Sensorimotor Coordination and the Structure of Space

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Abstract. Embedded in neural and behavioral organization is a structure of sensorimotor space. Both this embedded spatial structure and the structure of physical space inform sensorimotor control. This paper reviews studies in which the gravitational vertical and horizontal are crucial. The mathematical expressions of spatial geometry in these studies indicate methods for investigating sensorimotor control in freefall.

In freefall, the spatial structure introduced by gravitation – the distinction between vertical and horizontal – does not exist. However, an astronaut arriving in space carries the physiologically-embedded distinction between horizontal and vertical learned on earth. The physiological organization based on this distinction collapses when the strong otolith activity and other gravitational cues for sensorimotor behavior become unavailable. The mathematical methods in this review are applicable in understanding the changes in physiological organization as an astronaut adapts to sensorimotor control in freefall.

Many mathematical languages are available for characterizing the logical structures in physiological organization. Here, group theory is used to characterize basic structure of physical and physiological spaces. Dynamics and topology allow the grouping of trajectory ranges according to the outcomes or attractors. The mathematics of ordered structures express complex orderings, such as in multiphase movements in which different parts of the body are moving in different phase sequences. Conditional dynamics, which combines dynamics with the mathematics of ordered structures, accommodates the parsing of movement sequences into trajectories and transitions.

Studies reviewed include those of the sit-to-stand movement and early locomotion, because of the salience of gravitation in those behaviors. Sensorimotor transitions and the conditions leading to them are characterized in conditional dynamic control structures that do not require thinking of an organism as an input-output device. Conditions leading to sensorimotor transitions on earth assume the presence of a gravitational vertical which is lacking in space. Thus, conditions used on earth for sensorimotor transitions may become ambiguous in space. A platform study in which sensorimotor transition conditions are ambiguous and are related to motion sickness is reviewed.

Keywords: Mathematical, sensorimotor, gravitation, movement sequence, freefall

1. Introduction

On earth and in freefall, we move through a three-dimensional space, but the spatial geometries are irreducibly distinct because of the gravitational direction on earth and its lack in freefall. The organization of movement on earth and its relationship to gravity has been observed, experimented with, and characterized mathematically. For example, human walking involves the alternation of the two legs as support against gravity. In contrast, locomotion in freefall does not involve support against gravity. This paper is about the role of gravitation in sensorimotor organization and the possible differences in sensorimotor behavior without it.

The intent of the use of mathematical languages in these studies is to characterize the logic of physiological organization. In these studies, the focus is on logical structure, not numerical measures. The nervous system is considered to be an autonomous, self-organizing agent, rather than an input-output device. Although
numerical methods, including systems analysis, have been widely used in space studies, as in much of sensorimotor neurobiology, they will not be covered here. Instead, a broader range of mathematical languages is employed to directly express the physiological architecture. The studies have been chosen to show the way the role of gravitation on earth clarifies how its absence is felt in space. They will be covered in five sections:

1) The presence or absence of a gravitational vertical can only be addressed along with the horizontal (Fig. 1). That is, the basic geometry of the space must be characterized as a whole. The standard way to characterize the basic geometry of a space is using group theory. The mathematics of group theory is illustrated by a study of the disynaptic canal-neck projection [32].

2) Earth vertical and horizontal often play a tacit and essential role in movement studies. For example, in the sit-to-stand movement, the vertical is a goal and the movement is largely horizontal. A successful sit-to-stand movement follows one of a range of trajectories that reach the goal of erect balance [40]. Although the goal would be different in freefall, a similar dynamical approach can be used.

3) The dynamics of trajectories as perceived by the subject may differ from those perceived by an outside observer. A subject perceives self-motion in a subject-coincident fashion, that is, with coordinates centered on the subject but including velocity with respect to an external frame, such as the room [19]. The mathematics of subject-coincident coordinates developed for an earth environment will be reviewed, because self-motion perception has a strong effect on movements in freefall.

4) Many movements can be parsed into trajectories with transitions between them. In one example taken from a study of early walking, the gravitational vertical plays a striking role in transitions, similar to its role in the sit-to-stand movement [33]. This example serves to illustrate the use of invariant relations and the conditions for movement transitions. Because the dynamics of the movement change with conditional transitions, the mathematics used is called “conditional dynamics” [27,30,31].

5) Conditions for movements can be ambiguous to subjects lacking sensory cues. The conditions for a movement transition are selected by the subject in designing the sensorimotor control of the movement. However, conditions can become ambiguous because of a vestibular disorder or because habitual cues are absent, especially gravitational cues [29]. One type of ambiguity leading to motion sickness is illustrated from a study of vestibular patients [35].

