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MOVING IN THREE-DIMENSIONAL SPACE: FRAMES OF REFERENCE, VECTORS, AND COORDINATE SYSTEMS

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INTRODUCTION

We move in a three-dimensional world. What are the motor commands that generate movements to a target in space, and how is sensory information used to control and coordinate such movements? To answer these questions, one must determine how spatial parameters are encoded by the activity of neurons. Within the last decade, experimenters have begun to study a variety of movements in three-dimensional space. Among these are "reflexive" (or postural) eye, head, and body movements elicited by vestibular and visual stimuli; orienting movements of the eyes, head, and body subserved by the superior colliculus (or in lower vertebrates, the optic tectum); and arm movements with their neural correlates in motor cortex.

The neural systems that are involved in the production of each of these movements must deal with aspects that are particular to that task, and specialized reviews are available on each of these topics (Georgopoulos 1986; Knudsen et al 1987; Simpson 1984; Sparks 1986). Nevertheless, the question of spatial representation is a theme common to each of these

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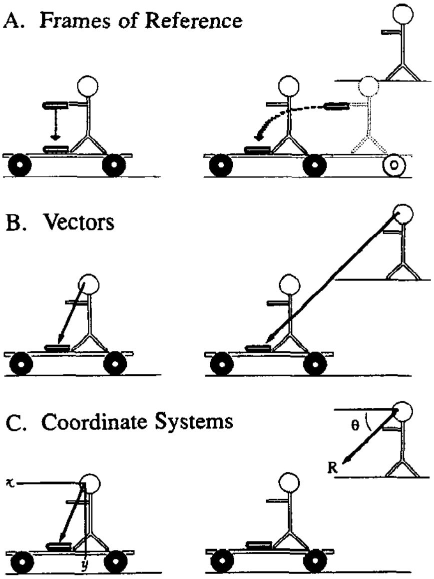
areas, and in this review we focus on that question. We show that multidimensional information can be, and is, represented in a variety of ways such as topographically, vectorially, or in coordinate systems. Underlying each of these representations is the notion of a frame of reference. We begin by defining these terms. Then, we summarize experimental data for each of the above-mentioned tasks and attempt to identify how spatial parameters are represented. We conclude by examining some common concepts that have begun to emerge from the study of this variety of motor tasks.

DEFINITIONS

Frames of Reference

Central to any spatial description is the concept of a frame of reference. As a textbook example of a frame of reference, consider a passenger standing on a moving train and an observer watching the train go by. We can imagine two frames of reference: one fixed to the train, the other fixed to the earth (Figure 1*A*). The passenger is moving in the earth's frame of reference, but is stationary in the train's frame of reference. If the passenger


A. Frames of Reference

B. Vectors

C. Coordinate Systems

Figure 1 Schematic illustration of the spatial representations of objects in frames of reference (*A*), vectorially (*B*) and by coordinate systems (*C*). On the left, the frame of reference moves with the passenger; on the right, the observer's frame of reference is fixed to the earth.

drops a book, it will fall straight down in the train's frame of reference. However, from the perspective of the observer in the earth's frame of reference, the book will drop along a curved path.

Closer to the problem at hand, we can imagine a retinocentric frame of reference, i.e. one fixed to the eye. We can also imagine other frames of reference fixed to the head, to the trunk, and to the earth. As was demonstrated by the simple example above, our (or a neuron's) description of events depends on the frame of reference that is adopted. The criterion for identifying a frame of reference is straightforward. For example, if a neuron encodes the location of an object in a retinocentric frame of reference, then the neuron's activity should remain constant as long as the object's image falls on the same locus on the retina, irrespective of the eye's position in the head, or the head's position on the trunk.

Vectors

Once we have defined a frame of reference, one way to define the location of any point in this frame of reference (e.g. the book in Figure 1*B*) is by means of a vector, with a direction and an amplitude. To do so, we must first define an origin for the frame of reference. In the illustrated example, the origin is the eye of the passenger (*left*) or of the observer (*right*). The amplitude of the vector is its distance from the origin, and its direction is given by the line that connects the origin with the point.

Coordinate Systems

Sometimes, it is convenient to define a coordinate system within the frame of reference by choosing a set of base vectors. Any point in the reference frame is now defined in terms of an amplitude along each of the base vectors (coordinate axes). In Figure 1*C*, a coordinate system in the passenger's frame of reference might be given by the horizontal (x) and vertical (y) axes, i.e. a Cartesian coordinate system. In the observer's frame of reference, a coordinate system could be defined by the distance from the observer to the book (in the radial direction, R), the angle between the radial direction and the horizontal (elevation, θ), and a second angle that defines the deviation of the radial direction from the sagittal plane (azimuth), i.e. in a spherical coordinate system.

COORDINATE SYSTEMS DEFINED BY NEURAL ACTIVITY

Are coordinate systems defined by neural activity? If so, how can one recognize them? These questions are more easily answered at the periphery of the nervous system, where coordinate systems (sensory and motor) are clearly defined by the geometry of the sensory receptors or the musculoskeletal system. The base vectors of the motor coordinate system are provided by the direction in which each of the muscles exerts force (Pellionisz & Llinás 1980). Sensory coordinate systems are defined by the direction of the stimulus that most effectively activates peripheral receptors. For muscle stretch receptors, the coordinate axes would also coincide with the direction in which each muscle exerts force. For semicircular canal afferents, the coordinate axes would be defined by the axes of head rotation that provide the most effective stimuli (Robinson 1982).

