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Short-term memory effects on the representation of two-dimensional space in the rhesus monkey

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Abstract Human subjects represent the location of a point in 2D space using two independent dimensions (x - y in Euclidean or radius-angle in polar space), and encode location in memory along these dimensions using two levels of representation: a fine-grain value and a category. Here we determined whether monkeys possessed the ability to represent location with these two levels of coding. A rhesus monkey was trained to reproduce the location of a dot in a circle by pointing, after a delay period, on the location where a dot was presented. Five different delay periods (0.5–5 s) were used. The results showed that the monkey used a polar coordinate system to represent the fine-grain spatial coding, where the radius and angle of the dots were encoded independently. The variability of the spatial response and reaction time increased with longer delays. Furthermore, the animal was able to form a categorical representation of space that was delay-dependent. The responses avoided the circumference and the center of the circle, defining a categorical radial prototype around one third of the total radial length. This radial category was observed only at delay durations of 3–5 s. Finally, the monkey also formed angular categories with prototypes at the obliques of the quadrants of the circle, avoiding the horizontal and vertical axes. However, these prototypes were only observed at the 5-s delay and on dots lying on the circumference. These results indicate that monkeys may possess spatial cognitive abilities similar to humans.

Keywords Categorization · Spatial cognition · Short-term memory · Rhesus monkey

Introduction

The perception and memorization of the spatial location of objects are elementary abilities that are critical for the survival of moving organisms. Hence, an extensive amount of information has been accumulated regarding the capacity of human subjects to solve spatial memory tasks. For example, it became obvious from the early work of Attneave (1955) that the perception of the location of visual stimuli presented on a circle is biased towards the middle of the quadrants. Subsequent studies confirmed the existence of a bias reproducing memorized spatial location in a circle (Dale 1973; Nelson and Chaiklin 1980). The basic observation is that when subjects are asked to reproduce the location of a point on a circle after a delay of few seconds, their responses reveal two kinds of bias. One bias is in the radial dimension, such that responses avoid the circumference and the center of the circle, whereas the other bias is in the angular dimension, such that responses are away from the horizontal and vertical axes, crowding the obliques. Huttenlocher and collaborators (1991) integrated this phenomenon in a meaningful model. This model assumes that the estimation of spatial location in short memory is represented at two levels of detail, namely a fine-grain value and a category. The model claims that the actual performance of the subjects depends on the weighted combination of these two levels of representation. In the absence of a memory load, the fine-grain value has a higher weight than the categorical value, whereas under a high memory load the categorical value has a greater influence on the performance, producing the observed angular and radial biases. The formation of a category bias may improve the overall consistency of response by decreasing the variability of the reports. In fact, these authors have demonstrated formally that the use of systematic bias increases overall accuracy when compared with that based on a fine-grain recollection alone in human

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subjects. Finally, it has been demonstrated that the adult capacity of coding simultaneously the categorical information of angle and radius emerges at ages above 9 years. Children of 5–7 years can only form categorical representations of one dimension (radius or angle) (Sandberg et al. 1996).

Monkeys are animals with perceptual and motor abilities that are very similar to those observed in human subjects (Georgopoulos et al. 1981; Mountcastle 1990; Merchant et al. 2003). In the present study we determined the capacity of a rhesus monkey to memorize the location of a dot in a circle. The objective of this experiment was to determine how monkeys represent spatial locations, and specifically whether they used fine-grain and categorical levels for coding space in a short memory task.

Methods

Animal

A male rhesus monkey (*Macaca mulatta*, 5 kg BW) was used in this study. The animal was on a regulated water schedule. 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 animal protocols were approved by the Institutional Review Board.

Visual display

A computer touch screen monitor (Elo Touch Systems Entuitive 2125C, 21" CRT) was used to display the visual stimuli, and to record the end point location of the monkey's reaching. The monitor was placed 20 cm in front of the animal, had a white background, and ran at a 60 Hz refresh rate. There were two main visual conditions called sample circle and response circle. The sample circle consisted of a black circle 20.32 cm in diameter that contained a black dot 1.91 cm in diameter. This dot could appear in one of 49 possible positions inside the circle or lying on the circumference. The 49 dots were arranged in polar coordinates with five radius levels or distances from the center (0, 5.08, 10.16, 15.24 and 20.32 cm), and 12 angular positions (separated every 30°) for all but the central dot (Fig. 1A). The response circle was identical to the sample circle except that it appeared in another location of the screen and did not contain the target dot (Fig. 1B). The center of the circles could be displayed in the following four positions in the

screen relative to the top-left corner of the monitor: (1) $x=10.2$, $y=9.4$ cm; (2) $x=10.2$, $y=5.6$ cm; (3) $x=14.6$, $y=9.4$ cm; (4) $x=14.6$, $y=5.6$ cm. Eight combinations of sample–response circle positions were used (see Table 1).

Apparatus and behavioral task

The monkey was seated in a primate chair during the execution of the task. At the beginning of the trial, the animal pressed a push-button with the right hand upon the appearance of an empty circle (20.32 cm in diameter). Once the button was pressed the sample circle (with the dot) was displayed for 1 s. Then the sample circle disappeared, and the monkey was required to keep the push-button pressed during a fixed delay period. Five delay period durations were used (0.5, 1, 2, 3 and 5 s). The end of the delay period was signaled by a beep (500 Hz, 500 ms duration) and the simultaneous appearance of a response circle. The monkey then released the push-button and touched the screen at the relative circle position where the dot had appeared in the sample circle. There was no dot in the response circle, and the monkey could use only the circle itself as a reference frame because the sample and response circle position differed (Fig. 1B). The trial was considered correct and the animal received a reward if the screen touch position was inside a circle of 8 cm of diameter, centered at the relative position of the sample dot. In addition, the monkey could receive one or two extra rewards if the response was inside a circle of 2.8 and 1.9 cm respectively.

Experimental design

All possible combinations of dot positions and sample–response circle locations were interleaved and presented in pseudorandom order in a block. Therefore, a block consisted of 392 trials (49 dot positions \times 8 combinations of sample–response circle positions). On average the monkey performed two blocks of trials every day. Ten blocks were collected for each delay duration. The monkey was trained in the task for more than 12 months. The data were collected once the monkey reached the top of the learning curve (the percent of correct trials was $>75\%$) for all delay durations. Blocks of short and long delay durations were intermingled throughout the acquisition.

