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CHAPTER

Behavioral and Neural Aspects of Motor Topology

Following Bernstein's Thread

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In his article "The Problem of the Interrelation of Co-ordination and Lateralization," Bernstein (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:

"There 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, 1935; see Whiting, 1984, p. 109)

This insight of Bernstein's, from 45 years ago, into the "directional engram" is remarkable. In a way, our work during the past 20 years on the neural coding of motor direction can be seen as addressing precisely this issue (i.e., the extraction of directional information from the impulse activity of single cells and cell populations in cortical areas). The discovery of directional tuning provided the key link between neural activity and the direction of movement and made possible the neural construction of a motor trajectory in space (Georgopoulos et al., 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 (1935), who stated that "the higher engram . . . is extremely geometrical, representing a very abstract motor image of space" (Whiting, 1984, 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 are of fundamental importance for its drawing.

In this chapter, I review the results of recent studies that have dealt with issues at the heart of Bernstein's concerns: motor topology and the neural representation of direction, size, and location of movement in space. Specifically, I discuss the results of behavioral studies of drawing geometrical figures and then turn to the issue of representation of topological features and how these can be invariantly extracted from neuronal populations irrespective of attributes of size, location, and the muscles effecting the motor trajectory. Finally, I discuss applications of such neurally inspired operations to artificial neural networks trained to draw figures.

Drawing Figures: Bernstein's Perspective

A major theme in Bernstein's thought was "motor topology." By that he meant the *relative* spatial features of a drawn figure—relative, that is, among its parts and irrespective of the size and location of the figure or the dynamic aspects of the movement, such as speed of drawing. These invariances have profound implications for the motor system, for they correspond to drastically different configurations of joints and patterns of muscle activations. Thus, a square can be drawn large or small, in different parts of space, at different speeds, in movement or isometric force space, and in different sequences of drawing its sides, while always retaining the proper relative proportions among its parts that make the figure a square. Although the *execution* of motor commands is ultimately specified in terms of torques or muscle length-tension curves (Hinton, 1984), the *representation* and *planning* of the rela-

tive spatial aspects of the motor command in terms of different joint and/or muscle configurations, and even different effectors, make figural invariances a very special case. First, I deal with a specific aspect of Bernstein's motor topology: the classification of figures according to their spatial features.

Motor Topology

Figures can be classified according to different sets of features. In discussing this topic, Bernstein wrote: "As topological properties of a linear figure, for example, we may discuss whether it is open or closed, whether the lines composing it intersect with each other as in a figure eight or whether they do not intersect as in the case of a circle and so on" (Bernstein, 1935; see Whiting, 1984, p. 103). The key outcome of any classification scheme is grouping figures (and objects in general) together according to their common features. Now, there may be a multitude of such features (e.g., perimeter, number of sides, orientation, openness), some of which may covary with others such that classification schemes rarely rely on a single feature. Moreover, this discussion is obviously most clearly applicable to percepts of figures rather than their motor drawings. Therefore, another approach is needed beyond the parametric, feature-based procedure. Indeed, a very general, nonparametric, all-encompassing concept in this regard is that of *similarity*. Apparently, objects are commonly grouped according to how similar they are, and although groups of dissimilar objects might be distinguished on the basis of differing distinct features, it is usually combinations of features, rather than single features, that underlie dissimilarity judgments. However, the important point is that, as Shepard (1980) pointed out, "Without any quantitative information about the physical properties of colors, tones, speech sounds, or words, we can learn something about how humans process such stimuli from an analysis of ratings of perceived similarity" (p. 390).

Let me now turn to the application of these ideas to motor topology. First, I want to draw attention to the possibility that the same figures might be grouped differently depending on whether one refers to their percepts or motor drawings. This is because the same features (e.g., perimeter, number of sides) might have a different impact on the perception or the motor drawing of a figure. My colleagues and I (Averbeck et al., 1998) investigated this problem in a recent study in which we analyzed perceptual and motor dissimilarities among nine geometric figures of approximately the same surface area. In the motor experiment, subjects were shown a figure and asked to copy it using a handheld joystick; in the perceptual experiment, subjects were shown pairs of figures and were asked to indicate in an analog scale the degree of perceived dissimilarity between the two figures by positioning a pointer along a line. The perceptual experiment yielded direct pairwise dissimilarity judgments; motor dissimilarities were derived from the figure drawings by calculating the area of nonoverlap between pairs of figures.

