

# Attention versus Intention in the Primate Premotor Cortex

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**One challenging issue in cognitive neuroscience has been to dissociate a variety of mental processes from one another in order to elucidate brain functions. Attention, in particular, has been a recurrent issue because of its strong links with perceptual, cognitive, and motor performances. This paper reviews data from neurophysiological experiments designed to dissociate neuronal activity related to visuo-spatial attention from preparatory activity in the monkey brain. Cell activity was recorded from the dorsal premotor area (PMd) and compared to the dorsolateral prefrontal cortex (DLPf), from which it receives inputs. PMd has been implicated in the planing and execution of voluntary movements (PMd), and the majority of its cells are active during tasks with instructed delay time. However, the activity of many PMd cells is not specifically correlated with movement preparation, as is observed when the animal is attending to a visual stimulus, although the proportion of attention-related cells is much lower than in the DLPf. The distribution of attention-related and intention-related neurons within PMd tends to vary along the rostrocaudal axis, with the former more frequent rostrally (PMdr) and the latter more predominant caudally (PMdc). In a functional magnetic resonance imaging (fMRI) study in humans, we compared the premotor activation in two tasks: a spatial attention/memory task and a motor preparation task. The results suggest a rostrocaudal specialization within PMd of the human brain, with attention-related activation rostrally and medially and intention-related activation caudally. These studies indicate strong similarities in the functional organization of dorsal premotor cortex of human and monkey.** © 2001 Academic Press

**Key Words:** spatial attention; neurophysiology; fMRI; monkey; human.

at it to analyze its features and locate it in space, reach toward it and grasp it. Because attentional, perceptual, cognitive and motor processes are intimately linked both in time and space, it has been challenging for neuroscientists to dissociate them under experimental conditions in order to understand their neural underpinning. This chapter focuses on the dissociation between spatial attention and/or memory from motor preparation (termed intention) in the dorsal premotor cortex of monkey and human.

Since the early 1980s, lesion experiments and single cell recordings in the monkey have shown that the primate premotor cortex plays a major role in sensorimotor and cognitive processes that lead to the selection and execution of voluntary actions (Passingham, 1985; Petrides, 1985; Wise, 1985). Early neurophysiological studies have confirmed that premotor cortex cells discharged in relation to movement planning and execution (Weinrich *et al.*, 1984; Wise, 1985; Godschalk *et al.*, 1985; Wise and Mauritz, 1985; Riehle and Requin, 1989). More recently, experimental designs have been developed in order to dissociate neuronal activity related to movement per se from spatial attention and sensory processing (Boussaoud and Wise, 1993a,b; di Pellegrino and Wise, 1993; Crammond and Kalaska, 1994). Several reviews have been focussed on the premotor cortex (e.g., Kurata, 1994; Boussaoud *et al.*, 1996; Wise *et al.*, 1997). Here, I will concentrate on the attention/intention dissociation. I will first summarize the main neurophysiological findings of single cell recordings from PMd and dorsolateral prefrontal cortex (DLPf) of awake monkeys (Fig. 1). Then, I will review evidence for the distinction between rostral (PMdr) and caudal (PMdc) subdivisions and show new evidence in support of a functional specialization within PMd in both monkey and human.

## INTRODUCTION

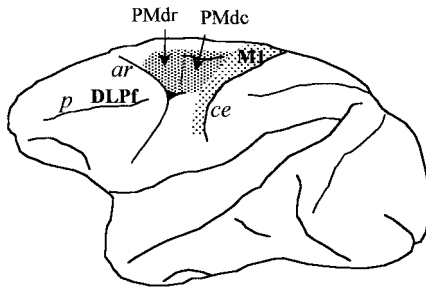
In the course of daily life, a particular object of the environment attracts our attention. We may then gaze

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## NEUROPHYSIOLOGY

### *Behavioral Task*

The task design has been described in detail elsewhere (Boussaoud and Wise, 1993a,b; Boussaoud and Kermadi, 1997). Briefly, monkeys were trained to perform a conditional visuomotor task where the color of a



**FIG. 1.** Lateral view of a macaque brain showing the dorsal premotor cortex (PMd) with its caudal (PMdc) and rostral (PMdr) subdivisions, dorsolateral prefrontal cortex (DLPF) and primary motor cortex (M1). Abbreviations used: ar, arcuate sulcus; ce, central sulcus; p, principal sulcus.