The monkey received 1–3 drops of juice (0.1 ml) every time it performed a correct trial. Since the monkey was on a regulated water schedule, its motivation was high at the beginning of the day and dropped slightly throughout the recording session. This was consistent for all delay period durations. We assured that the data analyzed in the present study were collected when the monkey was motivated by aborting sessions where the error rate became higher than 30% or the monkey was visibly distracted.

Fig. 1 **A** Spatial distribution of the dots inside the circle. The dots are distributed in polar coordinates. **B** Sequence of events during trial in the task

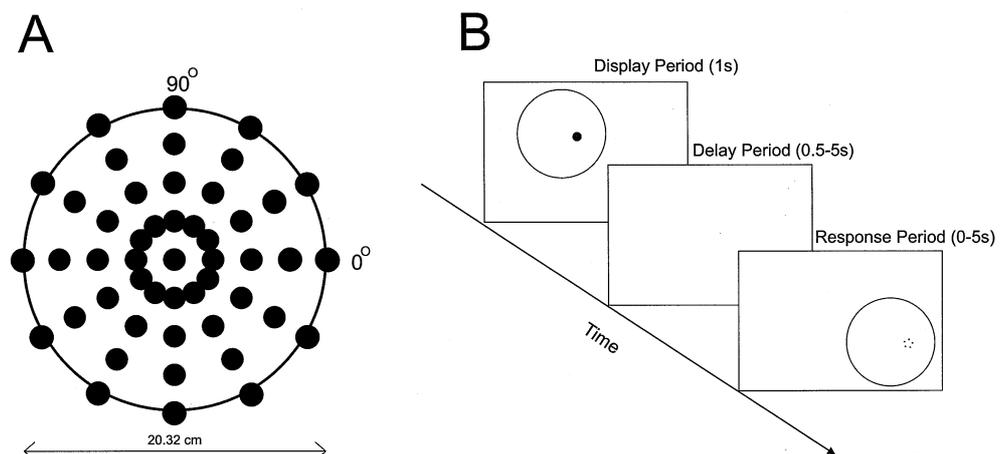


Table 1 Number of screen positions of the sample–response circles for the eight combinations used in the experiment. The number of screen position corresponded to the following screen coordinates in the screen: (1) $x=10.2$, $y=9.4$ cm; (2) $x=10.2$, $y=5.6$ cm; (3) $x=14.6$, $y=9.4$ cm; (4) $x=14.6$, $y=5.6$ cm

Number	Sample circle location	Response circle location
1	1	2
2	2	1
3	2	3
4	3	2
5	3	4
6	4	3
7	1	4
8	4	1

Data analysis

General

Standard statistical techniques were used for data analysis including analysis of variance (ANOVA) and linear regression (Snedecor and Cochran 1989). The level of statistical significance to reject the null hypothesis was $\alpha=0.01$. The SPSS statistical package (version 10, SPSS, Chicago, Ill., 1996) was used for the statistical analysis.

Radial bias

The radial bias was defined as the signed difference between the radius of the target dot and the radius of the response value in the sample and response circles, respectively.

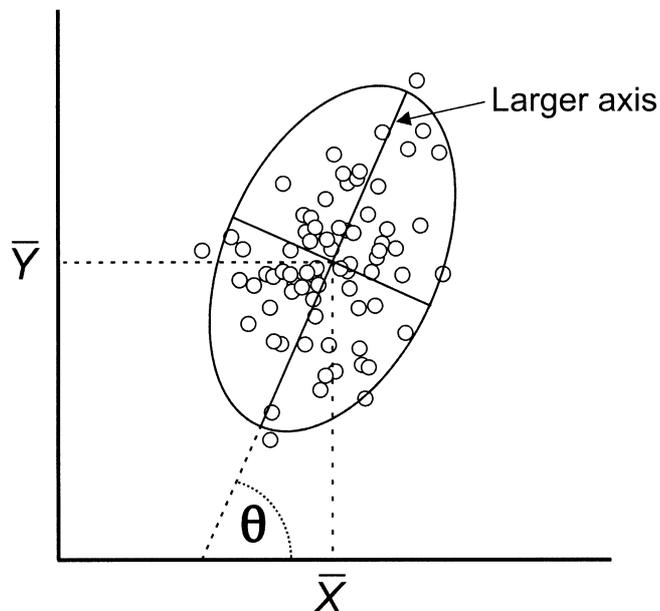


Fig. 2 Elliptic bivariate normal distribution that is used to explain the variability of the responses. The ellipse is centered at the x - y mean \bar{X}, \bar{Y} of the responses. The length of its axes is proportional to the square root of the two eigenvalues of the x - y variance-covariance matrix. These axes were scaled to that they include 95% of the bivariate distribution. The angle θ defined the orientation of the larger axis of the ellipse

Angular bias

The angular bias was defined as the signed difference between the angle of the target dot inside the sample circle and the angle of the animal response in the response circle.

Response variability

The variability in the response was determined using the x and y components of the end point of the responses in the touch screen. The two dimensional variability was characterized using an elliptic bivariate normal distribution (Fig. 2). In this figure, the ellipse is centered at the x - y mean \bar{X}, \bar{Y} and the length of its axes is proportional to the square root of the two eigenvalues of the x - y variance-covariance matrix. The two axes are orthogonal, and are equivalent to the variances along each axis (i.e. the larger axis corresponds to the axis of larger variance). We scaled the axis using the constant $X_p^2(\alpha)$ where $X_p^2(\alpha)$ is the upper (100α) th per-centile of the chi-square distribution with k degrees of freedom. This leads to an ellipse that contains the $(1-\alpha)\times 100\%$ of the distribution probability, where $\alpha=0.95$ (Fig. 2). Finally, the orientation of the ellipse was defined by the angle θ that was equal to the arctangent of the x and y elements of the eigenvector from the larger eigenvalue (Johnson and Wichern 1998).

Results

Short-memory effect on spatial location

The hypothesis in the present study is that the estimation of spatial location during short-memory situations depends on the interaction of two separate processes (Huttenlocher et al. 1991). The first process is assumed to reflect an unbiased fine-grain representation, which is to say that the inexact fine-grain representation in memory is considered as a normal distribution of values centered at the true value. The variability of the fine-grain values depends on two factors: (1) the degree of imprecision during encoding, and (2) the extent of loss of information from memory decay. The second process is a categorical one, defining a category as a bounded region that covers a range of fine-grain values. The boundary value specifies the endpoint of the range of values included in the category and is defined covertly by the subject (i.e. is it not physically present). The central value of the category is called the category prototype. Both the boundary and prototypic values have some degree of inexactness. It has been demonstrated that a system combining these two processes, in spite of introducing bias, reduces variability across trials and, therefore, may be an adaptive strategy of accessing spatial information from memory. The total error has two components: the variability around the mean of the reports (variance) and the bias that corresponds to the difference between the true value and the mean of the samples. Thus, even though the bias increases, the total error will decrease if the variability decreases by a greater amount. It has been shown that the use of angular and radial prototypes improves accuracy with respect to the reports assuming recollected fine-grain values alone (see Huttenlocher et al. 1991 for a formal description).