The vestibular system plays an essential role in the relationship between sensorimotor control and spatial structure, both physical and physiological. Some studies in this review involve the vestibular system explicitly; others, implicitly. The studies address concrete, practical issues indirectly, by focussing on the physiological organization of space and sensorimotor control. Each study is presented in four subsections: description of the biological problem, framing of the mathematical problem, technical fundamentals of the mathematical approach, and results in theoretical neurobiology of the physiological organization.

2. Framing space: Physical and physiological organizations

Vertical does not exist outside of its relationship with horizontal (Fig. 1). This relationship forms the framework for many sensorimotor behaviors, such as turning to look at something without falling over. This is a physical relationship, as are the relationships between the three directions of rotation. Physical relationships are maintained whether or not they are recognized by physiology. In incorporating or mimicking the physical relationships between horizontal and vertical and among the three rotational directions, the vertebrate nervous system quite naturally grounds these relationships in the vertebrate directions, right-left, front-back, and up-down. Although vertebrates have adapted to the physical world, physical relationships are not necessar-
ily represented in nervous systems in the way physicists conceptualize them. Rather, physical relationships can be inseparable from physiological elements of organization.

2.1. Biological problem: Structure of inertial space

Vertical and horizontal provide cues for many movements. For example, vertical, erect stance can be sensed by the equality of pressure on the two feet when they are evenly placed on a horizontal support surface. The completion of the sit-to-stand movement is signalled by proximity to vertical, whether sensed by vision, proprioception, or inertial sensors. However, the sit-to-stand movement involves important horizontal components. It is essential to the movement to distinguish vertical from horizontal.

Many terrestrial movements are structured according to the vertical and horizontal. The basic postures of standing and sitting are aligned to the vertical, whereas lying down is primarily horizontal. Walking and bicycling are forms of locomotion in which the body’s relationship to the vertical and horizontal is carefully regulated. In handling objects, we respect vertical alignment in lifting heavy objects carefully and avoiding letting breakable items fall. Altogether, we move in an environment strongly structured by the horizontal and vertical.

When the distinction between horizontal and vertical can no longer be made in freefall, astronauts experience sensory illusions [17,39]. They handle objects differently, because they can leave them in midair without them falling. Overall, astronauts’ movements are different, for example, they float from one place to another rather than walking. Upon returning to earth, astronauts are less adept at vertical-horizontal distinctions, for example, they mistake tilt for translation [17,39]. Illusions and movement errors involving the vertical and horizontal also occur when the inertial senses are disturbed, as in vestibular disorders [25]. For example, vestibular patients may feel a constant sensation of falling. Also, a horizontal head turn – for example, in response to being addressed from behind – may cause a vestibular patient to fall down, having lost track of the vertical.

2.2. Mathematical problem: Characterizing space

The relationship between vertical and horizontal is a basic geometrical structure of physics at the earth’s surface. It is best characterized by the symmetries of movement near the surface of the earth. For example, short ballistic trajectories – as in throwing a ball – depend on the initial angle to vertical and not on the direction in the horizontal plane. Thus, any rotation about the vertical axis leaves a predicted trajectory fixed. Any transformation – in this case, a rotation – that leaves an object fixed is a symmetry. Thus, rotations about the vertical axis are symmetries of physical movement near the earth’s surface.

Physiological movements have further organizational structure. The vertebrate body is largely organized into similar right and left sides. The right and left sides are approximately symmetric in the mathematical sense that the vertebrate body can be reflected right-left without essentially changing it. Although they do not have mirror symmetry, there are two other natural body directions: front-back and along the vertebral, rostral-caudal body axis. These physiological directions provide distinctions in humans between the somersault, the cartwheel, and the action of stepping in a turn about the body axis. The point here is not to simulate movements, but to analyze the physiological organization that constructs the internalized geometry of space. Although nervous systems must take into account the physical geometry of space, a physiological geometry can provide more physiologically relevant information about body movement.

The physiological geometry can be evaluated by determining the symmetry transformations expressed in nervous systems. An example familiar to many is the double push-pull organization of the principal vestibular innervations of the extraocular muscles (Fig. 2A). To analyze the symmetries mathematically, a first step is to simplify the diagram (Fig. 2B). Then transformations can easily be diagrammed (Fig. 2C). Reflecting or exchanging right-left then exchanging inhibition and excitation returns the innervation diagram to its original pattern, providing a symmetry (Fig. 2C). This symmetry binds the canal pair and muscle pair into push pull relationships with each other. Such an evaluation of a physiological organization provides both a characterization of the logical structure of the projection and also a means for comparing that logical structure to that of behaviors or of physical space itself.

2.3. Mathematical approach: Group theory

A standard method for characterizing basic features of spaces is group theory. A group has only one operation, giving it the suppleness to compare basic geome-
tries between very different entities, such as physical and physiological spaces.

