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Brain Mechanisms of Praxis

APOSTOLOS P. GEORGOPOULOS

ABSTRACT This chapter deals with the neural mechanisms of *praxis*, that is, purposeful motor actions. Three typical praxis tasks were used: copy geometrical figures, find exit routes in mazes, and construct objects from component parts. These tasks are commonly used in clinical neurology to determine the presence, and evaluate the severity, of constructional apraxia. Brain mechanisms were investigated using various methods and in different species, including experimental psychology (in human subjects and monkeys), functional magnetic resonance imaging (in human subjects), and single cell recordings from multiple sites (in monkeys). The results obtained provided new insights into how the brain deals with dynamic visuomotor processes and carries out purposeful *eupractic* motor actions.

Apraxia and constructional praxis

Apraxia has been defined as the "inability to perform certain subjectively purposive movements or movement complexes with conservation of motility, of sensation and of coordination" (Wilson, 1909). Apraxia typically is the result of parietal lobe damage, and occurs in three main forms. In *ideational* apraxia (Liepmann, 1920) there is a failure to perform a complex series of actions (e.g., to fold a piece of paper and place it inside an envelope); in *ideomotor* apraxia (Liepmann, 1920), the subject cannot execute a familiar action (e.g., a gesture on command or by imitation); and in *constructional* apraxia there is a disturbance "in formative activities such as assembling, building and drawing, in which the spatial form of the product proves to be unsuccessful, without there being an apraxia for single movements" (Kleist, 1934), or the "inability to assemble component parts into a coherent whole" (Koski, Iacoboni, and Mazziotta, 2002). In the first two forms of apraxia affected individuals have difficulty reproducing previously well-learned motor tasks. Thus, the mechanisms thought to underlie ideomotor apraxia have been considered to be disconnections between language and frontal areas (Geschwind, 1975) or, in addition, damage to stored representations of learned movement engrams (Heilman and Rothi, 1985; Gonzalez- Rothi, Ochipa, and Heilman, 1991; Poizner et al., 1995). In contrast, in constructional apraxia affected subjects have difficulty reproducing visual figures. Constructional apraxia is a fairly common neurological disorder (Gainotti, 1985; Förstl et al., 1993; Kirk and Kertesz, 1993). A crucial deficit in this disorder is the inability to copy a visual model (Benton, 1962, 1967; Gainotti, 1985) or assemble a two-dimensional or three-dimensional object from its component parts (Benton and Fogel, 1962). Although early studies pointed to a special role for the right cerebral hemisphere in constructional apraxia (Piercy, Hécaen, and Ajuriaguerra, 1960; Benton, 1967; Mack and Levine, 1981), more systematic later work (reviewed in De Renzi, 1982; Gainotti, 1985) supported the notion that this function is most probably subserved by both hemispheres.

Although constructional deficits are most often observed following damage to posterior parietal cortex, there is broad consensus that constructional deficits and other forms of apraxia also result from cortical damage that is confined to the prefrontal cortex (Luria and Tsvekova, 1964; Benton, 1968; Gainotti, 1985; Koski, Iacoboni, and Mazziotta, 2002). The fact that lesions in widespread cortical areas can cause constructional deficits led Benson and Barton (1970) to suggest that "drawing, by itself, is a reasonably good test for detecting brain damage." In fact, copying objects has been used as a probe to detect brain damage since early in the twentieth century (Poppelreuter, 1917). One possible reason why constructional ability is easily disturbed is that it is a complex task requiring the functional coordination of many different processes, including visuospatial perception and spatial motor planning. These factors are commonly tested in a different context, namely, route finding in simple drawings of mazes (Porteus Maze Test; Porteus, 1965). Interestingly, the performance of right-hemisphere-damaged patients in copying is highly correlated with their performance on route-finding tasks (Angelini, Frasca, and Grossi, 1992). These processes, then, collectively define *constructional praxis*.

Recently, we have studied the brain mechanisms underlying constructional praxis using three tasks, copying, mental maze solving, and mental object construction. The following discussion reviews our results and inferences that can be drawn from our studies.

COPYING Our first praxis task was copying shapes. To make a copy of a figure, one has to translate a visual pattern

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to a closely corresponding motor pattern. It is useful to contrast copying with tracing. In the case of tracing, the movement trajectory is *on* the visual template, whereas in the case of copying the movement trajectory is at a different spatial location. In tracing there is a close spatial proximity of the hand movement to the visual shape, and this enables the continuous visual guidance of the hand. In copying, on the other hand, the movement trajectory describes, ideally, the same figure as the visual shape, but is not superimposed on it. In other words, although there is a spatial correspondence between the visual figure and the movement, this correspondence is not immediately given but has to be imparted to the movement trajectory so that it conforms to the figure shown. Therefore, there are at least three key features of the function of copying: (1) the identification of the spatial characteristics of the figure, (2) the generation of a movement trajectory possessing the same spatial characteristics, and (3) in certain cases (e.g., handwriting) following a serial order in copying. Major theoretical contributions to these aspects were made by two great researchers of the twentieth century: N. Bernstein, on spatial aspects, and K. S. Lashley, on serial order.