Coding fine-grain location

There are two coordinate systems that can be used to code location, namely, the Cartesian and the polar. The former involves distances along the x and y axes, whereas the latter involves a radius and an angle. The results of the present study indicated that the monkey used a polar rather than a Cartesian fine-grain coordinate system. This was suggested by the finding that the errors in response location varied with radial distance, at all angular locations. Figure 3 shows examples of response values at dot locations with different radii and angles. Errors were smaller close to the circumference, and increasingly wider away from it, towards the center. In contrast, they did not vary with the polar angle and were very similar across angular locations. This error pattern is in agreement with a polar rather than a Cartesian coding scheme (see Huttenlocher et al. 1991). If the monkey was using a Cartesian coding system we would expect the shape of the distribution to be relatively circular at the diagonals (where the x and y coordinates are equal) and elliptical at other locations (x and y are unequal) and to diminish in size as it nears the reference frame (there is a decrease of the uncertainty of both x and y). This pattern was not found in the present data.

We quantified the spatial error pattern at a given location by calculating the ratio of the larger over smaller axes of the ellipse that corresponded to the bivariate variance of the response values (see Methods). We then log-transformed these ratios to make their distribution symmetric and stabilize their variance (Snedecor and Cochran 1989) and used them as the dependent variable in statistical analyses. The log ratio of the ellipse axes increased as a function of the dot radius (Fig. 4A). These results indicate

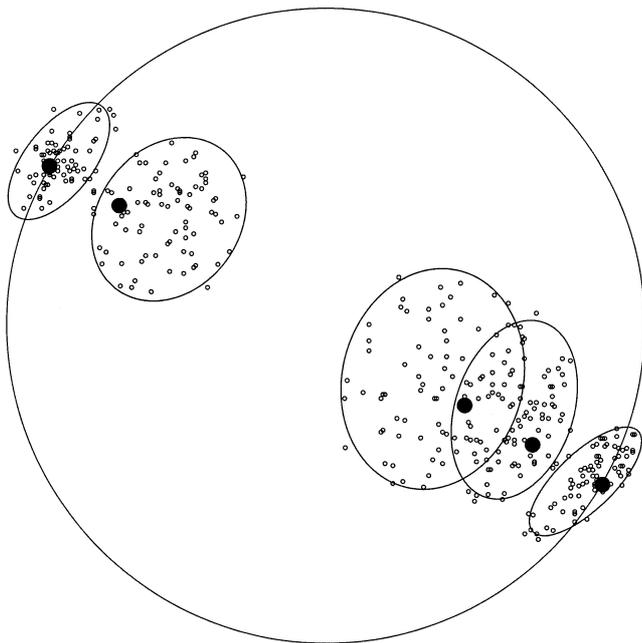


Fig. 3 Graphic displays of the response values and the variance ellipse associated to them, for dots in five different locations

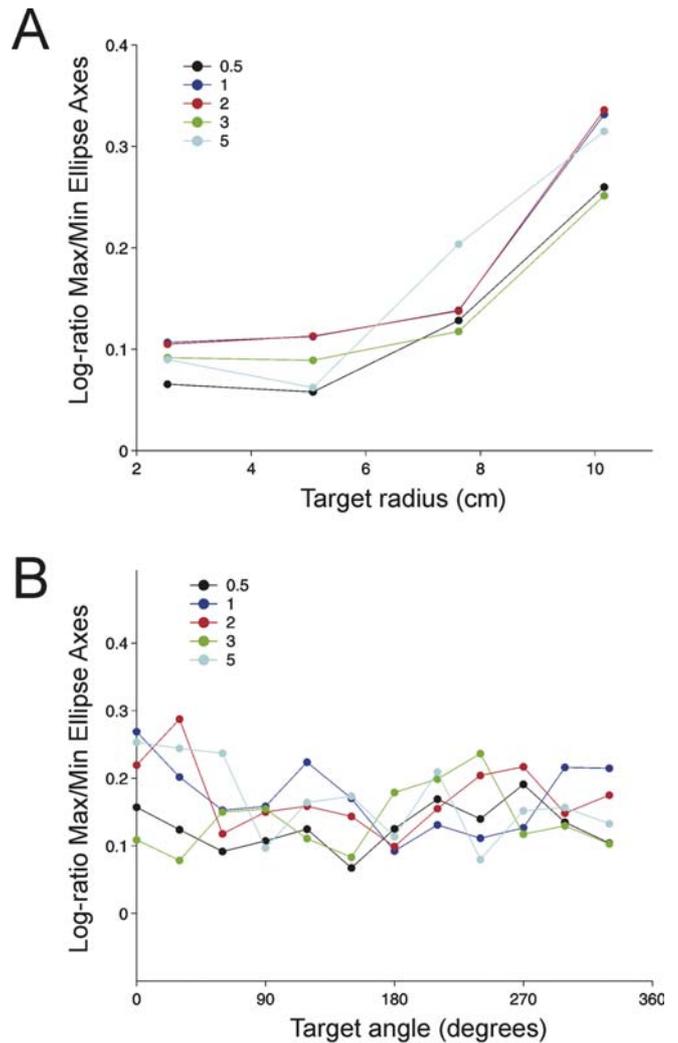


Fig. 4 Mean of the log ratio between the maximum and minimum axes of the variance ellipse as a function of the dot radius (A) or the dot angle (B). The data for the different delay periods are color coded