Formally, a group is a set of elements $G$ together with a binary operation $G \times G \rightarrow G$ such that: i) this operation is associative $(a(bc) = (ab)c$ for all $a, b, c$ in $G)$, ii) there is an identity element $u \in G$ with $uu = u = au$ for all $a \in G$, and iii) for this element $u$, there is to each element $a \in G$ an inverse element $a^{-1} \in G$ with $aa^{-1} = u = a^{-1}a$ [26]. A symmetry of object $O$ is a mathematical transformation that leaves specified properties
of $O$ fixed, whether or not it exchanges the elements of $O$. A symmetry group is a group whose elements are symmetries of the same object, where the group operation is composition (multiplication) of the symmetry transformations. A group expresses the completeness of the symmetries identified for an object.

2.4. Theoretical neurobiology: Structure of rotations in the disynaptic canal-neck projection

Group theory was introduced into neurobiology to characterize the complete set of locomotor gaits in terms of symmetries [11,12,14,41]. The symmetries are among leg movements in gait; for example, in quadrupeds the physiological symmetries among right-left and fore-hind limb movements predict the range of quadruped gaits.

In the vestibular studies, the physics of space and rotations are known. More research is required to evaluate the physiological spaces that include or mimic the physical space. These are expected to differ among neural centers and projections. The symmetries of the disynaptic canal-neck projection as recorded experimentally [42–44,48] have been evaluated directly from the data [31]. To evaluate the symmetry group of the disynaptic canal-neck projection, the first step is to diagram the projection as a whole, directly from the data (Fig. 2D). Each recorded neck muscle motoneuron received projections from all six canals, in three excitatory/inhibitory pairs. Because each pair can project with either sign, excitatory/inhibitory or inhibitory/excitatory, there are $2^3 = 8$ possible combinations of canal pair projections. This is more clearly seen in Fig. 2E, which is analogous to Fig. 2B. Eight muscle types were found, four on each side [42–44]. The eight muscle types exhibited exactly the eight possible canal pair projections.

The three canal pairs provide coordinates for physical rotations. However, the directions provided by the semicircular canals in the skull are external to the nervous system and do not determine a neural coordinate frame. Rather, the nervous system, by its own organization, determines whether sensory activity forms or maintains a coordinate frame. Coordinate axes may move separately or they may rotate, maintaining their relationships with each other.

Symmetry group evaluation can be used to provide information about whether the innervations are present to allow a vestibular projection to maintain a rotational coordinate frame. The symmetry group evaluation is done by defining transformations (as illustrated in Fig. 2C) and using the mathematics of symmetry groups (§2.3). In the case of the disynaptic canal-neck projection, symmetry group evaluation results in the framework of a rotational space in which the three rotational degrees of freedom are bound together, besides having a vertebrate right and left that does not exist in the physical world [32].

This space provides a unified logical structure including both the rotational geometry of the canals and the rectangular geometry of the neck muscles and the vertebrate body. The physiological right/left, front/back organization is added to the physical rotational symmetries. One manifestation of this addition is the organization of the projection as a cube rotating in a sensorimotor space as the head rotates on the shoulders. Physiological rotation augments physical rotation with physiologically useful organizational information. This physiological organization of rotation is not a model designed to simulate behavior, but a direct characterization of the physiological organization inherent in the data themselves [42–44,48].

Further evaluations of the spatial group structure of physiological organizations will be required to encompass the way gravitational information is incorporated physiologically. The canal projection studied omits the gravitational distinction between horizontal and vertical; in the absence of gravitation, the physiological symmetry group of inertial space may reduce to what is presented here.

3. A range of trajectories satisfies a behavioral goal

We shift now from intrinsic physiological organization to requirements for fulfilling sensorimotor tasks. These two are related, because body geometry and symmetries constrain sensorimotor performance. In addition, environmental factors constrain performance and may frame the task. For example, the vertical axis and horizontal plane frame the sit-to-stand movement, in which horizontal and vertical movements place the body in erect stance.

3.1. Biological problem: Sit-to-stand trajectories

The terrestrial structure of space, divided into gravitational horizontal and vertical, frames the sit-to-stand task. However, that spatial structure allows a range of solutions to the problem of arriving at standing, starting from sitting. The body is not required to arrive in an exact position via a particular trajectory. Instead,
the goal is a region of standing positions; they can be reached via a range of sit-to-stand trajectories. Similar statements are true of other goal-oriented tasks, such as grasping a handle or facing a conversation partner: the goals of these movements are not physical points, but regions in which the functional goal is satisfied. The physiological system does not need to be organized to create trajectories, but to select ranges that serve its purposes.

For the sit-to-stand movement with the feet on the ground (Fig. 3A), trajectories must arrive in the region of body positions and momenta in which standing balance is possible. Otherwise, the body will sink back to sitting or continue on to a forward fall. So the movement control problem is to set the body in motion on a trajectory that will reach standing.