visual cue presented on a video monitor instructed a limb movement. To initiate trials, monkeys had to put their hand on a touch pad located at arm's reach, orient gaze to a central fixation point, and maintain fixation thereafter until the end of the trial (Fig. 2). Then, a red or green square appeared at a given location on the monitor and the monkey had to attend to that location, without moving gaze, in order to solve a later phase of the trial. This first stimulus is termed spatial attentional and/or mnemonic cue (SAM). After a delay, the SAM cue went off, and a motor instructional conditional cue (MIC) appeared. The MIC cue was often composed of both a red square and a green one (identical to those used as attentional cues), one of which was at the same location as the previous SAM cue (Fig. 2, trial 3). The response rule required the monkey to select the square at the SAM cue's location, discriminate its color and make a limb movement according to a conditional rule: red meant to contact the left touch pad, green meant to contact the right one. Occasionally, the MIC cue consisted of a single square presented at the same location as the SAM cue, and in some trials, it had the same color as well (Fig. 2, trial 1). The MIC cue lasted for a variable delay period, and its offset served as the go signal. The monkey then had to rapidly contact the appropriate pad in order to receive a reward. Different types of trials were presented in a random order and the monkey could not anticipate the location or color of the upcoming SAM cue. Before the MIC cue was presented, the animal could not predict the direction of the motor response, on the basis of the SAM cue alone, nor whether the forthcoming MIC is one square or two squares. In this situation, when the SAM cue was followed by an identical stimulus as the instructional cue (MIC), the same visual stimulus guided spatial attention and/or memory during the first part of the trial and instructed a limb movement during the second part of the same trial (Fig. 2, trial 1). A neuron whose discharge rate is higher following SAM cue than after the identical stimulus presented as a MIC cue is considered to be related to spatial atten-

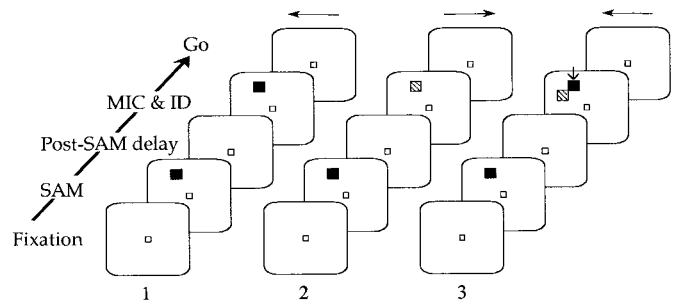
tion and/or memory. In the opposite case, the neuron is considered to be related to motor preparation (loosely termed hereafter, intention). Finally, neurons whose activity is not different following SAM and MIC cues is interpreted as reflecting sensory processing.

#### *Attention versus Intention in PMd*

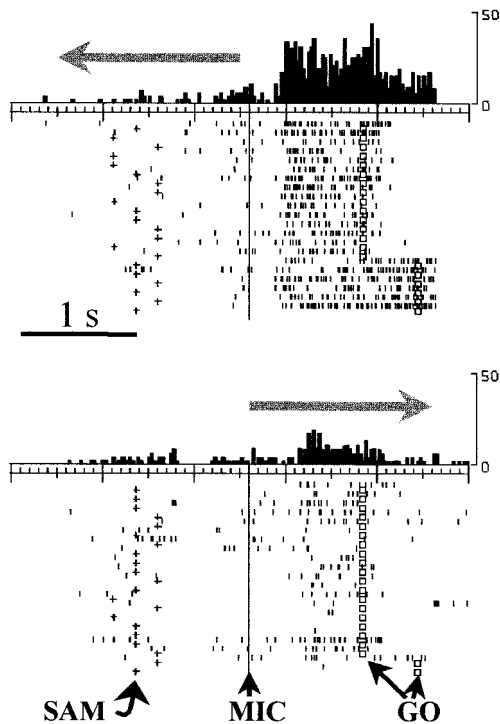
The main point in using the task described above was to determine whether PMd neurons discharge in relation to movement preparation as suggested by earlier studies, or whether their activity can be triggered by spatial attention alone. As expected, we found that for the vast majority of cells (70%), the activity was specifically related to movement preparation. For example, the cell illustrated in Fig. 3 is active during the instructed delay period, but was completely silent following the presentation of attentional stimuli. Furthermore, the discharge rate of most neurons varied depending on movement direction. The absence of activity following SAM cues, together with selectivity for movement direction are strong arguments in favor of the involvement of MIC-related cells in motor preparatory processes. However, for the remaining PMd cells (30%), the activity was triggered by the SAM cues, either preferentially or exclusively.