As Pellionisz & Llinás (1980, 1982) first pointed out, motor and sensory coordinate systems usually have nonorthogonal axes. In such a case, it becomes necessary to distinguish between the two types of coordinate representations, which are illustrated in Figure 2. Although sensory (receptor) representations are formed by projections onto coordinate axes (Figure 2*A*), and motor (effector) actions follow the rules of vector summation (Figure 2*B*), both cases predict a cosine tuning of neural activity around a "best" direction. In the bottom half of Figure 2, the amplitudes of the x and y components of point P are plotted as a function of the angle between the x axis and a vector from the origin to the point. The best direction is the angle for which the amplitude is the largest, and one might expect this best direction to correspond to the maximal neural activity. For vector summation (Figure 2*B*), the best directions do not coincide with the coordinate axes.

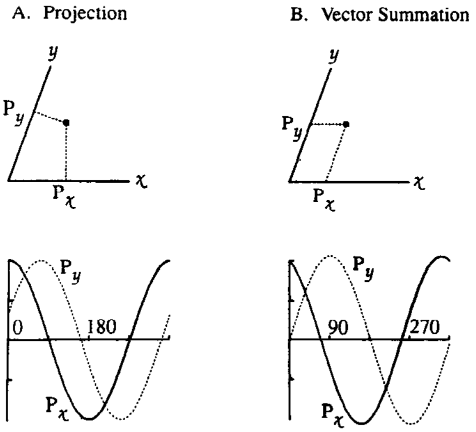


Figure 2 In coordinate systems with nonorthogonal axes, the coordinates of a point can be defined by projection onto the coordinate axes (*A*) or by vector summation (*B*). In both types of representation, the amplitudes of the x and y components vary sinusoidally with the angle between the x-axis and the vector from the origin to the point.

Thus, independently of whether a coordinate system is defined by projection or by vector summation, a neural representation in such a coordinate system should generally define a best direction along which activity is maximal. Neural activity should decrease by an amount proportional to the cosine of the angle, for inputs or outputs oriented along directions other than best directions. A vectorial code should exhibit tuning characteristics that are similar to one encoding a coordinate system, with one major difference: A coordinate system is defined by a limited number of base vectors; therefore, the number of best directions in a population of neurons should be similarly limited. In a simple vectorial code, one might expect the best directions to be more numerous and widely distributed.

In summary, to understand central processing of information in sensorimotor systems, it might be useful to begin by first identifying the frame of reference in which the information is encoded. The next steps would be to determine whether parameters in that frame of reference are encoded vectorially, and to ascertain whether the vectorial code also implies a coordinate system. If the criteria can be satisfied, it then becomes possible to describe neural processing in geometric terms, i.e. transformations from one frame of reference to another and transformations between coordinate systems within a single frame of reference. In the following sections we examine several examples in which this approach has been useful for understanding the neural representations involved in sensorimotor transformations.

VESTIBULO-OCULAR COORDINATE SYSTEMS

The semicircular canals and the extraocular muscles provide the clearest example of coordinate systems imposed by the geometric arrangement of the sensors and the motor apparatus. The afferents are linked to the efferents by a three-neuron arc (the vestibulo-ocular reflex), which acts to rotate the eyes in the direction opposite to the head rotation sensed by the semicircular canals.

Each of the three canals defines a plane; head rotation about an axis perpendicular to this plane is the most effective stimulus, whereas rotations about axes lying in this plane are ineffective (Blanks et al 1972; Estes et al 1975). Canal planes have been determined anatomically for several species (Ezure & Graf 1984a; Reisine et al 1988).

There are six extraocular muscles for each eye, and the pulling directions of these muscles have been computed from anatomic measurements (Ezure & Graf 1984a). The neural innervation of muscle pairs is organized in a push-pull fashion (Baker et al 1988a); thus, one can combine the antagonistic action of muscle pairs to define three axes of eye rotation, each evoked by activation of one of the three pairs (Robinson 1982). These three axes are not perpendicular to each other and they do not align exactly with the axes of the semicircular canals. In this nonorthogonal motor coordinate system, the axis of eye movement for which each muscle pair is most active does not coincide with the axis defined by the muscles' pulling directions (Baker et al 1988a), as predicted in Figure 2*B*. Also in accord with the prediction, the amplitude of the modulation in eye muscle activity in response to sinusoidal head rotation decreases as a cosine function of the angle between the best direction and the direction of rotation (Baker et al 1988b).

Thus, both the semicircular canals and the extraocular muscles define three-dimensional coordinate systems in a reference frame fixed to the head. Furthermore, because the axes of the two coordinate systems do not coincide, a coordinate transformation is implied. As there are only three neurons in the reflex arc, the coordinate transformation can occur in only two places: by convergence of vestibular afferents from different canals onto vestibulo-ocular relay neurons in the vestibular nuclei, or by convergence of these relay neurons in the oculomotor nuclei. This problem has received considerable attention, both theoretically (Pellionisz 1985; Pellionisz & Graf 1987; Robinson 1982) and experimentally (Ezure & Graf 1984b; Peterson & Baker 1991). Experimental evidence indicates that part of the coordinate transformation occurs at both sites.

The function of the vestibulo-ocular reflex is to stabilize gaze in an earth-fixed frame of reference. Visual input also contributes to stabilizing gaze, and there is substantial convergence of vestibular and visual inputs in the vestibular nuclei (Dichgans & Brandt 1978). Although the geometry of the semicircular canals and the eye muscles virtually imposes a coordinate system on the vestibulo-ocular pathway, retinal receptors do not define a coordinate system. How, then, is motion of the visual image encoded centrally? Is it also defined by a coordinate system? If so, what are the coordinate transformations on this visual input?