3.2. Mathematical problem: Finding the range of trajectories

Bodies vary in height and proportion, so the same numerical positions and trajectories will not suit all bodies. From infancy, we learn to judge our body position with respect to horizontal and vertical. Furthermore, we learn to judge the results of momenta and trajectories in attaining sitting and standing positions and in maintaining upright movements such as walking.

The desirable mathematical approach relates a simple judgment process to the precise body mechanics. Such a mathematical approach clarifies the way the physiological organization of the sensorimotor behavior can relate to the physical task. Although the mathematical approach is presented with details specific to the sit-to-stand movement, it applies similarly to many movements.

3.3. Mathematical approach: Topological biodynamics

The most salient variables for the sit-to-stand movement are the leg and trunk angles to vertical, so attention can be focussed on the two-dimensional phase space they determine. Topological considerations determine the form of the dynamics on this space, consistent with the older Hamiltonian and Lagrangian methods, which specify movement styles by means of constraints (Fig. 3A) [27,40].

In a topological approach we specify the type of space and then apply theorems that have been proven in the literature. We require a structurally stable solution. For structurally stable dynamical spaces, the Bloch theorem [5,34] allows us to limit consideration to a limited region of phase space (technically, a compact isolating block). This is an essential step, because
it allows investigation of body movements in modular fashion, rather than having to specify the individual’s movement, along with the rest of the universe, for all time.

Within the region of interest, trajectories converge only in limited areas, called attractors or limit sets. The nature of the limit sets is specified by the Poincaré-Bendixon theorem [1]. The limit set in the sit-to-stand phase space is the goal region of standing.

The next step is to determine the arrangement of non-converging trajectories in the phase space. Let the left-hand boundary of the phase plane be the sitting region and lift-off area. With insufficient momentum, the trajectory returns to sitting. A threshold must be crossed before reaching the range of trajectories arriving at the standing limit cycle. Therefore there is a saddle point between the sitting and standing regions, that separates the two ranges of trajectories. This determined, Peixoto’s theorem [1,15] limits the possible forms of the dynamics by ruling out trajectories connecting saddle points. Of the resulting six forms [40], only one includes trajectories that return to sitting, trajectories that arrive at erect stance, and trajectories that overshoot and fall forward (Fig. 3A).

3.4. Theoretical neurobiology: Ranges of trajectories

By using topology to determine the form of the dynamics, the essential properties of the phase space are specified without irrelevant quantities, such as height and proportions that vary from individual to individual. Any person rising from the sitting position using momentum (but not the arms of the chair) must select the correct trajectory range for a successful sit-to-stand movement. The middle range of trajectories loses just enough momentum to bring the body to a stable erect stance (Fig. 3A) [40]. With lower initial momentum, the trajectories return to sitting. With excessive initial momentum, the trajectories continue on beyond the standing position to a forward fall. The mechanics of the sit-to-stand movement divides a continuous space into discrete ranges according to the destinations of the trajectories. Physics provides the trajectory ranges; motor control must select among the ranges that physics offers.

In freefall, movements are not framed by gravitational horizontal and vertical, so trajectories are grouped by different criteria. For example, locomotion in space may consist of trajectories segmented by touching the wall of the vehicle. In analogy to the grouping of trajectories rising from a sitting position (Fig. 3A), astronauts may group trajectories according to the desirable amount of momentum and body rotation (Fig. 3B). Excessive momentum or body rotation may lead to unpleasant encounters with the opposite wall, making the transition to the next trajectory phase difficult. The criteria and goals for movement determine the way trajectories in freefall are grouped into desirable and undesirable for selection by the sensorimotor control system. As in the sit-to-stand movement, physics determines the trajectory ranges, and senses must be used to identify and monitor desirable trajectories.

4. Self-motion perception of velocity and acceleration

Trajectories are movement opportunities provided by physics and selected by the sensorimotor system. On earth, gravitation is involved in both the physics of the trajectories and the sensory cues by which they are selected. To understand self-motion perception in more unusual cases such as freefall, sensory function must be examined more rigorously.

4.1. Biological problem: Combining senses to provide self-motion perception

Self-motion perception – as opposed to the detection of motion of an insensate object – typically involves the capacity to detect velocity and acceleration information through vision, proprioception, and inertial senses. Sensory systems such as the vestibular and visual systems are physiologically separate at the periphery and may be accessed separately for modality-specific responses. However, their self-motion information is integrated in multiple neural centers, including the vestibular nuclei, the cerebellum, and the parietal lobe.