Spatial aspects. In his article, "The Problem of the Interrelation of Co-ordination and Lateralization," Bernstein in 1935 drew attention to invariances in the shape of drawings made under very different conditions, such as using different effectors or different combinations of muscles and joints. He called these invariances "topological" and contrasted them with other, "metric" aspects of movement, such as size and location in space. He then speculated on the brain representation of motor topology, as follows:

> . . . [T]here is the deeply seated inherent indifference of the motor control centre to the scale and position of the movement effected. . . . It is clear that each of the variations of a movement (for example, drawing a circle large or small . . .) demands a quite different muscular formula; and even more than this, involves a completely different set of muscles in the action. The almost equal facility and accuracy with which all these variations can be performed is evidence for the fact that they are ultimately determined by one and the same higher directional engram in relation to which dimensions and position play a secondary role. (Bernstein, 1984 [1935], p. 109)

Work in our laboratory over the past several years has addressed precisely these topics, namely, the neural coding of spatial motor parameters. Initial work on the motor cortex led to the discovery of directional tuning in space (Georgopoulos et al., 1982), which in turn made possible the neural construction of a motor trajectory in space (Georgopoulos, Kettner, and Schwartz, 1988; Schwartz, 1994). This "neural trajectory" proved to be an accurate and isomorphic representation of the actual motor trajectory. Remarkably, this was also predicted by Bernstein. He wrote, "the higher engram . . . is extremely geometrical, representing a very abstract motor image of space" (Bernstein, 1984 [1935], p. 109). Indeed, space is pervasive in figure drawing. Unlike relatively pure temporal functions, such as tapping, figure drawing cannot be conceived apart from the spatial relations connecting the elements of the figure. Therefore, the geometric aspects of the shape become of fundamental importance for its drawing.

We recently studied the neural mechanisms of these more general spatial aspects in the prefrontal cortex of monkeys trained to copy simple geometric shapes using a joystick (Averbeck et al., 2002; Averbeck, Chafee, et al., 2003; Averbeck, Crowe, et al., 2003) (figure 35.1). The shapes were drawn as a series of oriented movement segments and therefore could be analyzed at different levels—for example, at the level of drawing single segments, at the level of the ordered sequence of segments, and at the level of the overall shape. The drawing trajectories that monkeys produced were divided into a series of discrete segments that varied in direction and length. We analyzed the neuronal activity of single cells by performing a stepwise multiple linear regression to identify those copy parameters that significantly influenced cell activity (Averbeck, Chafee, et al., 2003). We found that the copied shape (e.g., triangle, square) and the serial position of the segment within each trajectory were the most prevalent effects (in 46% and 43% of cells, respectively), followed by segment direction (32%) and length (16%). In contrast, significant effects of temporal factors (maximum segment speed and time to maximum segment speed) were less influential. These results demonstrate that prefrontal neurons encode global (i.e., shape), spatial (segment direction and amplitude), and serial order variables that define copy trajectories.

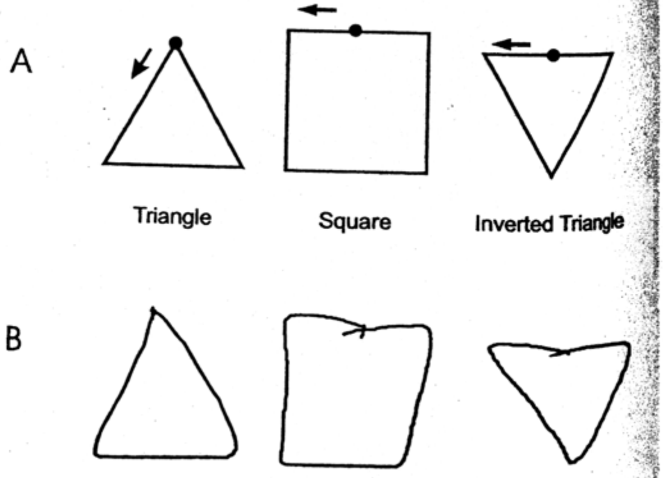

FIGURE 35.1 (*A*) Some shapes copied by monkeys. (*B*) Representative copies made by the monkeys. (Adapted from Averbeck et al., 2003a.)

