a clinical GE 1.5T magnet before surgery. Recording locations were verified by MRI after chamber implantation. Additionally, recording locations based on MRI were confirmed after the monkeys were sacrificed and the brains removed. All surgical procedures were done aseptically under isoflurane (2%) gas anesthesia.

Analyses

Population Vector Analysis

The neuronal population vector (Georgopoulos et al., 1983) was calculated as follows. First, the preferred direction of each cell was calculated using its discharge rate during the delay period following maze onset on trials with straight main paths (Crowe et al., 2004). Second, the population vector for the delay period was

$$\boldsymbol{P}_j = \sum_{i=1}^{N} w_{ij} \boldsymbol{C}_i \tag{1}$$

where $\boldsymbol{P}_j$ is the population vector for the j^{th} path direction, N is the number of cells included in the analysis, $\boldsymbol{C}_i$ is the preferred direction of the i^{th} cell, and w_{ij} is a weighting function:

$$w_{ij} = d_{ij} - \overline{d_i} \tag{2}$$

where d_{ij} is the average delay period firing rate of cell i on direction j, and

$$\overline{d_i} = \frac{1}{M} \sum_{j=1}^{M} d_{ij} \tag{3}$$

where M = 8 path directions. The time-varying population vector (every 10 ms) was calculated using the same formulas but applied to time bin k:

$$\boldsymbol{P}_{jk} = \sum_{i=1}^{N} w_{ijk} \boldsymbol{C}_i \tag{4}$$

$$w_{ijk} = d_{ijk} - \overline{d_{ik}} \tag{5}$$

$$\overline{d_{ik}} = \frac{1}{M} \sum_{j=1}^{M} d_{ijk} \tag{6}$$

Population Activity Time Course

Neurons were divided into four populations depending on the relation between their preferred direction and the one-turn path being processed. Preferred directions were expressed as angles relative to the orientation of the initial section of the path and in the direction of the turn. The four groups had preferred directions within a sector of 45 degrees centered on 0, 45, 90, and −45 degrees. Cells at 45 and 90 degrees had preferred directions in the direction of the path; those at −45 degrees had preferred directions away from the direction of the turn. Population activity associated with a given preferred direction was standardized to the average level of activity on the remaining preferred directions. The analysis was performed for each of eight possible one-turn path configurations and then averaged across the paths. Cell activation latencies were calculated for cells significantly tuned at $p < 0.01$. Activation was defined as the time that a cell's activity exceeded three standard deviations of the mean of the baseline activity (300 ms before maze display). Cumulative activity was determined by calculating cumulative sums after first subtracting average baseline activity.

Population Vector Rotation

In order to visualize the rotation of the population vector as one-turn mazes were solved, we combined the data from trials collapsed across path and turn direction as follows. First, the time-varying population vector for each path configuration was calculated. Then the direction of the population vector was re-expressed relative to the direction of the initial segment of the main path in each maze, defined as zero degrees in all cases. Vector angles in the direction of the turn in the path were defined as positive, and angles opposite the direction of the turn were defined as negative. This pooled the data across mazes containing main paths starting in each of the four possible directions.

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