At the behavioral level of analysis, the organism has access to self-motion information from all of the sensors. In some cases, the combination of self-motion information is fragmented and paradoxical from the physical point of view. For example, one may perceive motion along with a constant position. In other cases, there is a unified, physically-possible perception; sometimes it agrees with the physical motion and sometimes not. When self-motion perception is unified and physically-possible, how are the senses unified into a physically-consistent coordinate frame?
4.2. Mathematical problem: Self-motion coordinates

For unified self-motion perception, we seek a set of coordinates that travels with the subject while allowing both velocity and acceleration perception. Coordinates fixed with respect to an outside reference, such as the room, are typically used to unify information available to an experimenter. However, a subject’s center of reference travels with the subject’s body. A standard technique in physics in such cases is to use a moving frame centered on the object of interest; unfortunately, this is not appropriate for self-motion perception, because the self-motion in a moving frame is zero. Perception of physically-possible self-motions may be constructed physiologically in coordinates that are not typically used in physics.

For example, consider self-motion perception of a subject strapped securely in a centrifuge seat, facing forward into the motion, which has constant angular velocity. Visually, the subject sees constant forward motion. Because the subject perceives motion, the coordinate system is not a moving frame, at rest with respect to the subject. The derivative of the visually-registered motion is zero. However, the vestibular and proprioceptive systems provide non-zero radial acceleration information. Usually, coordinates in physics are chosen so that acceleration is the time-derivative of velocity. In contrast, the coordinates used by nervous systems both travel with the subject and allow motion with respect to the subject. In that sense, they are subject-coincident at every moment.

4.3. Mathematical approach: Subject-coincident coordinates

A finite version of subject-coincident coordinates would sample movement with respect to a fixed reference every moment, where a moment is a short, finite amount of time (not infinitesimal). For consistency with physics, an infinitesimal moment is required. A subject-coincident coordinate system is given by a set of coordinate axes fixed in position relative to the subject in question (such as the head), and for which the movement of the subject is specified at each moment in time according to an externally fixed reference. Thus, aspects of motion such as the linear velocity, linear acceleration, angular velocity, angular acceleration, and attitude with respect to gravity of the subject are given by their measurements in the (standard physics) coordinate system, but the external coordinates are shifted every moment to be coincident with the subject [19].

In this way, non-zero linear and angular self-motion velocity can be measured in a coordinate system that is oriented with the subject. Because the subject moves, the coordinate axes “catch up” with the subject at each instant. However, they are only used instantaneously, when they are both coincident with the head and fixed with respect to a reference object.

To study the mathematical nature of these coordinates that are instantaneously subject-coincident, it is of interest to investigate sustained motions. Motions that are sustained even briefly provide clues to the consistency of the disparate senses, in the form of requirements for the relationships between velocity and acceleration [19]. These relationships provide categories of sustained motion, along with a rationale for the nervous system to distinguish physically possible sets of sensory cues.

4.4. Theoretical neurobiology: Indistinguishable motions and movement planning

Using subject-coincident coordinates, aspects of physical motions can be calculated, from the subject’s point of view [18–22,27]. A basic issue is to determine which motions are physically indistinguishable. For example, two motions that are indistinguishable in the sense that they both have an acceleration of 1 g are 1) standing on the surface of the earth and 2) standing upside down in a spaceship near the earth, moving at twice the acceleration of gravity toward the earth. Given motions that are physically indistinguishable, an individual selects one plausible motion as an interpretation of self-motion cues.

Holly [18,20,21] has calculated the effect of this initial choice among indistinguishable possibilities on the subsequent perception of self-motion, in both 1-g and 0-g. In making the initial choice, the nervous system loses the information that the actual trajectory may be a different, but physically indistinguishable one. Thus, the initial perception strongly affects ensuing perceptions of the trajectory [23].

These effects are expected to be more pervasive in freefall, because there are fewer relationships providing clues to the physical consistency of sensory signals. By analyzing the coordinates natural to self-motion perception on earth, the mathematics of subject-coincident coordinates provides a way to express the sensory predicament of an astronaut lacking the gravitational attitude vector and to predict strategies by which felicitous sensorimotor decisions might be made.
5. Parsing motor control into trajectories and transitions

The previous two sections have addressed movement trajectories. Section 3 showed the way movement trajectories are selected as regions, according to physical criteria. Section 4 showed the way senses can be integrated to be consistent with physical trajectories. Both sections introduced discreteness, §3 in the distinctions between regions of trajectories and §4 in the choices of initial perception and their consequences.

The present section introduces the discreteness of shifting between one trajectory and another. Transitions between trajectories are conditional, depending on mechanical or physiological conditions. In this section, an example is presented in which the conditions are mechanical and depend on gravitation.