There are essentially two ways to analyze dissimilarity data: multidimensional scaling (MDS) and tree modeling (Shepard, 1980). These analyses address different

questions. Specifically, MDS aims at reducing a high-dimensional object space to, commonly, a two-dimensional (2-D) space while keeping the interobject distances in the reduced space similar to those in the high-dimensional space; the outcome of the analysis is a 2-D "object configuration" plot in which the objects are plotted at the coordinates derived by the analysis. In this plot, relative relations among objects can be visualized more easily, and if the new dimensions are readily interpretable, a meaningful remapping of the objects in the new 2-D space can be obtained. On the other hand, tree modeling aims at grouping the objects according to common properties. This analysis yields a tree with branches containing similar objects, but what it is that groups objects together is usually a challenge in interpreting the plots, much as the interpretation of dimensions is for MDS. We applied both of these analyses on the perceptual and motor dissimilarity data obtained in the experiment mentioned earlier. We found that perceptual judgments on, and motor drawings of, the nine figures used differed in their MDS object configuration space plot and in their additive tree modeling plot. This finding indicates that brain systems for perceptual analyses and motor drawings of figures rely on different aspects of the figures.

The methods of MDS and tree modeling provide useful tools with which to address experimentally the issue of what Bernstein called "topological class" (Bernstein, 1935; see Whiting, 1984). In his extensive discussion of this issue (Bernstein, 1935; see Whiting, 1984), Bernstein enumerates several features of objects, which he calls "topological properties" and which bear on classifying objects in different groups. He exemplified his train of thought by pointing out that "every printed letter is a separate topological class of the first order, while to the single class of letter *A* there belong letter *A*'s of all dimensions, scripts, outlines, embellishments, etc." (Bernstein, 1935; see Whiting, 1984, p. 104). Obviously, Bernstein's approach for classification is a mixture of explicit feature description and symbolic considerations; for example, the class of letter *A* is partly a symbolic one, for some *A*'s could conceivably be readily confused with another letter. This means that the allocation of a given object to a specific class might be ambiguous depending on the formal criteria used or the actual placement of the object in a specific class by a particular subject, irrespective of those formal criteria. It is precisely here that the assessment of dissimilarity by experimental methods becomes important; in a sense, the procedure is reversed: instead of classifying objects based on theoretical considerations of features, classification schemes are derived from experimentally assessed dissimilarities, and these schemes are then interpreted based on object features used by the brain. Now, since features may be fuzzy at times and frequently not entirely independent of each other, it is reasonable to suppose that dissimilarities may be based on more "holistic" aspects of the objects. Indeed, this state of affairs captures much better Bernstein's original intuition when he stated that "by the topology of a geometrical object I mean the totality of its qualitative peculiarities" (Bernstein, 1935; see Whiting, 1984, p. 103). It is this elusive totality on which the vague but powerful concept of (dis)similarity relies.

Effects of Brain Damage on Figure Copying

The translation of a seen figure to a drawing is accomplished by appropriate movements of the hand, produced, in turn, by the generation of suitable torques at various joints. This function of copying is frequently disturbed in patients with cortical damage who may be impaired in copying even simple geometrical figures such as a square. In some cases, copying is disturbed in the presence of normal object recognition (e.g., Cipolotti and Denes, 1989), whereas in other cases, figure drawing is normal in the presence of severe object agnosia (e.g., Behrmann et al., 1992). Finally, an additional dissociation concerns drawing from vision versus drawing from memory: either of the two can be intact while the other is disturbed (e.g., Servos and Goodale, 1995). All of this evidence indicates that the neural mechanisms underlying spatially patterned drawing are separate from those subserving perceptual recognition. Moreover, the disorder is not specific to drawing, for it is also manifested in assembly tasks, such as when a patient is asked to form a square by suitably arranging four matchsticks. This indicates that the problem is with the relative spatial (topological) relations of figural elements irrespective of the kind of motions (or effectors) used. This idea is also supported by the fact that, even in drawing, a square can be formed by drawing the sides in different sequences; in fact, a good-looking square was drawn discontinuously (i.e., by drawing nonadjacent sides) by a patient suffering from severe object agnosia (Behrmann et al., 1992). The neural mechanisms underlying these intrafigure spatial relations are essentially unknown. Although early studies pointed to a special role of the right cerebral hemisphere in constructional apraxia (Benton, 1967; Mack and Levine, 1981; Piercy et al., 1960), a disorder characterized by impairment in copying, more systematic later work (reviewed in De Renzi, 1982; Gainotti, 1985) suggested that both hemispheres are probably involved in this function.