#### *Comparison with the Prefrontal Cortex*

Direct comparison of neuronal properties of DLPF and PMd (Fig. 4) in the same animals shows that the proportion of SAM-related cells is higher in the prefrontal cortex (69% of the sample) than in PMd (30%).



**FIG. 2.** Behavioral paradigm illustrated by selected trials. Each diagonally oriented column represents one kind of trial among 56 types used. Time progresses from bottom left to upper right, as represented by the arrow on the left. In each screen (large panel), the small square at the center represents the fixation point, the larger squares indicate the location of the stimuli. A filled square indicates a red stimulus, a hatched square represents a green stimulus. From bottom to top, the first panel shows the state of the video screen after the monkey has initiated the trial and put its gaze on the fixation point (fixation); the following panels represent the presentation of the spatial attentional/mnemonic (SAM) cue, the post-SAM delay, the motor instructional cue (MIC) period including the instructed delay (ID) time, and finally the offset of MIC (the go signal). The horizontal arrows indicate the direction of arm movement on each trial. The vertical arrow in trial 3 points to the square to select.



**FIG. 3.** Typical activity pattern of PMd neurons. Raster and histogram displays of cell activity. Several trials are grouped by movement direction (indicated by the horizontal arrows), independently of SAM's color or location. In each raster, a vertical tick indicates the time of occurrence of an action potential. A line of vertical ticks represents the neuron's activity in one trial. The trials are aligned on the onset of the MIC cue (vertical line). Beneath each raster line, the + signs mark the times of onset of the SAM cue, the squares show the time of offset of MIC (the GO signal). Above each raster is a poststimulus histogram (in black); scale, impulses/s; bin width, 20.4 ms. Note the absence of activity during the SAM and post-SAM epochs, and the increase of activity after MIC onset and during the instructed delay period, especially for movement to the left (top).

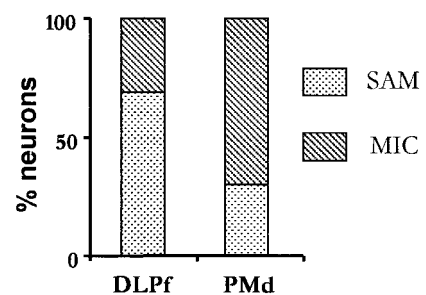
Conversely, the proportion of MIC-related neurons was higher in PMd (70%) than in the DLPf (31%). These findings support the view that DLPf is involved in spatial attention and/or memory (Funahashi *et al.*, 1990), whereas PMd is involved primarily during movement planning. Other aspects of the SAM/MIC design (see Boussaoud and Wise, 1993a,b; Boussaoud and Kermadi, 1997) allow the dissociation of activity related to stimulus versus movement parameters and support this view. In the DLPf, the activity of 57% of the cells is affected by changes in stimulus parameters, versus 2% of PMd cells. The proportions are reversed for movement effect, as relatively few MIC-related cells varied their discharge rate in relation to movement direction in DLPf, whereas more than 70% of PMd cells did so. Thus DLPf neurons are modulated by spatial attention/memory and process stimulus attributes, whereas PMd cells are less modulated by spatial attention/memory and specify movement direction.