Simpson (1984) and colleagues have addressed these questions by studying the rabbit's accessory optic system, which consists of three target nuclei that receive input from retinal ganglion cells and make efferent projections to the inferior olive and, hence, to the cerebellum (Maekawa & Simpson 1973). Neurons in this system respond preferentially to movements of large visual stimuli at slow speeds (Simpson 1984), i.e. to stimuli that would arise naturally during slow speed head motion in a stationary environment. Visual input to the accessory optic system could help compensate for the semicircular canal afferents' low gain at such speeds (Fernandez & Goldberg 1971).

In the accessory optic system, image motion is also represented in coordinates whose axes are aligned with the axes of the semicircular canals and the extraocular muscles (Simpson et al 1988; Sodak & Simpson 1988). Neural activity in the dorsal cap of the inferior olive and in the climbing fiber and mossy fiber inputs to the flocculo-nodular lobe of the cerebellum clearly defines a coordinate system (Graf et al 1988; Leonard et al 1988). One class of neurons in the dorsal cap responds best to rotation of the visual field about a vertical axis, i.e. to rotation in the plane of the horizontal canals. Two other types of neurons respond best to rotation about horizontal axes aligned with the axes of the anterior and posterior semicircular canals. One axis is located anterior at 45° to the sagittal plane, the other is oriented in the opposite direction (posterior, 135° to the sagittal plane). Climbing fiber activity in Purkinje cells shows the same preferential orientations (Figure 3*A*), as does simple spike activity.

Visual input to vestibular nuclei neurons (which, in turn, project to extraocular muscles) also defines a coordinate system aligned with the semicircular canals (Graf 1988). As shown in Figure 3*B*, one type of neuron, which also receives input from the posterior semicircular canal, shows a polarization in line with that of the posterior canal. (A second type responds best to rotations of the visual surround about the axis of the anterior canal.) The visual receptive field of these neurons is bipartite in nature, as indicated by the hatching in the right part of Figure 3*B*. Upward movement in one part of the receptive field is excitatory, as is downward movement in the other part. Rotation of the visual surround about the axis of the posterior canals (as indicated schematically in Figure 3*B*) would lead to upward motion on one side of the axis and downward motion on the other.

Activity of retinal ganglion cells is not in a vestibulo-oculomotor coordinate system; therefore, a coordinate transformation is required to go from retinal ganglion cell activity to the activity of neurons in the accessory

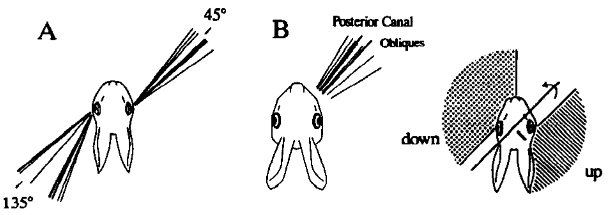


Figure 3 Coordinate axes defined by neural activity in cerebellum (*A*) and vestibular nuclei (*B*). Each line defines the best direction of one neuron for rotation of the visual surround. (*A*) is redrawn from Graf et al (1988), (*B*) from Graf (1988).

optic system or the vestibular nuclei. Simpson and coworkers have also worked out some of the details of this coordinate transformation. In the rabbit, which is a lateral-eyed animal, there are retinal ganglion cells that exhibit tuning for movement in one of three directions (Oyster et al 1972). One axis of this coordinate system is oriented anteriorly, i.e. it is aligned with the plane of the horizontal canals. This horizontal coordinate axis is maintained at subsequent stages in the terminal nuclei of the accessory optic system and beyond. The other two coordinate axes of retinal ganglion cells are oriented superiorly and slightly posteriorly, and inferiorly and slightly posteriorly. These vertically oriented axes undergo a transformation. The tuning of neurons in the accessory optic system nuclei is similar, but their orientation selectivity suggests a monocular combination of excitatory input from superior retinal ganglion cells with inhibitory input from inferior retinal ganglion cells, and vice versa (Sodak & Simpson 1988). More interestingly, a few neurons in the medial terminal nucleus exhibited bipartite monocular receptive fields (Simpson et al 1988), which would be stimulated by rotation of the visual surround about a horizontal axis between the two receptive fields (see Figure 3*B*). Thus, several distinct coordinate systems can be associated with the accessory optic system, providing for a gradual transformation of information about linear image motion to information about image rotation in a coordinate system aligned approximately with that of the semicircular canals.

COORDINATE SYSTEMS FOR POSTURAL RESPONSES

Afferent activity from the semicircular canals also contributes to stabilizing the head in an earth-fixed frame of reference by means of the vestibulocollic reflex. This reflex exhibits a considerable increase in complexity over the vestibulo-ocular reflex: There are many more muscles involved (about 30 in the cat, see Pellionisz & Peterson 1988); there is apparently more extensive convergence from other sensors (muscle stretch receptors and vestibular macular afferents), and the neural circuitry underlying this reflex is more complex.

Are there sensorimotor transformations to align the signals from the different sensors in a common frame of reference? How are these signals transformed to activate the neck muscles? Investigators have begun to address these questions experimentally and theoretically. The pulling directions of the neck muscles exhibit a wide range of orientations (Pellionisz & Peterson 1988). There is no unique solution for the manner in which the activation of neck muscles should vary with the axis of head torque, as there are more muscles than degrees of freedom. Theoretical activation vectors (best directions) for the muscles have been predicted (Pellionisz & Peterson 1988), based on the idea of coordinate transformations from canal coordinates to neck muscle coordinates to minimize the extent of muscle coactivation. As one would expect (Figure 2*B*), these vectors are not colinear with the muscles' pulling directions. When patterns of neck muscle activation in response to whole body rotation (activating vestibular receptors) were measured by Baker et al (1985), and compared with the theoretical predictions (Peterson et al 1988, 1989), they were found to be in good qualitative agreement.