Neural Coding of Figure Elements

In contrast to the paucity of knowledge concerning the brain mechanisms of motor figures as wholes, the neural coding mechanisms underlying the drawing of the elements of a line figure (i.e., the drawing of simple lines) have been well investigated and partially elucidated. The approach has been to train monkeys to draw lines in different directions and amplitudes and then record the activity of single cells in the brain during drawing. Such studies have provided the following information (see Georgopoulos, 1995, for a review). First, the activity of single cells in several motor structures is tuned with respect to the direction of movement in space. Specifically, there is a particular direction of movement for which a cell would discharge at the highest rate, called the cell's *preferred direction*. Second, cell activity is also modulated by the amplitude of the movement (Fu et al., 1993). The directional tuning is observed during both the reaction time and the movement time, whereas the modulation with movement amplitude is observed mostly during the movement time (Fu

et al., 1995). Third, the preferred direction of a cell is usually stable (e.g., it is invariant for different movement amplitudes (Fu et al., 1993), but it can be influenced by the posture of the arm, such as when the initial position changes (Caminiti et al., 1990) or when the posture is explicitly altered by a special mechanical arrangement (Scott and Kalaska, 1997). These findings indicate an orderly relation between cell activity and spatial movement parameters. However, the directional tuning by itself does not provide for a unique coding of the direction of movement at the single cell level since the tuning is broad (but not as broad as previously thought [Amirikian and Georgopoulos, 2000]) and the preferred direction can be affected by posture. Any unique information, then, should rely on the neuronal ensemble of directionally tuned cells. Indeed, this information can be extracted by various kinds of population vector codes (Georgopoulos et al., 1983, 1986; Salinas and Abbott, 1994). The outcome of these decoding schemes is the vector sum of weighted vectorial contributions of individual cells, called the *neuronal population vector* (NPV) (Georgopoulos et al., 1983, 1986, 1988), which has the following useful characteristics. First, the direction of the NPV is close to the direction of movement in space. Thus, the population decoding transforms aggregates of purely temporal spike trains into a directional signal, isomorphic to the direction of movement. Second, the calculation of the NPV is a rather simple procedure, for it (a) rests on the directional selectivity of single cells, which is apparent; (b) involves weighting of vectorial contributions by single cells on the basis of the change in cell activity, which is reasonable; and (c) relies on the vectorial summation of these contributions, which is practically the simplest procedure to obtain a unique outcome. In fact, an important aspect of the population vector analysis is that it relies on the directional tuning as defined operationally by the procedures mentioned earlier; no special assumptions are made or required as to how this tuning comes about. Finally, the NPV is robust. It is a distributed code and as such does not depend exclusively on any particular cell. Its robustness is evidenced by the fact that it can convey a good directional signal with only a small number of cells (Georgopoulos et al., 1988; Salinas and Abbott, 1994). However, a much more important property of the NPV is that it is an unbiased predictor of the direction of movement when the posture of the arm changes (Caminiti et al., 1990; Kettner et al., 1988; see also figure 1 in Georgopoulos, 1995), even when the preferred directions of individual cells may change with different movement origins (Caminiti et al., 1990). The NPV then provides posture-free information about the direction of movement in space.

This spatial invariance of the NPV shines when it is used to construct "neural trajectories" of continuous tracing movements (Schwartz, 1994). In these experiments, monkeys are trained to track a moving light along a predetermined trajectory, such as a spiral, circle, ellipse, or figure eight. The NPV is calculated at short time intervals (e.g., 10-20 ms) and strung tip-to-tail to form a neural trajectory. This neural trajectory has consistently been found to be an excellent predictor of the actual trajectory. The reason for this is that not only does the direction of the instantaneous NPV predict the direction of the movement but also its intensity predicts the instantaneous amplitude of the movement (i.e., speed for a fixed time bin) such

that the spatially arranged NPV time series yields the upcoming movement trajectory in space.

All of these findings show that accurate and robust information about movement direction can be extracted from an ensemble of directionally tuned neurons in the form of the NPV, which is invariant with respect to the posture of the arm and which, in drawing movements, carries information about the whole trajectory.