## INTRINSIC ORGANIZATION OF PMd

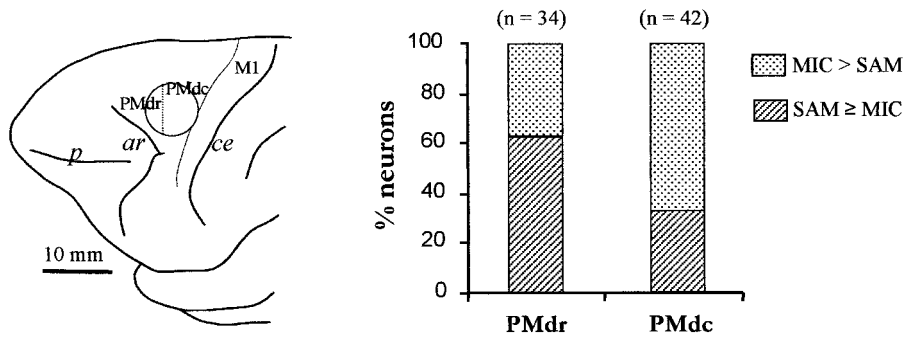
Evidence from a variety of studies suggests that PMd can be subdivided into at least a rostral (PMdr) and a caudal (PMdc) subdivision. Anatomically, prefrontal inputs appear to be concentrated in PMdr (see Boussaoud *et al.*, 1996, for review), which does not send appreciable projections to either the primary motor cortex or the spinal cord. By contrast, PMdc receives weak inputs from the prefrontal cortex but projects strongly to both M1 and the spinal cord. In addition, these two subdivisions of PMd receive differential inputs from the parietal cortex (Tanné *et al.*, 1995; Johnson *et al.*, 1996; Matelli *et al.*, 1998; Shipp *et al.*, 1998).

Physiologically, intracortical microstimulation elicits movements of the forelimb when applied to PMdc, whereas PMdr is not microexcitable (Sessle and Wiesendanger, 1982; Weinrich and Wise, 1982; Godschalk *et al.*, 1995). This is compatible with the anatomical connections described above. Furthermore, single cell recordings in awake monkeys reported differences in the neuronal properties of the two subdivisions (Johnson *et al.*, 1996; Tanné *et al.*, 1995). Cells in PMdr display activity in response to instructional cues, whereas cells in PMdc are less active in relation to the cues but discharge rather during the preparatory phase of movement as well as during movement execution.

Additional evidence to this physiological distinction comes from the SAM/MIC task. We analyzed the distribution of SAM-related and MIC-related cells within the explored zone of PMd in a monkey, where the recording chamber was implanted above PMdc and a portion of PMdr (Fig. 5). It appears that 65% of PMdc neurons were preferentially active in relation to MIC cues, versus 38% of PMdr cells. Conversely, 38% of PMdr cells were preferentially active in relation with SAM cues, versus 23% of PMdc cells. The remaining cells were equally active with both cues. Thus, cells with spatial attention/memory properties tend to be found rostrally, whereas intention-related cells are mostly found caudally in PMd, in agreement with the anatomical and physiological data reviewed above.



**FIG. 4.** Comparison of the proportion of SAM-related and MIC-related cells in the dorsolateral prefrontal cortex (DLPf) and the dorsal premotor cortex (PMd). See text for details.



**FIG. 5.** Functional specialization within the dorsal premotor area (PMd). The drawing of the macaque's left hemisphere shows the location of the recording chamber (circle). The dotted line depicts the approximate border between PMdr and PMdc. The graph shows the proportions of cells with SAM versus MIC activity. Cells assigned to PMdr are anterior to the dotted line, those assigned to PMdc are caudal to it. N, number of cells active with at least one of the two cues. Abbreviations used: See Fig. 1.

These data suggest that in the monkey, PMdr and PMdc play different roles in movement planning. Given its links with the prefrontal cortex and posterior parietal areas, PMdr might play a role in high order, cognitive processes that precede action plan such as selecting the goal of action and/or its temporal organization. By contrast, PMdc, which is connected with M1 and the spinal cord, would be more directly involved in movement preparation and execution.

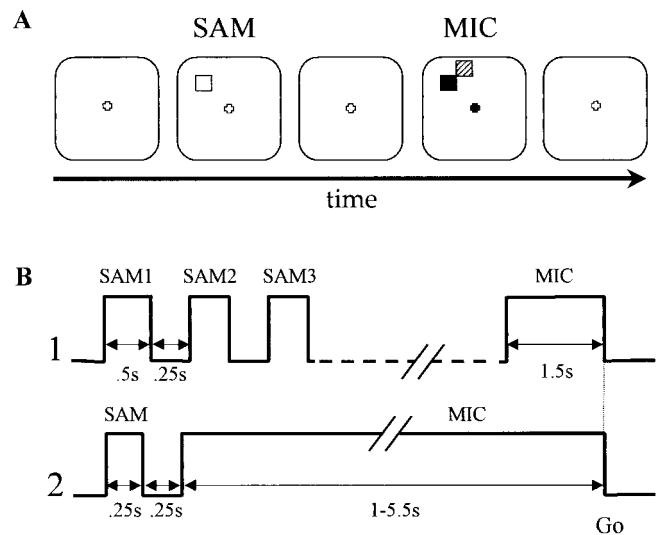
### Human Brain Imaging (fMRI)