Less is known about the intermediate stages in this sensorimotor transformation and the extent to which signals from other afferents are aligned with those from the semicircular canal afferents. Wilson and colleagues (Kasper et al 1988a,b; Wilson et al 1990) have begun to record activity in vestibulospinal neurons during head rotation about horizontal axes. The activity of most of these neurons defined a vector orientation for rotation, i.e. neural activity fell off as a cosine function of the angle between the axis of rotation and a best axis (see also Baker et al 1984). The orientations of these vectors do not appear to cluster about a few directions (i.e. to define coordinate axes), but they are also not distributed uniformly. Most appear to be oriented close to the roll (antero-posterior) axis or at a 45° angle to either side of this axis.

From the frequency response of the units, these investigators deduced contributions of otolith afferent input to some of the neurons. In most cases, the spatial orientation of the otolith and canal inputs was in alignment. Because the orientation of otolith response vectors to tilt shows a wide range of distributions (Fernandez & Goldberg 1976), such an alignment would not be expected by chance. About 50% of vestibulospinal neurons also responded to passive neck rotation; in most of them, the vestibular and neck response vectors were also in alignment, differing by close to 180°. These neurons do not respond to head rotation about a stationary trunk, as the vestibular and neck inputs would tend to cancel. They would respond to trunk rotation about a stationary head or to whole body rotation, i.e. movement of the trunk in an earth-fixed frame of reference. The tuning of the other 50% would be appropriate to signal head rotation in the earth-fixed frame of reference.

In summary, vestibulospinal neurons appear to provide a vectorial code of rotation in an earth-fixed frame of reference, of either the head or the trunk. In most instances, the vectors of each of the afferent inputs (semicircular canals, otoliths, and neck afferents) are in approximate alignment.

Responses in limb muscles evoked by perturbations to the surface of support during posture also involve concurrent input from a variety of sensors: vestibular, visual, and proprioceptive (Nashner & McCollum 1985). How postural information from limb proprioceptors is transformed into a common reference frame with visual and vestibular information remains to be determined (Droulez & Darlot 1990).

The control of limb musculature is apparently not effected muscle by muscle; instead, it has been suggested that global variables are controlled (Nashner & McCollum 1985; Lacquaniti et al 1990). Can these global variables be associated with a coordinate system? Nashner & McCollum (1985) have found it convenient to describe bipedal posture in terms of both the distance from the center of gravity to the base of support, and the ankle and hip angles. Maioli and coworkers (1988, 1989) have also suggested limb length to be one controlled variable in quadrupeds, along with the orientation of the limb relative to the vertical in the sagittal plane (see Figure 4). They found that these two variables remained constant when the base of support was tilted (around the pitch axis) or the location of the animals' center of gravity was shifted by adding weights. Subsequent work (Maioli & Poppele 1989) suggested limb length and orientation were controlled independently of each other. Thus, these parameters may provide two of the axes of a postural coordinate system in an earth-fixed frame of reference. At least a third axis would be needed to regulate the sideways tilt of the animal.

Ground reaction forces in posture also appear to define a coordinate system. Macpherson (1988) measured the tangential reaction forces on cat fore- and hindlimbs when the cats were subjected to translation of the support surface in different directions. During quiet stance, these forces were directed at angles of 45° or 135° relative to the anterior direction. Following perturbation, actively evoked reaction forces were also oriented along these two directions, irrespective of the direction of the perturbation, whereas passive forces were always aligned with the direction of pertur-

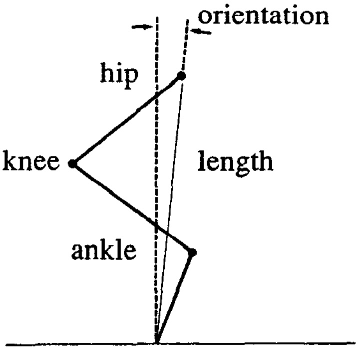


Figure 4 Limb length and orientation are two coordinates that can describe quadrupedal limb posture. A cat hindlimb is shown schematically; length is the distance from the base of support to the hip, and orientation is the angle of the vector from the base of support to the hip from the vertical axis.

bation. Thus, both limb kinematics (movements) and actively produced limb kinetics (forces) define coordinate systems in reference frames fixed in space. Whether these coordinate systems are independent of one another, or one is a consequence of the other, remains to be determined.

FRAMES OF REFERENCE AND COORDINATE REPRESENTATIONS FOR ORIENTING MOVEMENTS

Orienting movements of the eyes, head, and whole body can be evoked by visual, acoustic, and somesthetic stimuli. Information from each of these sensors is represented in a different frame of reference: visual in one fixed to the eyes, acoustic in one fixed to the head, and somesthetic in one fixed to the body. Because the eyes can move in the head, and the head on the body, the question arises: is information from these sensors transformed into a common frame of reference, and if so, what is it? How is information represented in each frame of reference? How are the transformations achieved?

The superior colliculus (or its analogue in lower vertebrates, the optic tectum) is a key structure for orienting movements. There is a topographic map of target location in the layers of the superior colliculus or the tectum (Knudsen et al 1987; Sparks 1986). Each neuron is preferentially activated by a stimulus located in one region of space. In the deeper layers, neurons respond to stimuli from more than one sensory modality, and the receptive fields defined by each sensory modality are approximately in register (Knudsen 1982; Meredith & Stein 1986; Middlebrooks & Knudsen 1984) when eyes, head, and body are in alignment. Visual and acoustic stimuli that are in spatial and temporal congruence enhance the response, whereas two stimuli that are spatially or temporally disparate can lead to a depression of the neuron's activity (Meredith et al 1987; Newman & Hartline 1981).