Figure Drawing by Artificial Neural Networks

The time-varying directional operations discussed previously have been modeled using a massively interconnected artificial neural network that consists of directionally tuned neurons and produces as an outcome the neuronal population vector (Lukashin and Georgopoulos, 1993, 1994a, 1994b). This network has been successfully trained to draw accurate geometric shapes (Lukashin et al., 1994, 1995) and has led to a novel hypothesis on how memorized trajectories of complex movements could be stored in the synaptic connections of overlapping neural networks (Lukashin et al., 1994). The idea is that there is a general-purpose network that is involved in all kinds of movements, memorized or not, but which carries no information about memorized trajectories of specific shapes (e.g., circles, ellipses, scribbles) and which, if activated alone, would produce straight line trajectories. It is now hypothesized that there are also networks highly specific to a particular trajectory (e.g., clockwise circle) that are interconnected with the general-purpose network; when a specific trajectory needs to be performed, the appropriate specific network fuses with the general-purpose network and, now as one network, produces the desired trajectory. Remarkably, the size of the specific network need only be less than 5% of the size of the general-purpose network for the desired trajectory to be effectively stored and reproduced (Lukashin et al., 1994). It is noteworthy that such very specific cells have been observed at low proportions in neurophysiological recordings during performance of memorized trajectories (Ashe et al., 1993; Hocherman and Wise, 1991).

The idea of the existence of very specialized networks raises the question of the degree of specialization and of how such networks are created in the first place. We can only speculate on these issues. With respect to the general-purpose network, it is reasonable to assume that it is present at birth since it is assumed to subserve all movements. There are several possibilities concerning the specialized networks. One possibility is that a number of small-size networks, specific for basic shapes (e.g., straight lines, curves, and some combinations thereof ["motor shape primitives"]), are present at birth. Then motor learning for other, complex motor acts would consist of adjusting the connection strengths between the general-purpose and specific networks. This idea implies that all of the specialized primitives are used routinely, although not as frequently as the general-purpose network. Another possibility is that innate specific networks code for more complicated shapes and are large in number. The mechanism of motor learning would

then be similar to that described previously; but in this case, only a small number of the specialized networks would be used. This means that a number of the complex specialized networks may never be used. This situation would be similar to that encountered in the immune system, in which there is a large potential for making a large number of antibodies, of which, however, only some may actually be made, depending on the exposure of the organism to specific antigens. In both cases there is a selection: selection of a specialized trajectory or selection of an antibody, both from a large ensemble available. Finally, an intermediate hypothesis would be that we start with motor shape primitives, but that the more complex trajectories resulting from the combination of these primitives with the general network become themselves very specialized and behave as such in the formation of other trajectories in novel associations.

Neural Representation of Memorized Figures

The neural mechanisms subserving well-learned, memorized, complex movement trajectories are elusive. This problem was investigated in a study (Ashe et al., 1993) in which monkeys were trained to perform from memory an arm movement with an orthogonal bend, up and to the left, following a waiting period. They held a 2-D manipulandum over a spot of light at the center of a planar working surface. When this light went off, the animals were required to hold the manipulandum there for 600-700 ms and then move the handle up and to the left to receive a liquid reward. There were no external signals concerning the go time or the trajectory of the movement. Following 20 trials of the memorized movement trajectory, 40 trials of visually triggered movements in radially arranged directions were performed. The activity of 137 single cells in the motor cortex was recorded during performance of the task. A high percentage (62.8%) of cells changed activity during the waiting period. Other cells did not change activity until after the 600-ms minimum waiting time was over, and occasionally cell activity changed almost exactly 600 ms after the center light was turned off. However, the most interesting observation was that a few cells changed activity *exclusively during the execution of the memorized movement* (see figure 5 in Ashe et al., 1993); these cells were completely inactive during performance of similar movements in the visually guided control task. These findings suggest that *performance of a movement trajectory from memory may involve a specific set of cells*, in addition to the cells activated during both visually guided and memorized movements. This idea is in accord with the results of the modeling studies summarized earlier.

Coding of Dynamic Isometric Force

Although the exertion of static force is not uncommon, as when we hold a book against gravity, the production of a change in force is almost universally present in