**MRI scanning and data analysis.** We used a 1.5-T scanner (Philips NT, Best, The Netherlands). A volume composed of 25 adjacent axial slices (4 mm thickness each) was measured 24 times during each epoch. The functional scans were performed by means of a gradient-recalled echo, echo-planar imaging MR sequence. T2\*-weighted images were acquired. The major MR sequence parameters were TR = 3700 ms, TE = 45 ms, pulse angle = 90°, acquisition matrix = 64 × 64, field-of-view = 256 × 256 mm<sup>2</sup>. Data were analyzed using SPM-96 routines (Wellcome Department of Cognitive Neurology, London, UK; see Friston *et al.*, 1995). Analysis of the main effect of each task relative to its baseline were made in each individual brain and for the group of ten subjects, and fitted into the Talairach and Tournoux (1988) stereotaxic reference space.

The dorsal premotor cortex of the human brain has also been subdivided into rostral and caudal divisions (see Preuss *et al.*, 1996). Functionally, brain imaging studies have shown that, in general, human premotor cortex is active during motor preparation tasks and have suggested a functional distinction between rostral and caudal premotor areas (Deiber *et al.*, 1996; Passingham, 1996; Lee *et al.*, 1999). We tested this hypothesis in human subjects using a modified version of the SAM/MIC paradigm (Fig. 6) under fMRI. As in the monkey, the task was designed to dissociate activation related to spatial attention and/or memory from

activation reflecting motor preparation (Simon *et al.*, unpublished data).

Ten right-handed volunteers participated in the study. They all trained to perform the tasks before the scans until their performance reached 90% correct responses with stable reaction times. Each subject held a response key with the index finger on one key and the middle finger on another. Visual stimuli were presented on a video monitor and consisted of a central



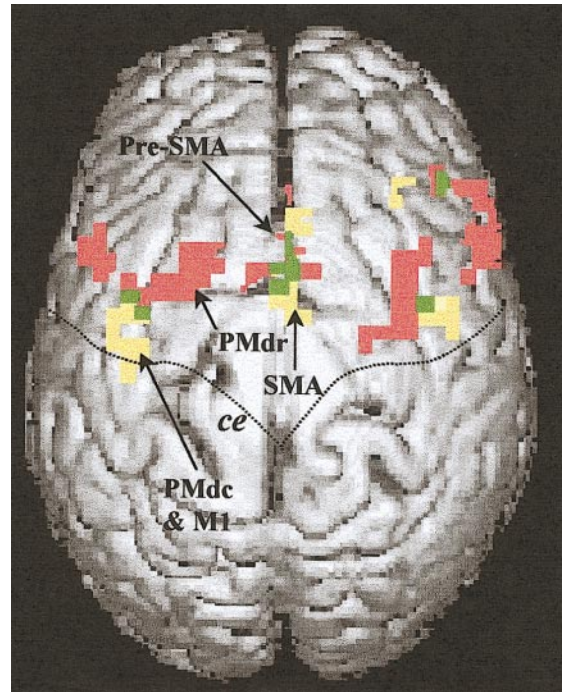
**FIG. 6.** Experimental design for functional magnetic resonance imaging (fMRI) experiment. (A) Basic structure of the task. Each panel represents the stimulation screen at a particular point in the task. First panel from left: a white cross at the screen center for fixation; Next, a white square (the SAM cue) is presented at a given peripheral location. After the delay (the last delay in the attention task), two squares were presented (MIC), one at the location of the previous SAM cue, the other at an adjacent location. They remain on for a fixed period of 1.5 s or for a variable period of 1–5.5 s. After this period, MIC was extinguished and, simultaneously, the cross changed color from white to either red or green. (B) Sequence of events for the *attention* (1) and *intention* (2) tasks. Note that in the attention task, SAM was presented 4, 8, or 12 times in each trial.

cross which served as a fixation point, and white, green and red squares ( $1.4^\circ \times 1.4^\circ$ ; eccentricity,  $29^\circ$  or  $40^\circ$ ) which served as the cues. There were four experimental blocs: the *attention task*, the *intention task*, and their respective baseline conditions.