The auditory map of space is synthesized from interaural time and intensity differences. In the barn owl, maps of interaural time difference (Carr & Konishi 1990; Sullivan & Konishi 1986) and maps of interaural intensity differences (Manley et al 1988) are formed in separate nuclei. Azimuth of target location is primarily related to interaural time difference, and target elevation to interaural intensity difference. However, the separation of the mapping between the two acoustic parameters and the two spatial parameters is not complete (Moiseff 1989). The elevation and azimuth of the location to which a barn owl turns its head depends in a linear fashion on both acoustic parameters. In any case, intensity and time information (or equivalently, elevation and azimuth) is combined in the superior colliculus.

In the barn owl, the range of eye movements is limited. Therefore, the problem of misalignment between the head-fixed auditory map and the eye-fixed visual map does not arise. Nevertheless, the auditory map is apparently in a visually defined frame of reference in this species. The auditory map remains aligned with the visual map when auditory input is altered by ear plugs (Knudsen 1985), or when the visual map is shifted by the use of displacing prisms (Knudsen & Knudsen 1989); the map is degraded when owls are raised with eyelids sutured (Knudsen 1988).

In cats and monkeys, the range of eye movement is much greater; thus, the potential for misalignment is also greater. Jay & Sparks (1984, 1987) have shown that the auditory map of space shifts with eye position. They trained monkeys to gaze at a fixation point and to make saccades (with the head fixed) to auditory and visual stimuli. They varied the fixation point and found that the receptive fields of neurons that responded to auditory stimuli shifted with the fixation point, i.e. with eye position. On average, the shift was by an amount smaller than the shift in eye position from one fixation point to another (Figure 5). Strictly speaking, the frame of reference for auditory space for these neurons is between a head-fixed and an eye-fixed one.

In the experiments of Jay & Sparks, the monkey, whose head was fixed, made only saccadic eye movements. What is the frame of reference of collicular maps when the head is also free to move? Is the frame of reference

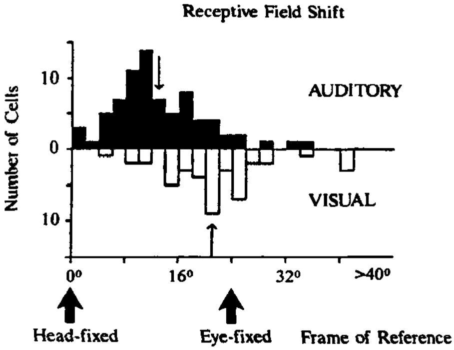


Figure 5 The reference frame of neurons in superior colliculus for representing the location of auditory and visual stimuli. The histogram describes the shift in neurons' receptive field after eye position (gaze) has shifted by 24°. The heavy arrows point to the amount of shift predicted if information were encoded in head-fixed (0°) or eye-fixed (24°) frames of reference. The median receptive field shift is indicated by the light arrows. Redrawn from Jay & Sparks (1987).

for eye and head movements the same? What is the frame of reference for the somesthetic map of body surface? These questions remain to be answered. Orienting movements of the eyes and the head only require information about the direction of target location (azimuth and elevation), but whole body orienting movements may also require information about the distance of the target (see below). Whether distance information is also encoded in the collicular map is not known.

Electrical stimulation of a site in the deeper layers of the superior colliculus evokes saccadic eye movements in the direction defined by the visual topographic map (Robinson 1972; Sparks 1986). The activity of neurons in the deeper layers is also correlated temporally with saccade onset (Sparks 1986). For these reasons, Sparks (1988) has suggested that the deeper layers represent a "motor map" for goal-directed movements (see also Grobstein 1988 for a discussion of this point).

The movement signal in superior colliculus, however, is not in the coordinate system of the muscles. For eye movements, the axes of the eye muscles' coordinate system are oriented vertically and horizontally (see above), and a separation of horizontal and vertical saccadic components in brain stem nuclei has been noted (Büttner & Büttner-Ennever 1988; Cohen et al 1985). There must be a transformation from the (coordinate-free) topographic map in superior colliculus to the different coordinate systems of eye, neck, and limb muscles. There is evidence (primarily from lower vertebrates) that this transformation involves an intermediate coordinate system whose axes are the spatial azimuth, elevation (and distance) of the movement (Grobstein 1988); this intermediate coordinate system is common to all effectors; and the transformation involves a population vector coding by collicular neurons (van Gisbergen et al 1987; Lee et al 1988).

Lee et al (1988) have demonstrated vector coding by reversibly inactivating small regions of the deep layers of superior colliculus and measuring saccadic error for eye movements in different directions. Saccades to targets lying within the center of the receptive field of the inactivated area were not in error, but those to targets at directions to either side were. These results imply that each collicular neuron provides a vectorial contribution to the code for movement; this contribution is in the neuron's best direction, and the movement is predicted by the vectorial average of the activity of all active neurons, i.e. a population vector code.