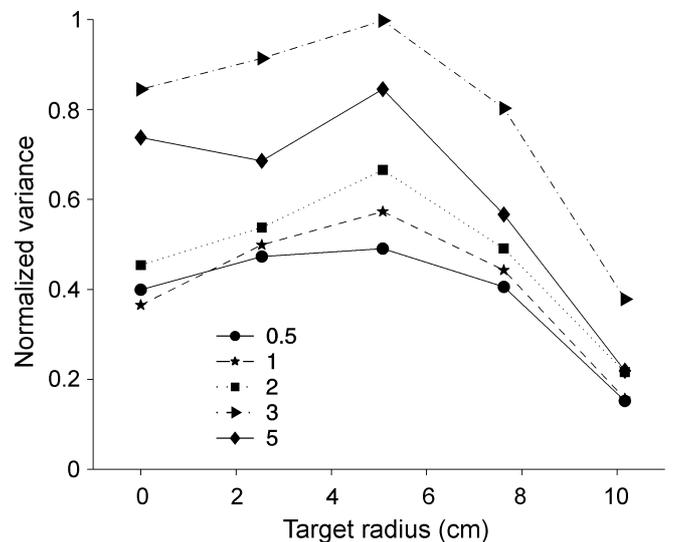
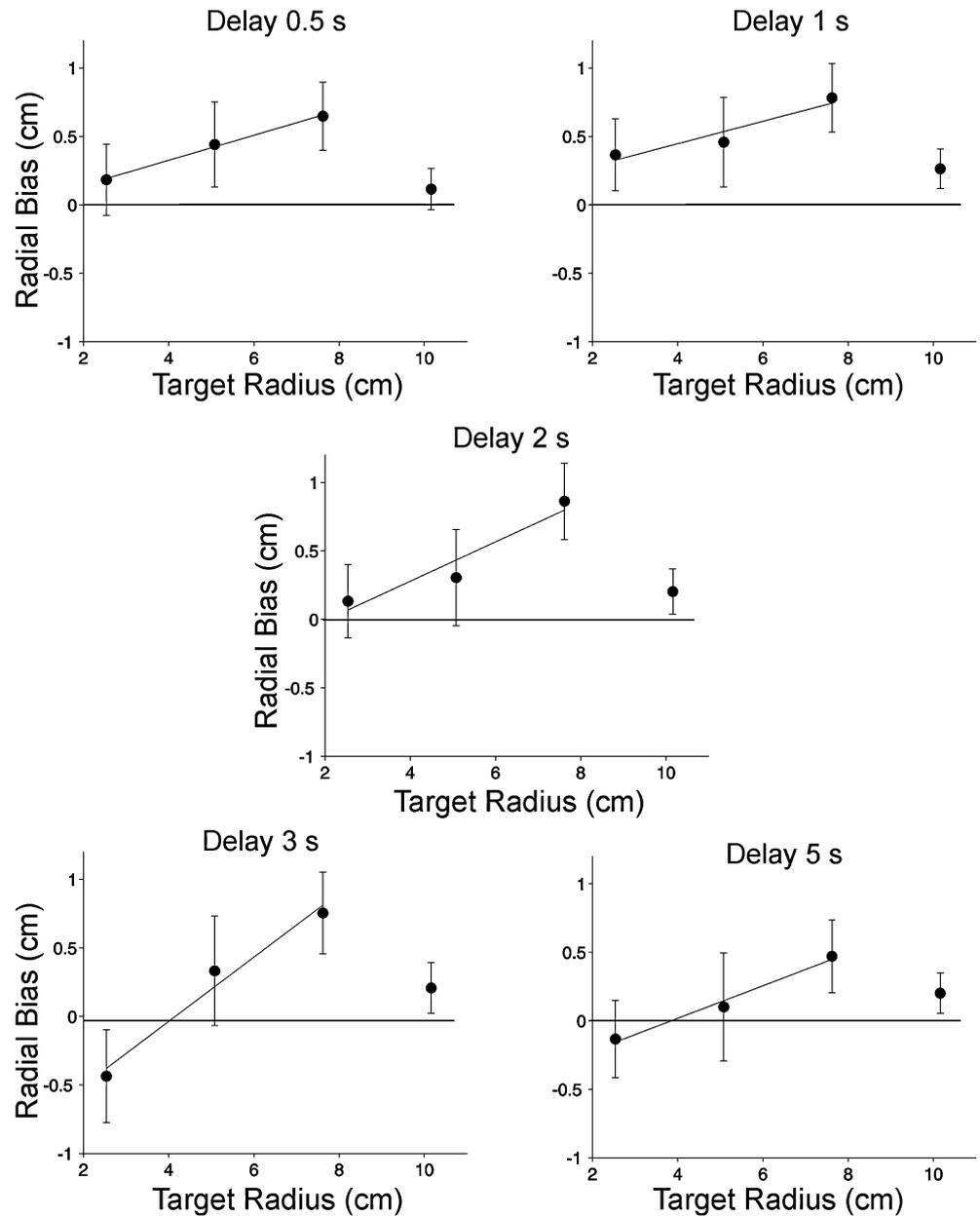


Fig. 5 Mean normalized area of the variance ellipse plotted against the dot radius for the different delay periods

Fig. 6 Mean \pm SD of the radial bias as a function of the dot radius, for the different delay periods. *Solid lines* correspond to the regression between these two variables for the first three dot radii