**Attention task.** Subjects were asked to fixate the cross and not move their eyes until the end of the bloc. After a delay of steady fixation, a SAM cue (white square) was presented 4, 8, or 12 times at various locations (Fig. 6B1), with intervals of 250 ms between two presentations. Subjects had to attend to each square, as the number of presentations was pseudo random. After the last square, two adjacent squares appeared, one of which was at the location of the SAM. As in the monkey experiments, subjects had to respond according to the color of that square: if red press with the index finger, if green press with the middle finger. The baseline bloc matched the attention bloc in all sensory and motor parameters (same visual cues, same motor responses), except that subjects had to attend to the cross to detect a change in its color from white to either green or red, and respond following the same conditional rule. Thus the paradigm establishes two situations: one where attention is directed to stimuli appearing at the periphery (spatial attention), the other where these stimuli were irrelevant to the performance of the task and are presumably ignored by the subject. Subtraction of baseline activation from the activation during the attention task should thus eliminate activation related to visual processing and to execution of movement, and leave activity that is correlated with spatial attention/memory.

**Intention task.** In the intention paradigm, movement preparation is emphasized (Fig. 6B2): as in the monkey experiments, a single SAM cue indicated where to attend to, followed by a delay (250 ms), and by the MIC cue which lasts for a variable period of 1–5.5 s during which the subjects awaited for the go signal (the offset of MIC) to make the appropriate key press. The baseline bloc was identical in all visual and motor parameters, except that subjects were told to respond as soon as possible after MIC onset, and keep fixating until the end of the trial. Subtraction of the baseline activation from the intention activation should thus eliminate activation due to visual stimuli and movement execution, and leave activity related to movement preparation.

**Specific activation within the lateral premotor cortex.** The data resulting from the group analysis of the main effect of each task relative to its baseline are shown in Fig. 7. Only regions of interest to the present review are shown, i.e., the premotor cortex in the general sense. As the figure shows, both tasks activated the middle frontal gyrus bilaterally, as well as medial premotor areas (SMA and pre-SMA). The attention/memory task activated, in addition, the superior frontal



**FIG. 7.** Brain activation in relation with spatial attention/memory versus intention, represented on a dorsal view of the human brain (Montréal Neurological Imaging template). Group analysis of the main effects of the two tasks relative to their baseline conditions. Red, attention minus baseline; yellow, intention minus baseline; green, overlap of the two activations. Abbreviations used: Pre-SMA, rostral part of the supplementary motor area (SMA). The dotted line shows the approximate location of the central (ce) sulcus. For other abbreviations, see the legend to Fig. 1. Orientation: the front of the brain is up.

sulcus. Of interest to this paper, there was a large degree of segregation between the two activations along the rostrocaudal axis of the dorsal premotor cortex, especially on the left hemisphere. The intention task activated the caudal portion of the left premotor cortex, extending into M1 (BA 6/4; Talairach coordinates:  $X = -33$ ,  $Y = -7$ ,  $Z = 49$ ), whereas the attention/memory task activated a more anterior and medial region (Talairach coordinates:  $X = -20$ ,  $Y = 1$ ,  $Z = 49$ ). These data suggest a functional specialization within the human dorsal premotor cortex, comparable to the one described in the monkey.

## CONCLUDING REMARKS

The dorsal premotor cortex of monkey, an area known for its motor function, is not a homogeneous area. The caudal region (PMdc) is a true premotor area, in the sense that it has strong connections with M1, and contains cells that clearly code limb movement parameters, such as direction in space. In contrast, PMdr is connected with the prefrontal cortex, and its neuronal properties reflect sensory and attentional signals. This region represents an intermediate level of

information processing between the prefrontal cortex and PMdc. The homologous PMd in the human brain shows a comparable functional specialization, as suggested by fMRI data. However, spatial attention and spatial memory were not dissociable in the reviewed studies. Future experiments should use tasks that dissociate attention from memory and determine more precisely the functional specificity within PMd.

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