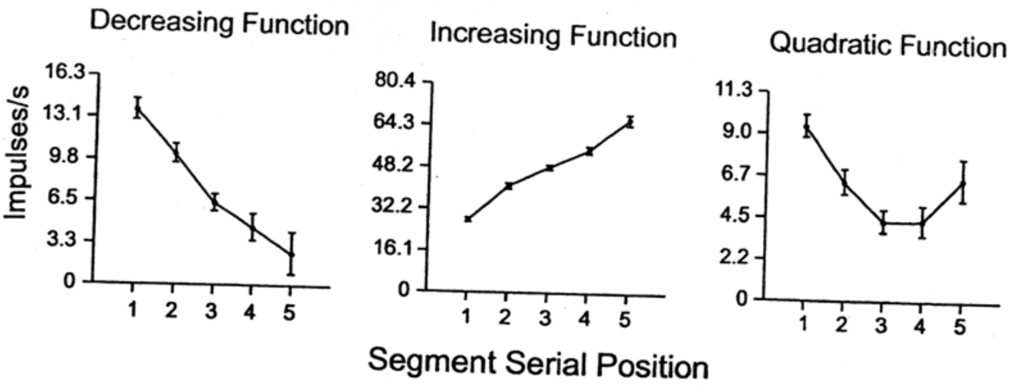

FIGURE 35.2 Typical curves of neural activity plotted against segment serial position. (Adapted from Averbeck, Chafee, et al., 2003.)

Serial order. In handwriting, letters and words are commonly written in an orderly, serial fashion similar to speech, where syllables and words are produced sequentially in time. Lashley (1951) pointed out that serial order is in fact fundamental to all forms of skilled action, from speech to reaching and grasping. He further believed that "[a]nalysis of the nervous mechanisms underlying order in the more primitive acts may contribute ultimately to the solution of the physiology of logic" (Lashley, 1951, p. 122). Speech is a prime example of elements organized serially at different levels: phonemes are uttered serially to make a syllable, syllables are strung together serially to form a word, words are uttered serially to make a sentence, sentences are combined serially to form a paragraph, and so on. In other motor actions, simple movements are executed serially to produce an integrated sequence (e.g., to reach for, grasp, and bring a cup to the mouth), a series of such sequences is performed to complete a task (e.g., get dressed), and so on.

One element common to all these examples is the serially ordered nesting of lower-order units of action (e.g., phonemes, simple movements) within higher-order units (e.g., syllables, integrated motor sequences such as drawing a shape). Lashley's major theoretical stance was the rejection of associative chaining theories and the suggestion of an alternative model based on parallel response activation. Much psychophysical evidence for this latter model has been gathered in speech and typing (MacNeilage, 1964; MacKay, 1970).

In the copying task we administered, monkeys copied the templates in a stereotypic order. Therefore, the serial order in copying consecutive figure segments was an integral aspect of the copying process. As noted earlier, the serial order in which the segment was presented and copied had a significant effect on prefrontal neural activity. In a subsequent analysis, we investigated whether this serial-order-related neural activity followed any systematic pattern. For this purpose we calculated adjusted means for the segments, that is, adjusted for the effects of all other main effects, except the serial position of the segment. This was done for all cells whose activity was significantly related to segment serial position in the regression analysis. We discovered that in many cells there was a systematic variation of neural activity with the serial position of the segment, described by monotonically increasing and decreasing functions as well as by parabolic functions (figure 35.2). These findings indicate that, within the copying task, the serial segment position is a key factor for neural activity in the prefrontal cortex. Monotonically increasing and decreasing functions were found in 38/245 (16%) and 89/245 (36%) of cells, respectively. Other functions were observed in 118/245 (48%) of cells (Averbeck, Chafee, et al., 2003).

Neural coprocessing of spatial attributes and serial order. The multiple regression analysis we performed identified the factors that had a significant influence on cell activity. A major finding of this analysis was that single cell activity is influenced significantly by global (i.e., shape), spatial (segment direction and amplitude), and serial order variables that define copy trajectories. Therefore, we wanted to find out whether, and to what extent, these effects occurred together (for a single cell); that is, whether they occurred more frequently together than would happen by chance. For this purpose, we constructed a number of 2 × 2 tables containing data for a pair of factors (e.g., segment serial position and segment direction) and their binary attributes (significant effects present or absent). Chi-square statistics (two-tailed) were used to evaluate the level of statistical significance of association between the effects of a pair of factors. Because each factor could have an effect independently of the other factor, we also wanted to calculate the odds by which the co-occurrence of the two effects exceeded the level of independent occurrence. For this purpose we used the odds ratio. Finally, we were interested in testing the hypothesis that single cells might coprocess more than two of the four attributes—shape, segment serial position, direction, and length. We used loglinear analysis in this case to assess the statistical significance of higher-order associations.

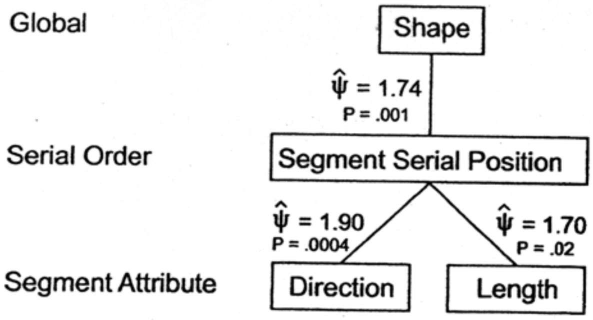

FIGURE 35.3 Systematic association in processing together various copying variables by single cells in the monkey prefrontal cortex. Numerical values are odds ratios. (Adapted from Averbeck, Chafee, et al., 2003.)