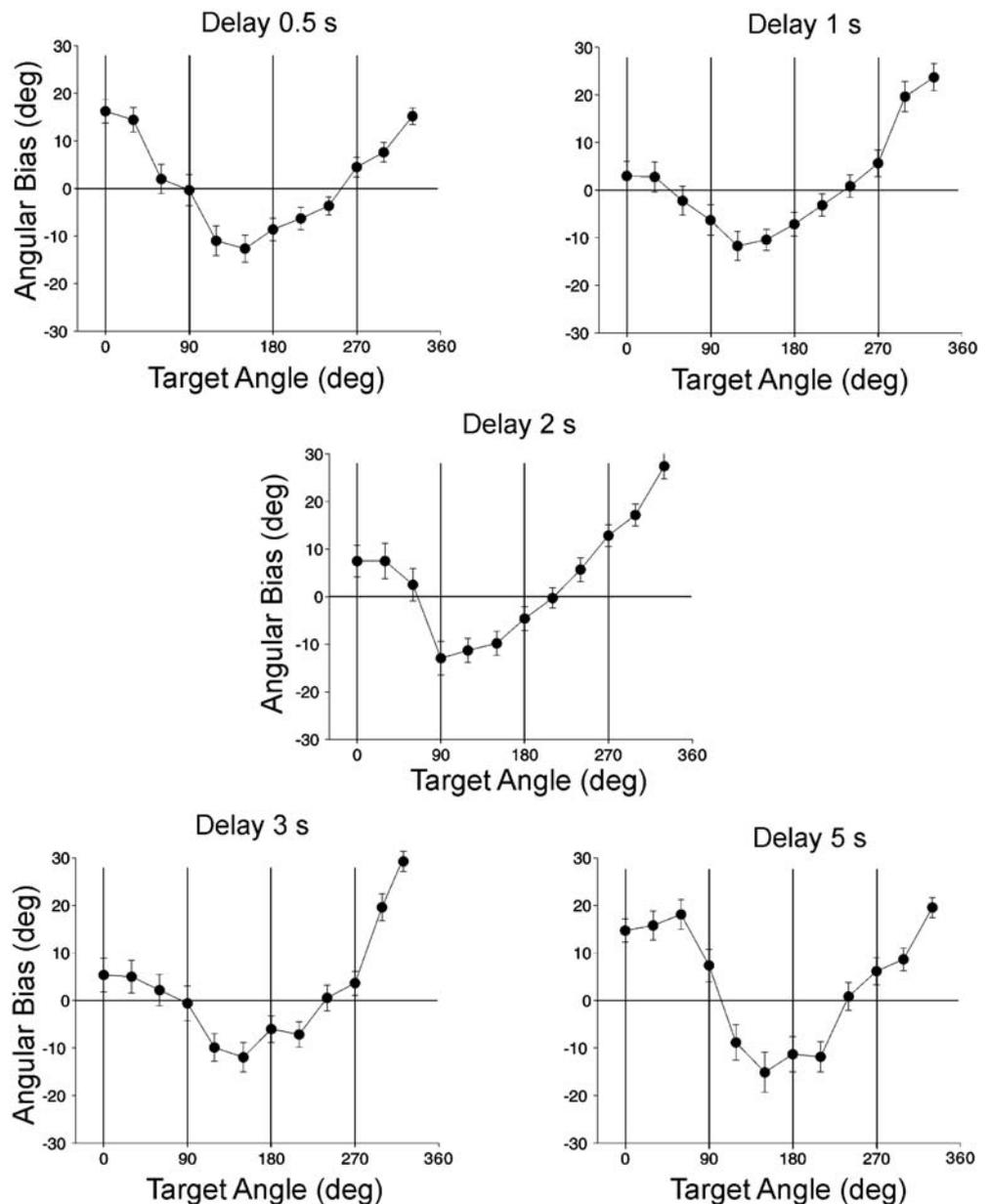


that the radial error was narrow close to the displayed circle (large ratio between the large and small axes of variability) and wider towards the center of the circle (with a log ratio close to 0). We performed an ANOVA using the log ratio of the ellipse axes as the dependent variable and the dot radius and delay as factors. The results showed a highly significant effect of the dot radius ($P < 0.00001$), but neither the delay nor the dot radius \times delay interaction were significant ($P = 0.29$ and $P = 0.17$, respectively). In addition, the log ratio of the ellipse axes did not show significant changes as a function of the dot angle, the delay or the dot angle \times delay interaction ($P = 0.33$, $P = 0.84$ and $P = 0.99$, respectively, ANOVA; Fig. 4B). The fact that the errors were smaller and most flattened at the circumference indicates that the monkey used the circumference as

a reference frame, whereas the lack of an angle effect stems most probably from the fact that no explicit angular information was provided to the monkey.

Next, we investigated whether the radial and angular information were coded independently. For that purpose, the correlation between the radial and angular bias was estimated on trial-by-trial data for each delay period. No significant correlation was found between these two measures. The Pearson's correlation coefficients were -0.006 , 0.008 , 0.044 , 0.044 , and -0.03 , for the delay values of 0.5, 1, 2, 3, and 5 s, respectively. Altogether, these results indicate that the monkey used a polar coordinate system, where the radial and angular components were independent. Therefore these measures were examined independently in the following sections.

Fig. 7 Mean \pm SEM of the angular bias against the dot angle for dots located inside the circumference