Evidence in favor of intermediate coordinate systems comes from two sources. Masino & Knudsen (1990) took advantage of the fact that there is refractoriness to electrical stimulation of the tectum—there is no movement evoked by the second of two stimuli presented in brief succession at the same locus (Robinson 1972). In the barn owl, they stimulated two different tectal sites in brief succession. The direction of the head movement evoked by the first stimulus was arbitrary; the direction of movement in response to the second stimulus was either horizontal or vertical, but never oblique (Figure 6*A*). For example, if stimulation of the first site evoked upward, leftward head movement, and stimulation of the second site in isolation evoked downward, leftward head movement, then the response to the second of the two stimuli presented in quick succession would be restricted to the downward direction, i.e. the direction that was not in common with the first movement. There was a refractoriness to the leftward component of the movement, as that was a coordinate axis common to the two tectal sites. The pulling directions of the neck muscles are widely distributed; thus, the horizontal and vertical axes of this intermediate coordinate system are not aligned with the coordinate axes of the neck muscles.

Experiments on whole body orienting movements in the frog suggest that the same spatial intermediate coordinate system may also be used to encode body movements. Presented with a worm, a frog orients its body to the target by turning (dependent on the azimuthal location of the target) and by hopping or snapping (dependent on the distance of the target from the frog). Large lesions in the optic tectum abolish this response, but hemisection of the caudal mesencephalon leads to a very different deficit (Kostyk & Grobstein 1987). Frogs still respond by hopping or snapping, but fail to turn if the stimulus is located to one side of the sagittal plane.

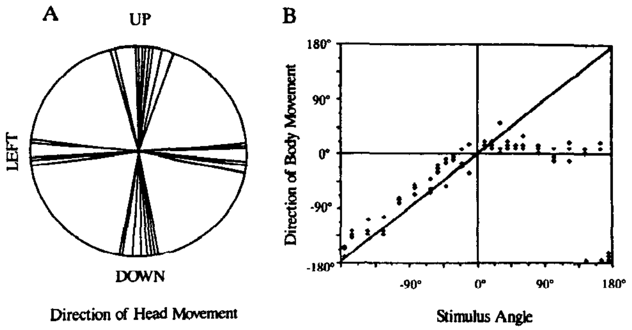


Figure 6 Intermediate coordinate systems for head and body orienting movements. (*A*) The directions of head movements evoked by the second of two electric stimuli to a region of the optic tectum in the owl are restricted to the horizontal or vertical directions. (*B*) Brain stem lesions in the frog abolish the horizontal (azimuthal) component of body orienting responses to one side. For stimulus angles greater than 0°, the direction of body movement was straight ahead. (*A*) is redrawn from Masino & Knudsen (1990), (*B*) from Masino & Grobstein (1989a).

Normally, there is a transition from snap to hop at a characteristic distance that depends on the azimuthal location. Lesioned frogs also exhibit this transition, but always at the distance characteristic of targets located straight ahead. That is, the frogs produce a behavior that would have been appropriate had the worm been located straight ahead. A similar deficit can be evoked by localized lesions at the junction of the medulla and the spinal cord (Masino & Grobstein 1989a,b) as shown in Figure 6*B*. An intact tecto-tegmento-spinal pathway is necessary to produce normal behavior.

ARM MOVEMENTS TO A SPATIAL TARGET

Arm movements to a spatial target also utilize sensory information that is initially represented in different frames of reference, and the sensory signals that specify target location need to be transformed into motor commands to arm muscles. Thus, the same questions concerning frames of reference and coordinate transformations that we have dealt with for eye, head, and body movements also arise in the study of arm movements. However, arm movements also illustrate an additional aspect of sensorimotor transformations: the distinction between forces and the movements that the forces produce.

For eye movements, a torque applied to the eye produces rotation about the torque axis. Therefore, forces and movements are colinear, and the coordinate system for forces and movements can be assumed to be the same. This is not usually the case for the arm, as illustrated in Figure 7. Consider a force directed downward (F_2) that is resisted by muscle activation. If the force is suddenly released, the arm does not begin to move

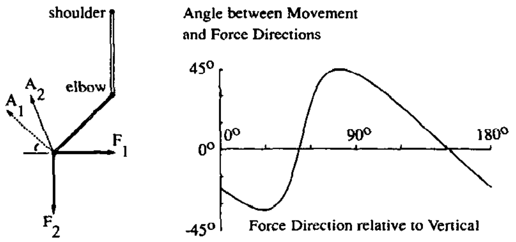


Figure 7 The directions of force and movement are not colinear for the arm. On the left, the dashed lines indicate the initial direction of hand acceleration (A) when a force (F) is suddenly released. On the right is shown how the difference between force direction and movement direction varies with the force direction. These results were computed from the equations of motion of the arm (Hollerbach & Flash 1982) by using typical values for the moments of inertia of the arm.

in the direction opposite to the force (i.e. straight up). Instead, the arm moves upward and forward (A_2). Similarly, release of a posteriorly directed force (F_1) also leads to forward and upward movement (A_1). The difference between the direction in which muscles exert their force and the direction in which the arm moves depends on the orientation of the force vector (Figure 7, *right*), on the posture of the arm, and on the arm's angular motion.

Thus, the transformation between kinematics (movement) and kinetics (forces) is nontrivial in the case of arm motion. Not much is known about how this transformation might be implemented by neural circuits. Mathematical formulations of the problem have been provided by several investigators (Hollerbach & Flash 1982; Hoy & Zernicke 1986; Zajac & Gordon 1989). Other investigators have quantified biomechanical factors, such as muscle stiffness (Mussa-Ivaldi et al 1985) and the changes in the muscles' lever arms with posture (Wood et al 1989), which also affect the relationship between force and movement.

Arm muscle activation vectors for isometric forces have been empirically determined (Buchanan et al 1986, 1989; Flanders & Soechting 1990b). In contrast to the patterns for neck muscle activation, static arm muscle activation sometimes deviates substantially from single cosine tuning functions, which suggests a complex vector code. Arm muscle activation onsets (Hasan & Karst 1989) and activation waveforms (Flanders 1991) have been empirically related to the direction of movement.