A major finding of this analysis was that specific groupings of significant effects tended to occur together in single neurons (Averbeck, Chafee, et al., 2003). Specifically, single neurons simultaneously processed the serial position of a segment within each trajectory along with the corresponding spatial (but not temporal) attributes of that segment (i.e., direction and length), as well as the overall shape to which the segments belong (figure 35.3). The effects were strong, as shown by the high values of the odds ratio. (In the absence of an effect, the odds ratio would equal 1.) For example, in the case of shape and segment serial position, the odds ratio of 1.74 means that the likelihood of these two factors being processed together was 74% higher than the likelihood of being processed separately.

Finally, the results of the loglinear analysis provided a clear result with respect to higher-order associations among the factors of shape, segment serial position, segment direction, and segment length. We found that the single four-way association among all of these factors was statistically significant ($P = 0.025$). This finding suggests that single cells also process all four factors concurrently. These findings underscore the central role of serial order, as well as the importance of global (shape) and specific spatial attributes (direction and length), for the neural mechanisms of copying in the prefrontal cortex.

Cotemporal representation of serial order. The results just described demonstrate the pervasive influence of serial order on neural activity at the single cell level. In a different analysis (Averbeck et al., 2002), we examined the simultaneously recorded activity in small neuronal ensembles to determine the time-varying representation of segment serial position. Specifically, we wanted to test Lashley's hypothesis that there is a cotemporal activation of serially ordered action units: "There are indications that, prior to the internal or overt enunciation of the sentence, an aggregate of word units is partially activated or readied" (Lashley, 1951, p. 119). Lashley also postulated a scanning mechanism by which these cotemporal representations would be translated int serial actions:

> [I]ndications . . . that elements of the [sequence] are . . . partial activated before the order is imposed upon them in expressio suggest that some scanning mechanism must be at play in regula ing their temporal sequence. The real problem, however, is th nature of the selective mechanism by which the particular acts ar picked out in this scanning process and to this problem I have n answer. (Lashley, 1951, p. 130)

In our experiments (Averbeck et al., 2002) we sought t (1) test Lashley's hypothesis on cotemporal activation o action representations, (2) seek a neural code for the seri order of these cotemporal representations, and (3) use thi code to investigate several aspects of serial order behavio For this purpose, we used a linear discriminant analysis t analyze the ensemble data recorded during copying an drawing of a sequence of segment, as follows. First, eac trial was divided into a sequence of epochs, with each epoc spanning the drawing of a single segment of a shape. The the average firing rate during the drawing of each segmen was calculated for all the cells in an ensemble (these pattern of ensemble activity can be considered neural representations of the segments). Next, the ensemble pattern for eac segment was averaged across correct trials and used to deriv discriminant classification functions for that ensembl namely, one classification function per segment. These functions were then used to classify particular ensemble activit patterns as belonging to a specific segment. For that purpos we calculated the posterior probability that the patter belonged to different segments, and the pattern was classified as belonging to the segment category with the highes posterior probability—that is, the "most probable" segment We imposed the constraint that ensemble activity patterns i a given trial were classified only to those segments belonging to the shape drawn on that trial.

The results showed that the rank of the strength of representation of a segment in the neuronal population durin this time predicted the serial position of the segment in th motor sequence. Moreover, an analysis of errors in copyin and their neural correlates supplied additional evidence fo this code and provided a neural basis for Lashley's hypothesis that errors in motor sequences would be most likely t occur when a subject was executing elements that had prio representations of nearly equal strength.

Mentally tracing a maze route

BEHAVIORAL AND NEUROPHYSIOLOGICAL STUDIES Ou second praxis task involved maze solving. In this task neithe copying nor construction is involved. Instead, the subject has to follow a route to exit a maze with blind alleys. Lik copying and constructing, then, this task involves a dynamic spatial process.

In recent studies we investigated the behavioral (Crowe, Averbeck, et al., 2000; Chafee et al., 2002) and neural (Chafee et al., 1999; Crowe, Chafee, et al., 2000, 2003) mechanisms underlying this process in the absence of explicit tracing of the maze path. Subjects looked at mazes with orthogonal distracters and were required to indicate which of several possible routes exited the maze (Crowe, Averbeck, et al., 2000), or to indicate whether a given route exited or not (Chafee et al., 1999, 2002; Crowe, Chafee, et al., 2000, 2003). In both tasks, the response time increased as a linear function of the length of the path and the number of orthogonal turns in the path (figure 35.4). This finding indicates that the postulated dynamic spatial process involves a mental tracing of the maze path. Direct neurophysiological evidence for that hypothesis was obtained from experiments in which neuronal activity was recorded in area 7a of the posterior parietal cortex of monkeys during mental maze solving (Crowe, Chafee, et al., 2000, 2003). In these experiments, monkeys were required to determine from a single point of fixation whether a critical path through the maze reached an exit or a blind ending. A delay period of 2–2.5 sec was imposed between the onset of the maze and the appearance of a go signal. We found that during the delay the activity of about 25% of neurons (N = 1200) in area 7a