5.1. Biological problem: Onset of locomotion

Both the sit-to-stand movement (§3) and walking are organized according to the gravitational horizontal and vertical. Both movements are largely horizontal; one attains and the other maintains vertical balance. Children learn that gravitation reduces vertical momentum by the time they learn to walk. The onset of locomotion is a critical time in learning certain physical principles [9,10]. In adult walking forms, physical principles, such as the conservation of angular momentum and the exchange of potential and kinetic energy by gaining or losing altitude, are smoothly integrated. The physical requirements of any successful walk are more rudimentary, including alternate support by the two legs, along with progress across the floor. At the onset of locomotion, a broad range of unusual walking forms are displayed. At the extremes of this range, walking forms display the mastery of certain physical principles and not others. In an investigation of the physics of early walking using conditional dynamics, one extreme type of early locomotion depended saliently on rising and then falling [33]. This is an example of a movement sequence in which gravity plays an important role in transitions from one movement phase to another.

In locomotion, the parsing of motor control into trajectories and transitions is familiar. Stance phase and swing phase are trajectories. Heel-strike is the transition between swing and stance phases. Toe-off is the transition between stance and swing phases. The physics of stance and swing phases involve both the momentum that continues the motion and invariants that maintain balance. The biological problem of the onset of locomotion addressed here is to understand the simple control structures that allow children to explore the physics of walking.

5.2. Mathematical problem: Specifying control structures

Each movement phase is identified by a maintained relationship or “invariant”. The swing phase of walking, for example, can be formalized by noting that the weight is on the stance foot and the swing leg moves forward with respect to the hip. During the swing phase, the opposite leg is in the stance phase. The mathematical problem is to specify the physiological organization of the movement in terms of the invariants and their relations with each other.

Many movement invariants have been observed experimentally. For example, Jacob Bloomberg has recorded in altitude-pitch space the invariant followed by the head in maintaining dynamic visual acuity while walking [6,7]. The invariant is a long, narrow region in altitude-pitch space, corresponding to the relationship between altitude and pitch that must be maintained for continuous visual fixation (Fig. 4). It is not an exact line, because the fovea has a small width; rather, it is a two-dimensional region. There are many more dimensions in the overall space of body movements as the subject walks on the treadmill; altitude-pitch space is a subspace of this much larger space [2,8,24,36]. Within a different subspace, each leg follows a cycle in joint angle space [2,8]; it engages and releases a support action against gravity, as it alternates between stance and swing phases.

Although the motion of each leg can be specified as following a trajectory in joint angle space, bipedal walking requires a larger sensorimotor space in which the motions of the two legs are integrated. Within this larger space, the overall control structure is not in a right, left, right, left, etc. sequence. Although stance and swing phases alternate linearly for one leg, stance phase for the right leg overlaps with swing phase for the left leg. Thus, in order to parse locomotion into trajectories and transitions, we require a mathematical approach that includes a large sensorimotor space, along with the ability to focus on included sensorimotor subspaces.

5.3. Mathematical approach: Conditional dynamics

The mathematics of ordered structures is helpful in specifying the relationships of the phases in locomo-
Fig. 4. Maintained Relationship in Dynamic Visual Acuity. The stick figure on the left shows the relationship maintained between the altitude and pitch angle of the head while fixating a stationary target [6,7]. The upper box contains a graph of the maintained relationship: the altitude and pitch angle remain within the shaded region. The solid lines denote inclusion by conventions of the mathematics of ordered structures. The lower boxes contain graphs of the pitch angle and altitude. The boxes with lines diagram a conditional motor space, which is a mathematical expression, like an equation. The diagram conveys: even though the head pitch angle and altitude are free to move through their physiological ranges, the relationship between them is maintained.

5.4. Theoretical neurobiology: Walking by falling

One simple method observed in the first two weeks of walking used falling as a primary way to power forward motion [33]. Falling releases potential energy – height – in favor of kinetic energy. After two steps, the child stops and rises on tiptoe to regain potential energy. Soon, toddlers learn the practical relationship between potential and kinetic energy as a lesson in locomoting in gravitation.

In terms of conditional dynamics, passing the vertical orientation serves as a condition for the transition between rising and falling (Fig. 5). The attainment of vertical orientation is the final phase of rising, and it serves as the condition leading to a transition in motor coordination, to falling.

Gravitation plays a crucial role in movement transitions between rising and falling. For example, in the sit-to-stand movement, there is a transition to standing balance when the body axis reaches vertical. In the sense that the gravitational vertical shapes everyday movements on earth, gravity is an essential feature of the geometry of the inertial world.