There is evidence (described below) that neurons in motor cortex, like those in the superior colliculus, encode the direction of movement by a population vector code. We now focus on three questions: What is the sensory information required to compute movement direction? In which frame(s) of reference is it represented? What is known about sensorimotor transformations for arm movements?

To move to a target accurately in the absence of visual guidance, the starting point of the movement, as well as the desired final point, must be sensed (Bizzi et al 1984; Hogan 1985), as is the case also for eye movements (Mays & Sparks 1980). Information about target location is provided by the visual system, whereas proprioceptors are adequate to signal initial arm posture. Because propriceptors sense muscle length and joint angles (McCloskey 1978), the initial frames of reference for kinesthesis are fixed to the limb segments, i.e. elbow joint angles are initially sensed in the frame of reference fixed to the upper arm. There is psychophysical evidence that this representation of joint angles is transformed to a frame of reference fixed in space (Soechting 1982). Soechting & Ross (1984) found that subjects were best able to match joint angles of their right and left arms when they were measured relative to the vertical axes and the sagittal plane (see also Worringham & Stelmach 1985; Worringham et al 1987). In particular, these experiments identified yaw and elevation angles as a spatial coordinate system for arm orientation.

Target location is initially defined in a reference frame centered at the eyes. Other psychophysical experiments indicate that the origin of this reference frame is shifted toward the shoulder during the neural processing for targeted arm movements (Soechting et al 1990). In this shoulder-centered frame of reference, target location is defined by three parameters: distance, elevation, and azimuth, i.e. a spherical coordinate system (Soechting & Flanders 1989a).

The direction of hand movement is the difference between initial hand location and the location of the target. An analysis of human pointing errors suggests that there is a coordinate transformation from target coordinates to hand (arm) coordinates. The intended, final arm position is computed from target location by a linear transformation that is only approximately accurate (Soechting & Flanders 1989b). This transformation involves two separate channels: Arm elevation is computed from target distance and elevation, and arm yaw is computed from target azimuth (Flanders & Soechting 1990a). Thus, visually derived target coordinates are transformed into a common frame of reference with kinesthetically derived arm coordinates (Helms Tillery et al 1991).

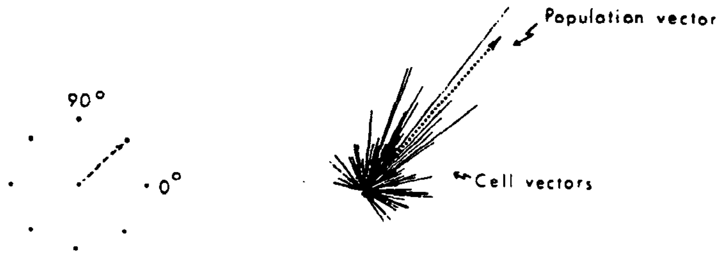
A model that synthesizes these observations (Flanders et al 1992; Soechting & Flanders 1991) ends at the point at which a movement vector is defined by the difference between the intended arm orientation and the initial arm orientation. Thus, the model provides a description of the kinematic coordinate transformations required for goal-directed arm movements, and the transformation to kinetics is beyond its scope.

Because these transformations involve cortical processing, it is interesting to consider which parameters the cortical activity encodes. Since the pioneering work of Evarts (1968), who studied one-dimensional movements, researchers have recognized that discharge of motor cortical neurons is strongly correlated with force (see also Humphrey et al 1970). This, plus the strong monosynaptic connections of pyramidal tract neurons to motoneurons of distal muscles (cf. Kuypers 1981), leads to the interpretation that kinetic parameters are encoded by motor cortical activity.

A different perspective has been provided by Georgopoulos and coworkers (reviewed by Georgopoulos 1986, 1990), who studied the neural correlates of two- or three-dimensional reaching movements. Activity in motor cortex and in area 5 was best correlated with the direction of the movement (i.e. the difference between the initial and final hand positions in space) in a vectorial code (Georgopoulos et al 1982, 1984; Kalaska et al 1983; Schwartz et al 1988). Each neuron's activity defined a direction in space (the "best direction"); for other directions, activity was proportional to the cosine of the angle between that direction and the best direction. The best directions were distributed uniformly in space.

From these observations, Georgopoulos et al (1984) deduced that the motor command for movement direction is determined by the discharge of the entire population (the population vector), and that each cell provides a vectorial contribution to this command. This vector is in the cell's best direction and has an amplitude proportional to the cell's discharge (see Figure 8). The neuronal population vector agrees well with the observed hand trajectories (Figure 8), even when it is computed every 20 ms (Georgopoulos & Massey 1988; Georgopoulos et al 1984, 1988).

Taken at face value, the results of Georgopoulos and coworkers imply that motor cortical activity encodes movement direction, i.e. a kinematic parameter. Kalaska (1991) has attempted to reconcile these findings with earlier observations that neural activity was correlated with force. He suggested that the population vector encodes a kinetic parameter, such as



Movement Direction **Neuronal Population Vector**

Hand Trajectories **Confidence Interval for Population Vector**

Figure 8 Movement direction is encoded vectorially by the activity of a population of motor cortical neurons. For hand movements in the 45° direction, each cortical neuron makes a vectorial contribution in its best direction (*top right*). The vector sum of the cell vectors is the population vector. The 95% confidence interval of the population vector (*bottom right*) approximates the variability in the hand trajectories (*bottom left*). Redrawn from Georgopoulos et al (1984).

the direction of force. He has interpreted his experimental evidence in favor of this suggestion. Kalaska et al (1989) applied static loads to the monkey's arm and found that the neural discharge was tuned to both the direction of the static load and to the direction of a planar arm movement. Although the best directions for movement and for static load were, on average, 180° apart, there was a broad distribution in the angular difference between the two directions.