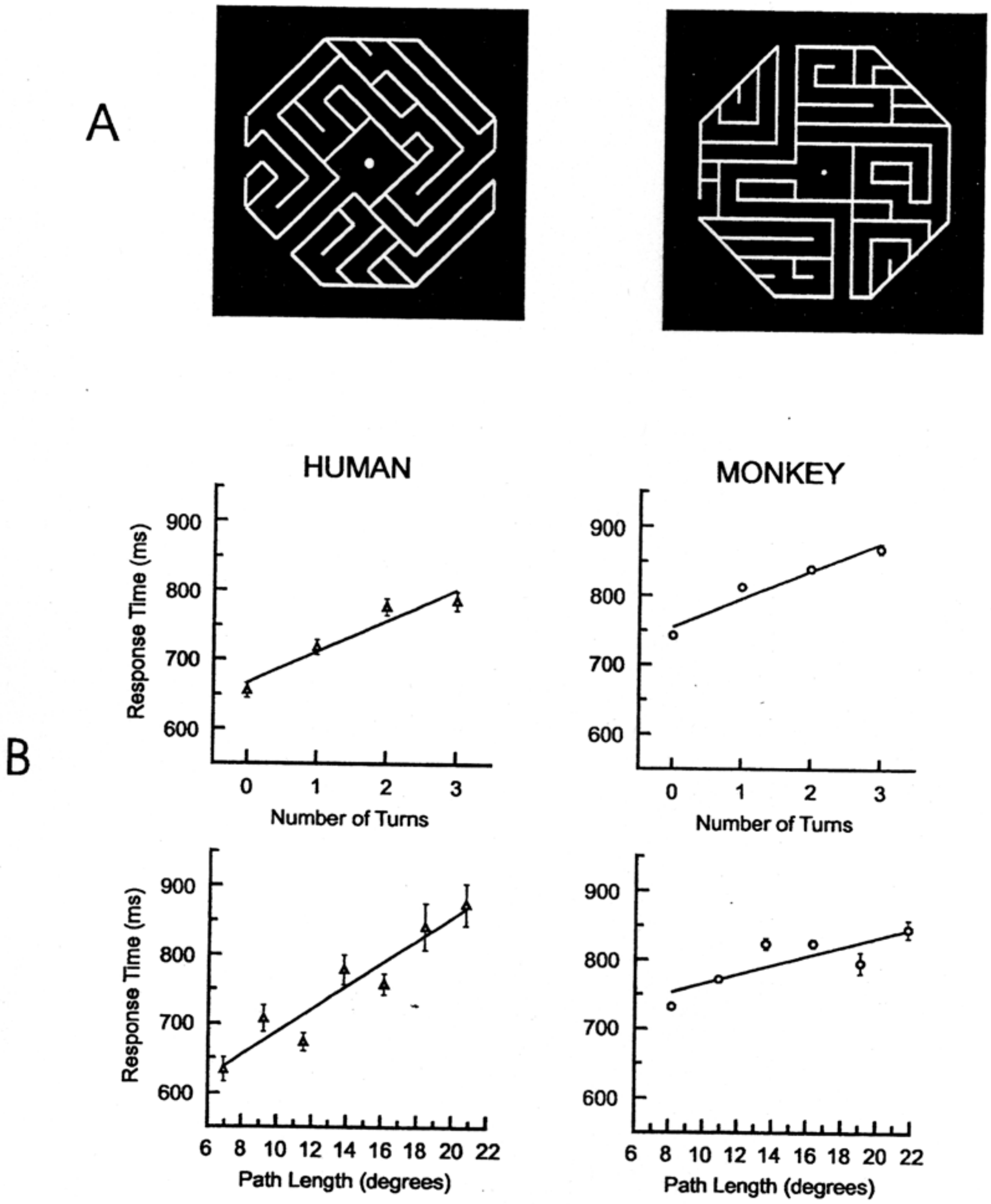

FIGURE 35.4 (*A*) Examples of mazes used. (*B*) Variation in response time with maze path length and number of turns in human subjects and monkeys. (Adapted from Chafee et al., 2002.)

was spatially tuned to maze path direction (Crowe et al., 2003). Clear evidence from control tasks indicated that the path tuning did not reflect a covert saccade plan, since the majority of neurons active during maze solution were not active on a delayed-saccade control task, and the minority that were active on both tasks did not exhibit congruent spatial tuning in the two conditions. We also obtained evidence that path tuning during maze solution was not due to the locations of visual receptive fields mapped outside the behavioral context of maze solution, in that receptive field centers and preferred path directions were not spatially aligned. Finally, neurons tuned to path direction were not present in area 7a when a naive animal viewed the same visual maze stimuli but did not solve them. These results support the hypothesis that path tuning in parietal cortex is not due to the lower-level visual features of the maze stimulus but rather is associated with maze solution, and as such reflects a cognitive process applied to a complex visual stimulus. Furthermore, an analysis of the ensemble activity using the neuronal population vector (Crowe, Chafee, et al., 2000) showed that time-varying population vectors traced the maze path, from the fixation point (at the center of the display) to the exit of the path. These findings are in accord with the behavioral evidence we obtained that mental maze solving is accomplished by mental tracing of the route.