The methods reviewed here are applicable to freefall in at least two ways. First, movements composed of trajectories and transitions can be formalized using conditional dynamics and specifying the conditions leading to transitions. Not only movements but more general behaviors can be formalized in this way. Second, specific results on movement in gravity can be examined to determine which movement transitions may be problematic in freefall. Movement transitions that depend on gravitation become ambiguous when gravitation is absent. For example, rising and falling are simply motions in freefall, not distinct classes of motions, as they are in gravity. A transition that depends on distinguishing rising and falling becomes ambiguous in freefall.
6. Control ambiguity and motion sickness

The absence of gravitation makes two conditions, such as rising and falling, equivalent as cues for movement transition. For example, a control system may use vertical rising as a condition for continuing to push upward, whereas vertical falling is a condition for putting a foot forward to transition to stance. If this control system is transferred to freefall, rising and falling become one equivalent movement, which leads to both continuing to push upward and putting a foot forward. An astronaut continuing to use a control system in which gravity makes crucial distinctions will be using an ambiguous control system.

Vestibular patients have been observed to use ambiguous control systems [35]. The same patients become motion sick in a way that is plausibly related to the ambiguity of control.

6.1. Biological problem: Shifting sensory coordination

In experimental studies using a movable platform, subjects coordinate the use of sensory orientation cues to avoid those that are unreliable. By manipulating the availability of reliable physical cues, observers can infer which sensory cues are used by subjects that balance successfully, and experimenters can encourage transitions in the use of sensory cues in subjects. These transitions in the use of sensory orientation cues on the posture platform have been demonstrated experimentally to be abrupt [38]. These experimental results do not contradict the belief that the vestibular system sums sensory inputs, but rather they demonstrate another facet of nervous system function: the ability to shift between mutually exclusive behavioral states, like those involved in walking and running or speaking Spanish and speaking Russian. Subjects in platform studies changed sensory states according to the physical conditions affording orientation cues.

The subjects were of four types: healthy subjects and three types of vestibular patients [3,4,35,37,38]. Although healthy subjects balanced in all platform conditions, vestibular patients fell in some. Given this information, the biological problem is to determine which sensory orientation cues are being used and which physical conditions lead to a transition in sensory use.

6.2. Mathematical problem: Consistent control

Healthy subjects are often unaware of their own abrupt transitions and the experimental manipulations that occasion them. In everyday life, these transitions function unnoticed. The mathematical problem is to develop a system of abrupt transitions with these closed and seamless properties. The abrupt transitions among states of sensory use are similar to those considered in the previous section among states of motor coordination. Sensory states are characterized by maintenance of relationships, such as alignment of the body to visual vertical.

The mathematical problem of transition among sensory states includes properties of the overall control structure. It must be consistent rather than ambiguous and containing impasses. Although no external condition can force a physiological transition, this is expected to be a simple system in which a match or mismatch of cues leads to a transition. In particular, a condition is never ambiguous: the same condition does not afford an opportunity for transition to different sensory states. In addition, no sensory state is a dead end: if the control structure leads to it, then it must also provide an exit.
6. Mathematical approach: Dyads in conditional dynamics

Conditional dynamics was presented in the previous section (§5.3) and used to denote the transition between the motor coordination states of rising and falling (§5.4, Fig. 5). Similar transitions form the control structure among sensory coordination states.

The requirement that the organism be able to enter and exit any state can be formalized as conditional completeness: Given a system of state transitions with states $S_n$ (n an integer), for every $S_i$, there exist states $S_j$ and $S_k$, along with trigger regions $t_{ji}$ and $t_{ik}$ such that $S_j > t_{ji}, > t_{ji}, S_i, > S_i > t_{ik},$ and $> t_{ik}, S_k >$. (That is, $S_j$ includes $t_{ji}, t_{ji}$ is contiguous to $S_i, S_i$ includes $t_{ik}$, and $t_{ik}$ is contiguous to $S_k$.)

The smallest nontrivial conditional space that is conditionally complete is a dyad, which consists of two distinct states, $S_1$ and $S_2$, with trigger regions $t_{12}$ and $t_{21}$ that represent conditions for transition, such that $S_1 > t_{12}, S_2 > t_{21}, > t_{12}, S_2 >$, and $> t_{21}, S_1 >$ [26–28]. Lack of ambiguity can be formalized in the following way: For distinct states, 1) if $S_1 > t_{ij}, S_j > t_{ji}, > t_{ij}, S_j >$, and $> t_{ji}, S_i >$, then $t_{ij} \cap t_{ji} = \phi$, and 2) if $S_1 > t_{ij}, S_j > t_{ik}, > t_{ij}, S_j >$, and $> t_{ik}, S_k >$, then $t_{ij} \cap t_{ik} = \phi$. The transitions in a dyad may be ambiguous or not.

6.4. Theoretical neurobiology: Ambiguous transitions and motion sickness

The sensory transitions of vestibular patients and healthy subjects were evaluated to determine the control structures by which they transitioned among sensory states [35]. Healthy subjects and the three types of vestibular patients used the same sensory cues, but used different conditions for transitioning among sensory states. For example, the data on Category I patients was consistent with the use of only the match or mismatch between the vestibular cue and the ankle angle cue as a condition for transitioning between two sensory states. Although all senses are active in all states, the two states differ in the sensory cue that is predominantly trusted, ankle angle or visual cues. Thus, motion of the support surface would lead to a transition to trusting vision. Even though there is no a priori implication from the motion of the support surface that vision is to be trusted, such a transition works within a conditional dynamic control system that is both conditionally complete and unambiguous.