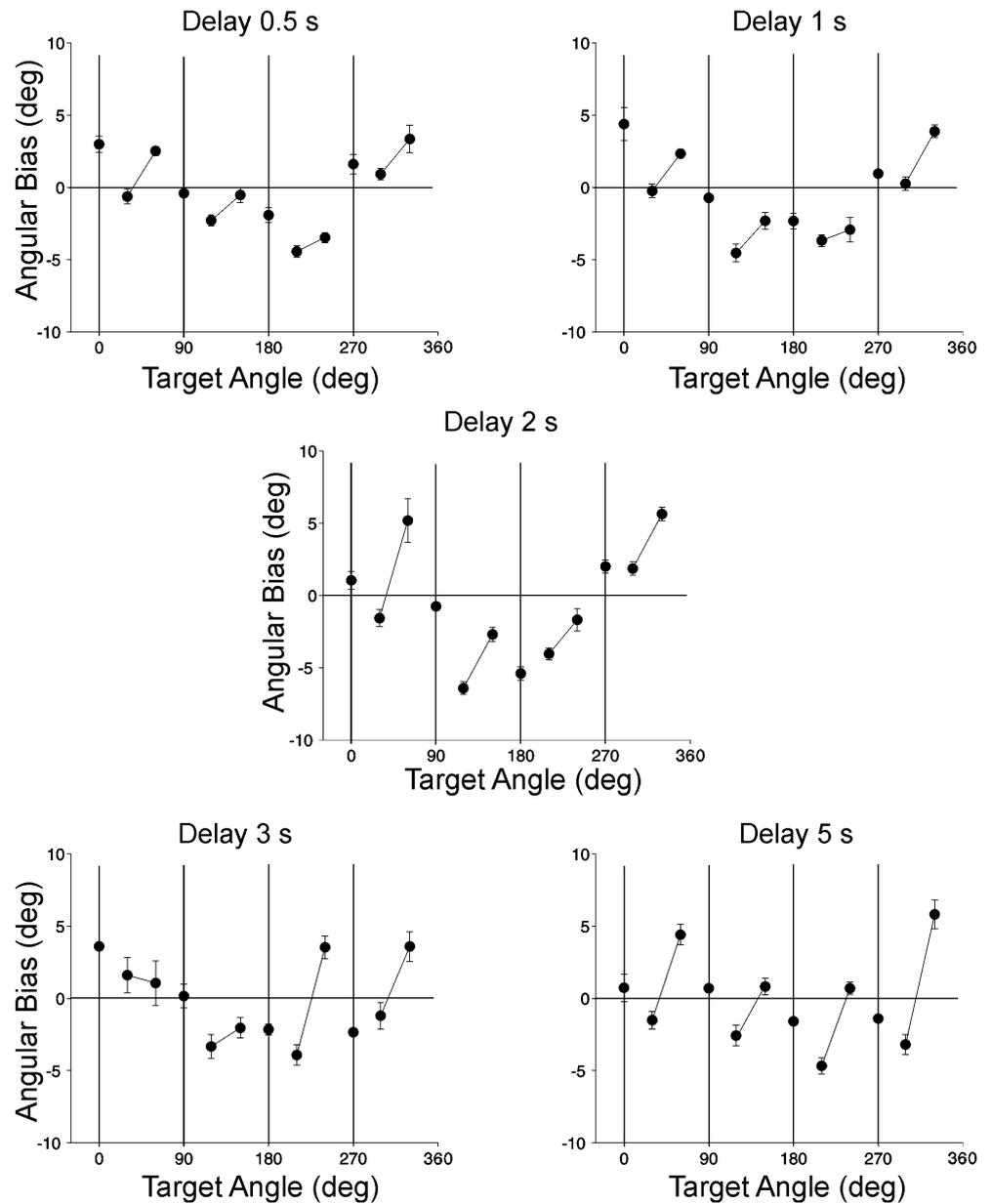


Finally, the overall variability in the response values was evaluated using the area of the variance ellipse. Figure 5 shows that the ellipse area increased with the length of the delay period until it reached a maximum at 3 s. With respect to the dot radius, the ellipse area was smallest for dots at the circumference (10.16 cm), reached its maximum at the mid-distance (5.08 cm) between the center and the circumference, and decreased again towards the center of the circle. An ANOVA using the ellipse area as the dependent variable, and the delay period and dot radius as factors, showed a significant effect in both factors and their interaction ($P < 0.0001$ for the three factors).

Categorical process

The formation of categorical prototypes and boundaries was evaluated for the radial and angular component of the monkey responses at various delay periods. The location of the radial and angular prototypes was defined as the point of zero bias within a particular category (see Appendix in Huttenlocher et al. 1991). Thus, we compared the radial bias as a function of the dot (target) radius in order to determine whether the monkey formed a radial prototype (Fig. 6). The results showed, first, that the radial bias was close to zero at targets lying on the circumference (radius of 10.16 cm), which indicated that the performance was quite accurate at these locations. Nevertheless, these values were not used to determine the radial proto-

Fig. 8 Mean \pm SEM of the angular bias against the dot angle for dots lying on the circumference. The *solid lines* are within quadrant regression lines of the angular bias as a function of the dot angle



type since the circumference acted as a reference frame. On the other hand, the response values for dots located inside the circle showed a substantial bias in the inward direction. This inward radial bias decreased linearly as a function of the target radius in all the delay periods (Fig. 6). Interestingly, the radial bias crossed zero (the radial prototype) only at delays of 3 and 5 s, which suggested that the formation of a radial prototype was delay-dependent (Fig. 6). In fact, a linear regression analysis was performed between the radial bias and the dot radius (at values of 2.54, 5.08 and 7.62 cm), and it was found that the radial prototypes were at 4.15 and 3.85 cm for the delays of 3 and 5 s, respectively. The regression models were statistically significant ($P < 0.0001$, F -test) in the five different delay periods, indicating that there was a systematic change in the radial bias as a function of the dot radius.

The accuracy was greatest on the dots located on the perimeter because the circumference was the reference frame. Although there was some degree of inward radial bias for the dot located in the circumference this bias was very small. The avoidance of the categorical boundary (in this case the circle) is probably the cause of this bias (see Huttenlocher et al 1991).

Regarding the angular prototype, the hypothesis was that the monkey formed categories by dividing the circle into four quadrants, using the horizontal and vertical axis as category boundaries and the diagonals as prototypes. The results showed that the monkey followed a different strategy depending on whether the dots were inside the circle or were lying on the circumference. For dots inside the response circle, the angular bias showed a characteristic pattern that was similar across delay periods (Fig. 7):

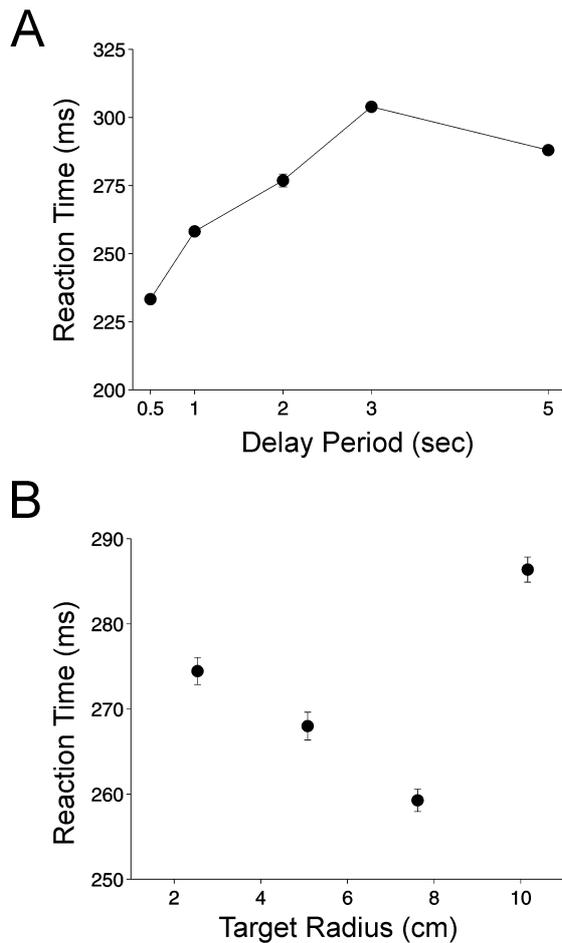


Fig. 9 Mean \pm SEM of the reaction time plotted as a function of the delay period duration (A), or as a function of the dot radius (B)

the angular bias was positive for the dots located in the right side of the circumference (for dot angles of 0–90° and 270–330°), and it was negative for the dots located in the left side (for dot angles 90–270°). In addition, the angular bias was close to zero at the dot angle of 90 and 270°. This pattern indicates that the monkey had a bias in the upward direction for all the dots and delay periods. Surprisingly, the upward bias at 300 and 330° was more pronounced than the adjacent angle of 0° for delays of 1, 2 and 3 s. Since this pattern was maintained across delay periods, it is likely that the angular bias changed depending on the relation between the sample and response circle, rather than on the formation of a category prototype (see discussion that follows).