FUNCTIONAL MAGNETIC RESONANCE IMAGING STUDIES The major and robust result of these neurophysiological studies was the finding of directional path tuning of single cells in the posterior parietal cortex. Prompted by this evidence, we carried out fMRI experiments in human subjects in which we focused on the superior parietal lobule during mental maze solving. Subjects solved the same kind of mazes that the monkeys solved. Octagonal mazes were shown for 300 ms. They had a straight main path that extended from the center to one of eight directions, every 45°; the rest of the maze was filled with random linear distracters. The main path was either open at the end ("exit maze") or closed by a line ("no-exit maze"); subjects had to indicate the exit status (present or absent) of the maze by pushing respectively the right or left buttons of a button press. High-spatial-resolution blood oxygen level-dependent (BOLD) activation images were acquired at high magnetic fields of 4 tesla (Tzagarakis et al., 2001, 2002, 2003; Gourtzelidis et al., 2003) and 7 tesla (Tzagarakis et al., 2003). In the 4-tesla experiments, the spatial resolution was $1.56 \times 1.56 \times 3$ mm, whereas in the 7-tesla experiment it was $1 \times 1 \times 1.5$ mm. On both experiments we found that the direction of the maze path had a significant effect on the BOLD signal in many voxels, and that a systematic variation of the pattern of activation with the direction of the maze path was also present. These results of the fMRI studies are in accord with those obtained from neurophysiological studies and, in addition, provide evidence for an orderly representati the direction of mental tracing in the human superior etal lobule.

Mentally reconstructing an object

Our third praxis task involved the mental construction o object out of its fragments. This task can be considered c plementary to copying: in both tasks the same picture be shown, but in copying, the component parts and spatial relations among them are replicated, whereas in structing, these relations are reproduced out of ready-m component parts.

We studied the process of object construction in its m abstract form, in dissociation from movements used to br component parts together. Specifically, we used 25 geom ric fragments of a square (figure 35.5) in two visual ima processing tasks requiring judgments on object construct (FIT task) or object sameness (SAME task). In initial beh ioral studies (Whang, Crowe, and Georgopoulos, 1999), su jects rated the FIT-ness or SAME-ness of the pairs and a indicated (in a different session) whether the two fragme in a pair could make a complete square or whether they w the same. A multidimensional scaling analysis of the num ical subjective ratings and response times for these judgme showed that within the same set of geometric objects, d ferent shape-related properties were emphasized under d ferent task conditions. The similarity judgment depend most on a representational dimension related to enclosure space, while the fit judgment depended to a greater exte on a dimension related to the symmetry properties of t fragments. This pattern of results was found in both the su jective ratings and the response times, as analyzed both MDS and by confirmatory classic statistics. These findin suggested that mental representations of the same visu image—that is, a fragment pair—are task dependent.

Next, we investigated the neural mechanisms underlyin these tasks in an fMRI study at 4 tesla (Georgopoulos et al 2001). In the FIT task, subjects had to indicate, by pushin one of two buttons, whether the two fragments could matc to form a perfect square, whereas in the SAME task they ha to decide whether the fragments were the same or not. In control task that preceded and followed each of these tw tasks, a single square was presented at the same rate and subjects pushed any of the two keys at random. We found tha the inferior temporal gyrus was activated exclusively durin the FIT task, whereas all other areas showed activatio during both tasks but to different extents. These results indicate that there are distributed, graded, and partially overlapping patterns of activation during performance of the two tasks. We attribute these overlapping patterns of activation to the engagement of partially shared processes, in accord with the results of neuropsychological studies, which

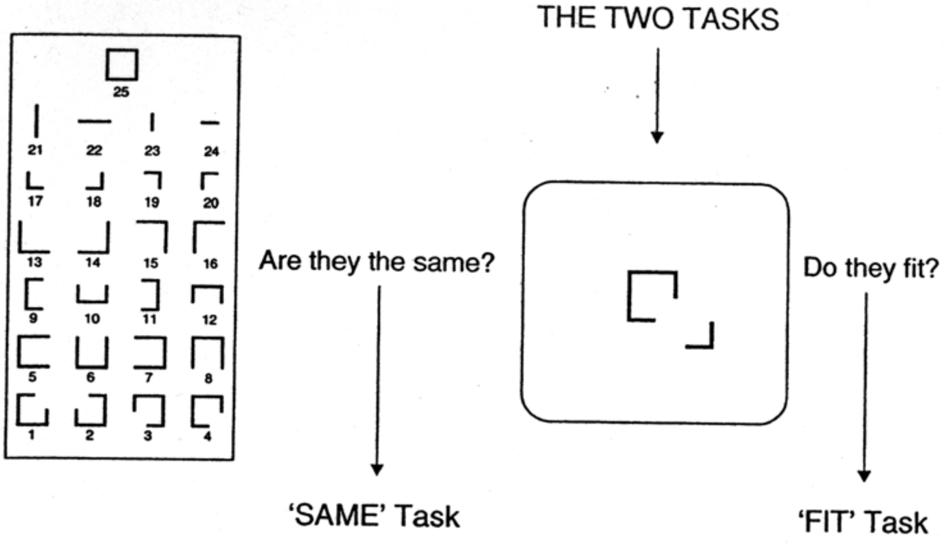

FIGURE 35.5 The 25 square fragments used in object discrimination and mental construction (left), and an example of the task (right). (From Georgopoulos et al., 2001.)