One would not expect such a broad divergence if the activity of each cell encoded a single parameter measured under two conditions. However, this divergence might be expected if the tonic and phasic activities of the cell were related to two different parmeters (i.e. static load direction and movement kinematics). Also, as shown in Figure 7, a cosine tuning to a kinematic parameter (such as movement direction) would not generally correspond with a cosine tuning of a kinetic parameter, such as force direction, because the difference between force and movement is a nonlinear function of force direction. Without a more precise kinematic and dynamic analysis of the movements, the results of Kalaska et al (1989) are inconclusive. Finally, the population vector does not reverse direction as it evolves over time (Georgopoulos et al 1984), but force does reverse direction as the movement is decelerated.

For these reasons it appears that a kinematic representation of movement direction in motor cortical neurons is compatible with experimental evidence, at least for proximal muscles. Connections between motor cortical neurons and proximal motoneurons are primarily via interneurons (Kuypers 1981; Preston et al 1967), such as the propriospinal neurons described by Lundberg (1979) and Alstermark et al (1981, 1986). These interneuronal circuits could provide the substrate for the transformation from movement kinematics to movement kinetics.

CONCLUDING REMARKS

We have discussed how spatial parameters may be represented by the activities of neurons involved in several different motor tasks. We applied geometric constructs borrowed from classical physics and outlined a stepwise procedure to answer this question. Central to the procedure is the concept of a frame of reference. We have given this term its traditional meaning, even though activity in the central nervous system may never conform exactly to the criteria outlined at the beginning of the review. For example, in the superior colliculus, the frame of reference for auditory stimuli is not exactly eye-fixed, and the direction vector of motor cortical neurons is not exactly in an earth-fixed frame of reference (Caminiti et al 1990). Thus, the concept of an eye-fixed frame of reference in the former case, and of one fixed in space in the latter, is only an approximation.

Nevertheless, reference frames provide a useful point of departure for understanding information processing by neural structures. This is not a given. For example, connectionist models can lead to a very different perspective. In such models, activity in both input and output layers is defined in specific frames of reference, but activity in intervening (hidden) layers need not be in any frame of reference. These hidden layers receive and send highly divergent and convergent projections from other layers. The synaptic weights of these connections are initially random and are then modified iteratively to produce the desired behavior (Sejnowski et al 1988). Because the initial pattern of connectivity is random, the receptive fields of elements in the network would be different from one implementation to the next. Each neuron would have its own idiosyncratic frame of reference. Such a model has been useful in interpreting the visual receptive fields of neurons in parietal cortex (Andersen & Zipser 1988). These receptive fields cannot be defined in any specific frame of reference; instead, they behave as if these neurons were part of an intermediate layer in the transformation from eye-fixed to head-fixed frames of reference.

However, in the examples reviewed here, approximate frames of reference do appear definable. Once a frame of reference has been identified, we can ask how information is encoded in that frame of reference. A variety of neural codes exist, such as topographic (place) codes, vectorial coding, and coding along coordinate axes. In any given system, these different codes may coexist. For example, the spatial coordinates (azimuth and elevation) of sound location appear to be segregated initially (i.e. as time and intensity differences), then combined in the optic tectum in a place code, only to be segregated again in the brainstem. Similarly, the representations of the target location for arm movements appear to be encoded topographically in the retina, in a coordinate system in the intermediate representation, and vectorially in motor cortex.

Coordinate systems have been identified for the three motor tasks we have discussed, either electrophysiologically (Peterson & Baker 1991; Simpson 1984) or behaviorally (Flanders et al 1992; Maioli & Poppele 1989; Masino & Grobstein 1989a,b). It may not be coincidental that in all three motor tasks, one of the coordinate axes was defined by the gravitational vertical. Another coordinate was defined by a sagittal horizontal axis. Thus, one may suggest that, ultimately, there is a common, earth-fixed frame of reference utilized for all motor tasks.

We move in a three-dimensional world dominated by the force of gravity and by the visual horizon. Although one may not be consciously aware of gravitational force (Lackner & Graybiel 1984), its influence on movement is readily appreciated when one observes the movements of astronauts under conditions of microgravity. The vestibular system provides a primary, but not sole (Berthoz et al 1979), indicator of the vertical direction, and one can suggest that other coordinate systems may be aligned with the one defined by the vestibular afferents. In this context, it is noteworthy that the head is usually stabilized in space (Pozzo et al 1990), thus providing an inertial platform for sensing the vertical.

One advantage of representing information in different parts of the brain in a common, spatial frame of reference might be that the exchange of information is facilitated. This would be especially true if the same parameters (e.g. the same coordinate system) were represented in each part. Electrophysiological data on superior colliculus and motor cortex (two major command centers for movement) suggest that this is the case. Neural activity in both structures appears to encode movement kinematics, specifically the movement direction (vector difference between initial and final position). A transformation from kinematic to kinetic parameters occurs much later, perhaps in spinal cord (Georgopoulos 1990).

Representations of kinematics can be effector-independent, whereas codes of kinetics (or muscle activation) are not. Thus, the same kinematic signal could be used to encode an orienting movement if it was effected by the eyes, the head, the body, or a combination of all three. The structure provided by kinematic codes in common coordinate systems can provide the ability for a system to process information from a variety of stimuli concurrently and to respond to one stimulus by a variety of movements.

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