In contrast, a clear delay-dependent effect was observed on the angular bias for the dots on the circumference (Fig. 8). First, at a delay period of 5 s the angular bias was small at the vertical and horizontal axes. In fact, the mean angular bias was 0.7, 0.69, -1.5 , -1.3 ° for the dots at 0, 90, 180 and 270°, respectively. Furthermore, in this delay, the angular bias showed a similar pattern within each of the four quadrants of the circle. Inside each quadrant, the response values were biased away from the

actual dot location in a direction toward the center of each quadrant. The quadrant centers or obliques are at 45, 135, 225 and 315°, and, indeed, the angular bias reached a value of 0° at dot angles that were close to these centers (Fig. 8). We carried out a linear regression analysis between the angular bias against the dot angle for each quadrant, in order to determine the angular prototypes. The results showed that the prototypic angular values from the within quadrant regressions were the following: 38, 152, 237 and 309° for the quadrants from 1 to 4, respectively. The linear regression fits were statistically significant for all circumference quadrants ($P < 0.0001$, F -test).

Reaction time

The RT was compared across delay periods and the target dot angle and radius. As expected, RT increased as a function of the delay period, peaking at the delay of 3 s (Fig. 9A). An ANOVA showed that the main effects of both the delay period and the dot radius on the RT were statistically

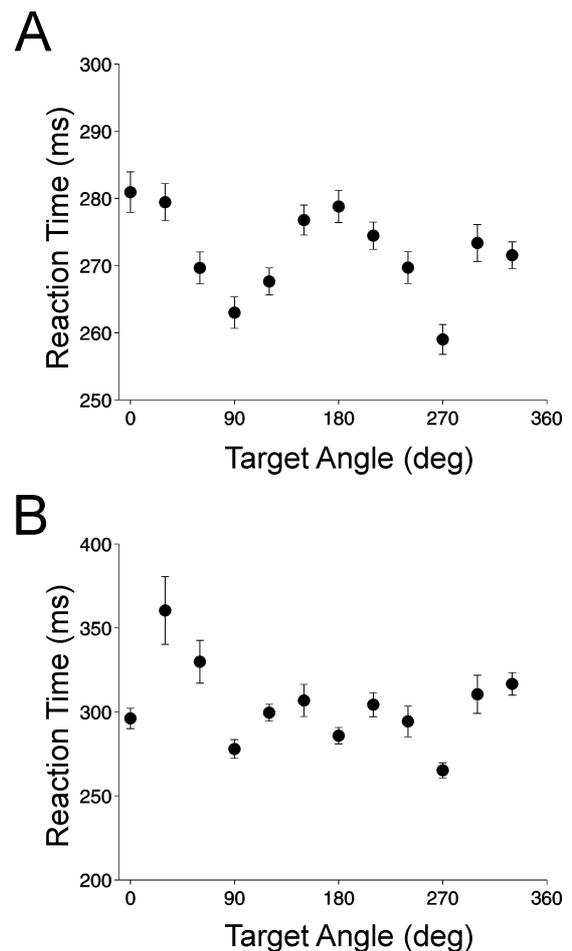


Fig. 10 A Mean \pm SEM of the reaction time plotted against the dot angle for all dot locations and delay periods. B Mean \pm SEM of the reaction time plotted against the dot angle for the dots located on the circumference and with a delay period of 5 s

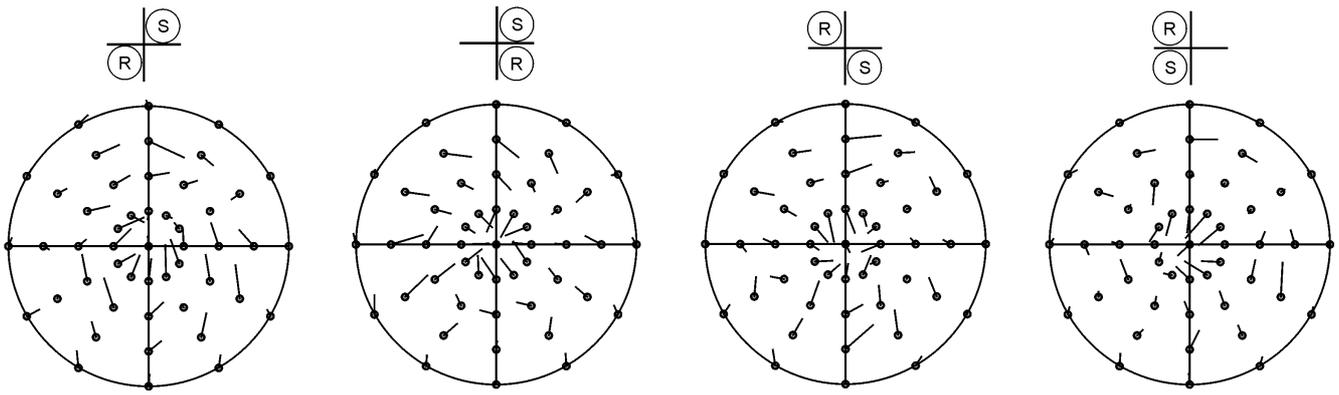


Fig. 11 Graphic displays of the vectors between the dot locations (*black circles*) and the mean response values (*open end*) for four different sample–response circle combinations. The relative position of the sample–response circles is illustrated in the *insets*

highly significant ($P < 0.0001$) but not their interaction ($P = 0.3$). In general, RT was longest for dots lying on the circumference (radius of 10.16 cm); it was shortest at the next radial value (radius of 7.54 cm), and then increased again for dots closer to the center of the circle (Fig. 9B).

Finally, the delay, the dot angle, and their interaction all had significant effects on the RT ($P < 0.0001$). Overall, the reaction time was shorter for dots located on the vertical axis, and gradually increased for dots located on the horizontal axis (Fig. 10A). Interestingly, the RT for dots located on the circumference followed a pattern that is congruent with the formation of an angular prototype, as follows. The RT was shorter at the dots lying on the vertical and horizontal axes, and longer for the dots at the obliques. However, this pattern was observed only at a delay period of 5 s that in fact, was the period where the angular prototypes were formed (Fig. 10B). A *t*-test indicated that there was a statistically significant difference in the RT between the dots in the axes and at the obliques ($P < 0.01$).