have shown that visuoperceptual, visuospatial, and visuoconstructive deficits can result from focal lesions in various cortical areas (Black and Bernard, 1984; Kertesz and Dubrowolski, 1981; Mehta, Newcombe, and Damasio, 1987).

A clustering analysis revealed three types of clusters with activated voxels: FIT-only (111 voxels), SAME-only (97 voxels), and FIT + SAME (115 voxels). Voxels contained in FIT-only and SAME-only clusters were distributed approximately equally between the left and right hemispheres, whereas voxels in the SAME + FIT clusters were located mostly in the left hemisphere (figure 35.6). With respect to gender, the left-right distribution of activated voxels was very similar in women and men for the SAME-only and FIT + SAME clusters but differed for the FIT-only case, in which there was a prominent right-sided preponderance for men (figure 35.7). Given that the two tasks involved the same visual stimuli (fragments of a square) as well as the same visual control stimuli (whole square), these results point to fundamental differences in the brain mechanisms underlying each task, as well as to basic differences between women and men in the visual object construction task. Specifically, we conclude that (1) cortical mechanisms common for processing visual object construction and discrimination involve mostly the left hemisphere, (2) cortical mechanisms specific for these tasks engage both hemispheres, and (3) in object construction only, men engage predominantly the right hemisphere, whereas women show a left-hemisphere preponderance.

Previous studies of the effects of sidedness and sex on the performance of visual tasks in people with brain damage focused on visuoconstructive abilities, best reflected in our FIT task, in addition to studies of language-related functions. With respect to lateralization of visuoconstructive function, it is generally believed that the right hemisphere plays a crucial role in that function (Piercy, Hécaen, and Ajuriaguerra, 1960; Smith, 1969; Benton, 1967; Gott, 1973; Nebes, 1978; Mack and Levine, 1981). However, there is substantial controversy regarding this matter (see De Renzi, 1982; Gainotti, 1985). Part of this controversy stems from the fact that differences may exist between women and men such that the effects of right- or left-hemispheric lesions may depend on gender. In men, right-hemispheric lesions seem to be more effective in producing visuoconstructive deficits, as compared to either left-hemispheric lesions in men or right-hemispheric lesions in women (McGlone and Kertesz, 1973; Lewis and Kamptner, 1987). In women, on the other hand, the effects of left-hemispheric lesions on visuoconstructive functions are similar to those of right-hemispheric lesions in women (McGlone and Kertesz, 1973; Lewis and Kamptner, 1987) but similar (McGlone and Kertesz, 1973) or worse (Lewis and Kamptner, 1987) than the effects of left-hemispheric lesions in men. Assuming a preponderant role of the right and left hemispheres in visuoconstructive and language skills, respectively, it has been proposed that a given task may be performed using spatial or verbal procedures, and that women, being more expert in language skills (Hobson, 1947; Meyer and Bendig, 1961; Wechsler, 1958), may tend to use preferentially verbal strategies (Kimura, 1969), hence their smaller dependence on the right hemisphere. Then, the gender differences are explained by postulating that men and women employ fundamentally different strategies to perform these tasks, based on spatial or verbal operations, respectively. A variant of this idea makes use of the concept of "synthetic" (nonverbal) and "analytic" (verbal) functions for which the right and left