all actions, for it precedes the beginning of the movement. Study of force change under conditions of limb motion is hampered by several factors that cannot be easily controlled experimentally (e.g., interaction forces). An experimentally "clean" case is provided by the exertion of an isometric force pulse (i.e., by the production of a rapid change in force in the absence of limb motion). Such a paradigm, which allows the study of the relation of neural activity to pure dynamic force change, was employed recently (Georgopoulos et al., 1992). The following experimental arrangement allowed dissociation between the dynamic and static components of the force exerted. Monkeys produced pure force pulses on an isometric handle in the presence of a constant force bias so that the net force (i.e., the vector sum of the monkey's force and the bias force) was in a visually specified direction. The net force developed over time had to stay in the specified direction and to increase in magnitude to exceed a required intensity threshold. Now consider the case in which the directions of the net and bias forces differ, for example, by being orthogonal. For the task to be performed successfully under these conditions, the animal's force has to change continuously in direction and magnitude so that, at any moment during force development, the vector sum of this force and the bias force is in the visually specified direction. Thus, this experimental arrangement effectively dissociated the animal's force vector, the direction of which changed continuously in a trial from the net force vector, the direction of which remained invariant. Eight net force directions and eight bias force directions were employed. Recordings of neuronal activity in the motor cortex revealed that the activity of single cells was directionally tuned in the absence of bias force, and that this tuning remained invariant when the same net forces were produced in the presence of different directions of bias force. These results demonstrated that cell activity does not relate to the direction of the animal's force. Since the net force is equivalent to the dynamic component of the force exerted by the animal, after a static component vector (equal and opposite to the force bias) is subtracted, these findings suggest that the motor cortex provides the dynamic force signal during force development; other, possibly subcortical, structures could provide the static compensatory signal. This latter signal could be furnished by antigravity neural systems, given that most static loads encountered are gravitational in nature. According to this general view, the force exerted by the subject consists of dynamic and static components, each of which is controlled by different neural systems; these signals would converge in the spinal cord and provide an ongoing integrated signal to the motoneuronal pools.

Conclusion: Neural Mechanisms of Copying

Copying is a rich activity that involves coordinated interaction among several areas of the brain. In a continuation of our behavioral studies described previously, we have investigated the neural mechanisms underlying the copying function. For that purpose, we trained monkeys to copy simple geometrical shapes, including triangle, square, inverted triangle, and trapezoid. We then used a multielectrode system to record the activity of single cells in the periprincipalis region of the prefrontal

cortex. We found the following (Averbeck et al., 2001; Chafee et al., 2001): Movement trajectories were segmented as evidenced by multiple positive-going zero-acceleration crossings. An analysis of covariance was used to assess the effect of various motor and shape variables on cell activity during the drawing of a segment. These variables included the serial position of the segment and shape drawn (as fixed factors), maximum segment speed, time to maximum speed, direction of segment in space, X-Y position of the segment's midpoint, average X-Y position of the eye during the drawing of a segment, and the sequential trial number. We found a significant relation to the serial position of the segment (46% of cells) and to the shape being drawn (51%). Smaller percentages of cells were related to other factors. Plots of adjusted neural activity means against the serial position of the segment revealed several types of systematic variation, including monotonically increasing and decreasing functions as well as parabolic functions.

These findings draw attention to the fact that usually simple shapes are drawn as a sequence of movements; in that respect, then, copying can be regarded as an instance of serially ordered behavior. A key idea in Lashley's formulation of the problem of serial order in behavior is the postulated neural representation of all serial elements before the action begins. We investigated this question by recording simultaneously the activity of small neuronal ensembles in prefrontal cortex during copying. As mentioned previously, the shapes were drawn as sequences of movement segments, and the drawing of these segments was associated with distinct patterns of neuronal ensemble activity. We found that these patterns were present during the time preceding the actual drawing. In fact, the rank of the strength of representation of a segment in the neuronal population during that time predicted the serial position of the segment in the motor sequence such that, for example, the segment with the highest strength was the first in the sequence, and so on. Lashley (1951) theorized that errors in motor sequences would be most likely to occur in the execution of elements that had prior representations of nearly equal strength. Now, in the previous analysis, the strengths of neural representation of middle segments in the drawing trajectory of a square, for example, were closer to each other than to the initial and last segments. A prediction based on this finding is that more errors would be committed in the drawing of middle segments in comparison to either the first or last segments. Indeed, more errors were committed during the drawing of the middle segments, and comparatively few were made during the drawing of either the initial or last segments. Specifically, over the entire data collection period, the monkey committed an average of 122, 249, and 165 errors during drawing of the initial, middle, and final segments, respectively. These findings connect the strength of the representation of the upcoming serial elements in copying to the actual performance and its variability with respect to errors committed. Overall, they provide additional evidence in support of Lashley's idea on the cotemporal representation of serial order and its effects on the serial behavior emitted subsequently. Finally, it is worth noting that this work has brought together the ideas of two great masters of the 20th century, Bernstein and Lashley, in the context of copying. And this is only one instance,

among many others, of their sharp and inspiring ideas and intuitions in the field of motor behavior.

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