Relative spatial reference frames

The animal was required to maintain in memory the relative position of the dot in the circumference of the sample circle for an interval up to 5 s, and then to indicate where the dot was relative to a circumference (response circle) placed in another part of the computer monitor. We used an ANOVA in order to determine whether the relative position of the sample and response circles in the monitor had an effect on the response values of the monkey. The ANOVA model included the sine and cosine of the angular bias as the dependent variables, and the sine and cosine of the angle formed between the central location of the sample and response circles as independent variables. The results showed that the angle between the sample and response circle did not have a significant effect on the angular bias for any delay period. Therefore, it was likely that the monkey learned to associate the dot location with

a spatial response that was centered on the circumference as the reference frame, rather than the absolute position of the dot in the computer monitor. A typical example is shown in Fig. 11, where the vectors formed between the dot position and the mean location of the responses are illustrated for the 49 dot locations, in four combinations of sample–response circles. It is evident that the mean response locations were similar across the four sample–response circle configurations.

Discussion

This study demonstrated the ability of a rhesus monkey to represent the spatial location of a point in a circle and to hold this information in memory, using a fine-grain and a categorical level of coding. These results indicate that memorization of spatial location in the rhesus monkey may follow the same principles observed in humans.

Previous studies have demonstrated that monkeys are able to memorize different attributes of visual, auditory and tactile stimuli (Hernandez et al. 1997; Miyashita and Hayashi 2000; Wright 2002). In addition, the spatial memory performance in monkeys has been analyzed in delayed-match-to-place paradigms (Rainer et al. 1998) or delayed memory saccade or reaching tasks (Fuster 1973; Smyrnis et al. 1992; Chafee and Goldman-Rakic 1998). To our knowledge, the present study is the first to address the problem of the formation of spatial categorical prototypes under conditions of memory load.

The short-memory value of particular variables (e.g. color, size, space, time, etc.) tends to fade with time. The longer the time that a value needs to be retained, the more inexact is the memory trace of it (for review see Nairne 2002). In fact, if information is simply forgotten, a default value may be reported. Huttenlocher et al. (1991) proposed a model, which postulates that the memory for spatial location is hierarchically organized. The model states that the representation of spatial dots in memory has two levels of detail, namely a particular (fine-grain) value and a category. The fine-grain representation in memory is defined as a distribution of values centered on the true value. In contrast, a category is defined as a range of values limited by boundaries and centered on a prototype. The optimal weight of a prototype depends on the relative inexactness

of the remembered fine-grain value: as a fine-grain value becomes more inexact with passing time, the prototype weight becomes larger. The present results are in accordance with the assumptions of the model of Huttenlocher (1991) and colleagues. First, we found that the monkey was encoding fine-grain information using a polar coordinate system. Second, the variance of the spatial responses increased as a function of the delay period. Finally, with the longest delay durations, we observed the development of angular and radial prototypes. This means, then, that during the recollection of inexact memorized values, the monkey used categorical prototypes that led to a bias across the entire range of values away from the boundaries of a category. The monkey avoided the circumference and the center of the circle (radial boundaries) and also avoided the horizontal and vertical axes (angular boundaries) for the targets lying in the circumference.

Coding the location of a dot in a circle requires the use of a particular reference frame. A point may be encoded with respect to the body, the arm or the monitor and still be located accurately from memory. In the present study we trained the monkey extensively (over a year) to use the circumference as a reference frame. In order to divide the circumference into quadrants to form four different angular categories a system of axes must be imposed on the circle itself and the center of the shape must be identified as the origin. The fact that the monkey apparently did not form angular prototypes for dots inside the circumference means that this arbitrary frame of reference consisting of vertical and horizontal axes was not established within the circle. In contrast, the monkey succeeded to form angular prototypes on the dots located on the circumference. Two possible interpretations can be offered for this discrepancy. One interpretation is based on the premise that the circumference provided unequivocal radial information. Thus, it is possible that the monkey formed angular categories when radial information was provided. This implies that the monkey could establish categorical prototypes in just one dimension. Interestingly, children of 5–7 years behaved in a very similar fashion in a practically identical task (Sandberg et al. 1996). At this age, the children are able to show a radial prototype, but do not show angular prototypes. However, when angle is the only dimension to be encoded, these children also formed angular prototypes. Alternatively, it is possible that the monkey developed angular prototypes for dots lying on the circumference, because the circle was not completely perfect; due to the resolution of the graphics program the vertical and horizontal axes could be identified as small rectilinear regions (2° of visual angle). If this is true, then, the monkey used an extrinsic cue to categorize the circle in quadrants instead of an intrinsic reference frame.

Radial categorization, on the other hand, may be easier for the monkey because it does not require a mental subdivision of the circle. Only one prototype is needed. In addition, radial distances may be represented at fine-grain and categorical levels without the need for a concept of vertical or horizontal axes. Nevertheless, the development of a radial prototype required the notion of boundaries

that in this case corresponded to the center and circumference. Interestingly, we found that the variability of the responses was smaller at these two levels, which suggests that the monkey used the circumference as a reference frame, and that he also had a concept of the center of the circle. It is important to mention, however, that the pattern of radial bias observed in the present study is somehow different from the radial bias reported in humans. In human subjects the bias decreased as the radial value of the dot increased. In fact, humans create a radial prototype that is around two thirds of the radial extent of the circle. In our case, the outermost dots showed the largest inward bias, and the bias decreased as the dot radius decreased. The radial prototype of the monkey was around one third of the distance between the center and the periphery of the circle. This effect is probably not due to the skewed spread of the target dots caused by the polar distribution, because the formation of a radial prototype is delay-dependent. Only after delays larger or equal to 3 s did the monkey use a radial prototype, avoiding the circumference and the center of the circular test area.

Finally at the neurophysiological level it is likely that the cortical areas engaged in the representation of the fine-grain and categorical levels of coding include the posterior parietal cortex and the prefrontal areas. These areas are intensively interconnected, and are part of a network where multimodal sensory information is processed and complex motor signals are integrated. In addition, the activity of spatially tuned neurons in prefrontal and posterior parietal areas increases during working memory in both areas, creating memory fields (Gnadt and Andersen 1988; Funahashi et al. 1989; Chafee and Goldman-Rakic 1998). Moreover, lesions in these areas produce severe spatial and memory deficits (Quintana et al. 1989; Chafee and Goldman-Rakic 2000). Hence, a working hypothesis could be that neural mechanisms engaged in the representation of the location of a dot in a circle, correspond to the weighted interaction of neural ensembles in prefrontal and posterior parietal areas that separately encode the fine-grain and categorical levels of representation. This hypothesis remains to be tested.

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