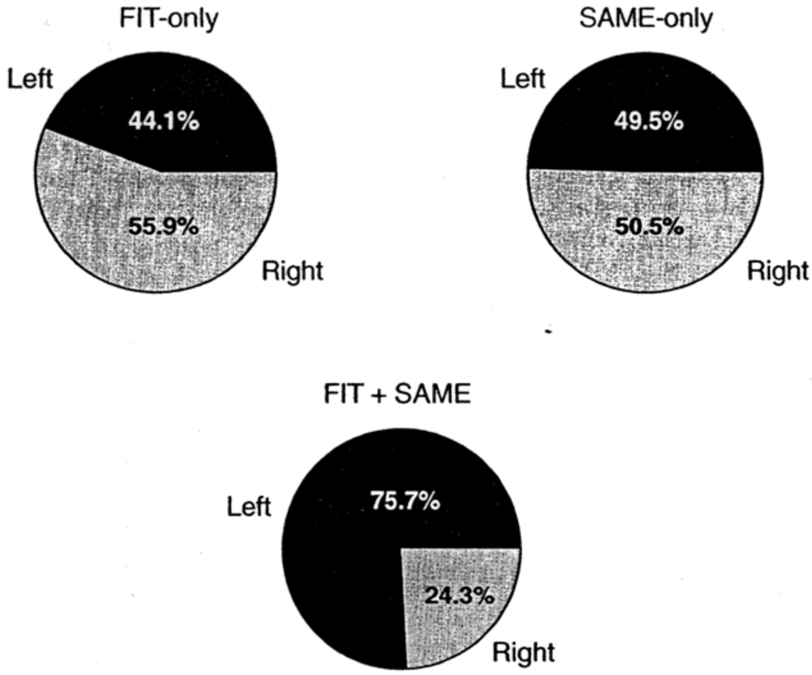

FIGURE 35.6 Percentages of activated voxels in the left and right hemisphere for the FIT-only, SAME-only, and FIT + SAME clusters. (Adapted from Georgopoulos et al., 2001.)

hemispheres are specialized, respectively (Levy, 1969). Specifically, it has been proposed that tasks involving perceptual synthesis rely on the right hemisphere in men, whereas tasks involving perceptual analysis or language skills rely on the left hemisphere in women (Tucker, 1976). The argument, then, can be formulated as follows: Men tend to use spatial/synthetic strategies, hence their right-hemisphere preponderance in solving visuoconstructive problems; in contrast, women tend to employ verbal/analytic strategies, hence their left-hemispheric preponderance. Although this is a plausible scheme with reasonable support, it includes a fair amount of speculation. What seems to be especially weak is the supposed reliance of women on verbal strategies in solving visuoconstructive tasks. Although this could be the case for fairly complex tasks, it does not seem plausible for simple ones. And specifically, it is difficult to believe that a piecemeal, analytic, verbal strategy would be the strategy employed to perform our FIT task, in which the individual visual stimuli were simple line drawings and the whole figure was the highly common square. Therefore, it is hard to attribute the apparent left-hemispheric preponderance in women to the use of verbal strategies.

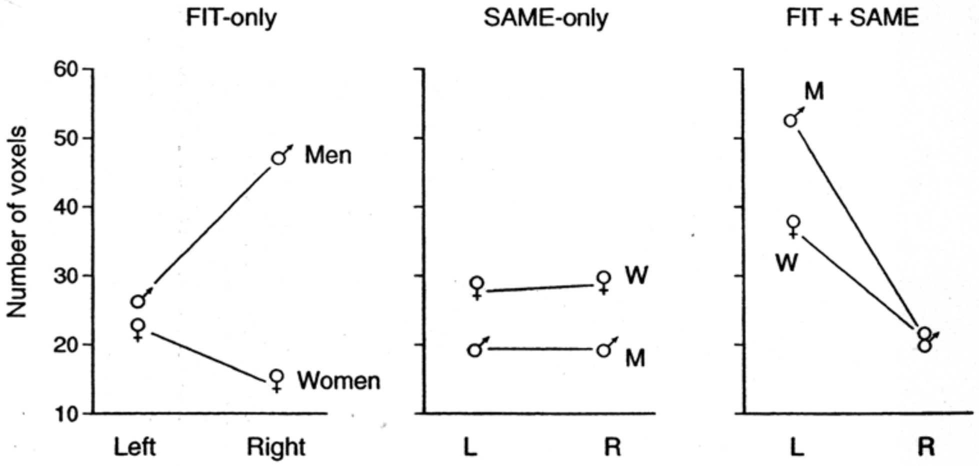

FIGURE 35.7 Number of activated voxels in women and in men for the FIT-only, SAME-only, and FIT + SAME clusters. (Adapted from Georgopoulos et al., 2001.)

We believe that, for our data, the crucial observation is not so much a preponderance of the left hemisphere as a substantial decrease in the involvement of the right hemisphere in women in performing the FIT task. Indeed, there was almost no difference between men and women with regard to *left*-hemispheric activation, whereas there was a major difference in the involvement of the *right* hemisphere, which was much more extensively activated in men than in women with regard to specific, FIT-only voxels (figure 35.7). Insofar as verbal strategies may not be plausible in our case, and assuming that right-hemispheric activation truly underlies visuoconstructive operations, it may be that women are much more efficient in using their right hemisphere than men, hence the reduced extent of activation of that hemisphere.

Concluding remarks

Constructional praxis tasks provide a rich behavioral set for probing the behavioral and neural mechanisms that underlie spatial cognition. They are nonsymbolic and therefore can be used in both human subjects and monkeys. In addition, they are suitable for studies using different technologies. In this chapter I have amplified on results obtained from behavioral, neurophysiological, and fMRI studies; studies using magnetoencephalography are ongoing (Georgopoulos et al., 2002). It is hoped that studying the same function across species and with a variety of complementary methods will lead to a better understanding of the brain mechanisms underlying such complex functions as constructional praxis.

ACKNOWLEDGMENTS This study was supported by U.S. Public Health Service grants NS17413 and NS32919, the MIND Institute, the U.S. Department of Veterans Affairs, and the American Legion Chair in Brain Sciences.

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