Category III vestibular patients, however, failed to follow a consistent control system. Unlike the vestibular patients who fell apparently unknowingly, these lurched to a fall. Because of this behavior and because no consistent control structure fit their pattern of transitions, an ambiguous control structure was proposed for them.

In an unambiguous dyad, the two regions that specify conditions for transition are distinct. For example, the visual surround moving is distinct from the visual surround not moving (Fig. 6A). The key ambiguity in the vestibular patients’ control structure was that two conditions were not distinct. The condition for trusting vision was for the visual surround to move [35]. The condition for trusting vision was for the support surface to not move. The two conditions are not distinct, because the visual surround and support surface can both move (Fig. 6B). In that case, the patient would continually reverberate between trusting and distrusting vision: when the subject trusts vision, the moving visual surround suggests a transition to distrusting vision, and when the subject distrusts vision, the moving support surface suggests a transition to trusting vision. This behavior fits the observed behavior [27,35]. These patients also became motion sick.

The logical cause of distress for these patients was the ambiguity of the transition cue. Astronauts still using earth transition cues for sensorimotor control face similar ambiguity. For example, rising and falling are not distinguished in space by the direction of the gravitational vertical. During this initial phase, astronauts become motion sick. It would be consistent with our study of vestibular patients’ control structures that astronauts become motion sick by using sensorimotor control structures which involve conditions for transition that depend on gravitation as a cue. When the gravitational cue is unavailable, the sensorimotor control structure becomes ambiguous, perhaps suggesting multiple, mutually exclusive actions. In such a case, it would make sense for an astronaut to overcome space sickness by restructuring sensorimotor control structures to use conditions that are unambiguous in freefall.

7. Discussion

The studies reviewed in this paper have sought the intrinsic organization in physiological systems and chosen mathematical structures that express that organization as directly as possible. The advantage of this approach is that it addresses the intrinsic organization of
physiological systems as directly as possible. Any of the approaches presented can be used in a quantitative way. However, quantification imposed for its own sake may obscure the intrinsic organization or introduce organization, such as an input-output structure, where it is alien. The effort to avoid imposing alien organization requires of the theorist a broad mathematical repertoire and sensitivity to the physiological system.

The intrinsic spatial properties of the physiological system are of direct relevance to vestibular and movement studies, on earth or in freefall. In Section 2, the disynaptic canal-neck projection was selected for evaluation because of its clear physiological organization. The mathematics of symmetry groups is well-known and standard for specifying spatial properties of empirical systems, so that results of this study are readily compared with the symmetry group properties of physical systems. In particular, the projection’s organizational structure binds the three separate rotational degrees of freedom into a three-dimensional rotation space, while adding physiological structure, especially right-left symmetry. Parsing the disynaptic projection out of the entire set of vestibulocollic projections limits the evaluation while providing the potential to understand vestibular projections as a concatenated or layered structure linked by related spatial subgroups. The discrete groups found are the necessary skeleton for continuous spatial perception or movement [32].

Given that the vestibular system has a fundamental spatial structure different from that familiar to physicists, it behooves those interested in motor behavior to consider the physics of movement in a way that does not impose a particular spatial structure on it. Section 3 presents the selection of movement trajectories by regions, rather than specific trajectories, using topology [27,40]. The topological approach specifies the dynamical properties of the movement space — in this case, the sit-to-stand movement — regardless of the particular body’s height or proportions. By specifying regions of movement space according to dynamics, the topological approach clarifies when variations in sit-to-stand trajectories have physiological meaning and should not simply be averaged together. The sit-to-stand study is presented as an example of the topolog-
ical approach and how to apply it to the trajectories of other physiologically-relevant motions in their physical setting, whether terrestrial or in space.

For self-motion perception, the study reviewed in Section 4 emphasizes the multiplicity of senses that integrate at the behavioral level of analysis [19,27]. Knowing the physical trajectory does not tell us what the self-motion perception will be; there are motion illusions and paradoxical, physically-impossible motions. Understanding these requires a physiologically-sensitive understanding of self-motion perception. Although the physiological system has accommodated itself to the physical world, the intrinsic physiological organization is fundamental in neural mimicking of physics. Subject-coincident coordinates provide a meeting point for physics and physiology; they are continuous and provide physically accurate expressions, which physiological self-motion perception does not always do.

In particular, sensorimotor behavior is often abruptly segmented. Section 5 addresses sensorimotor cues for transitions between movement phases, using conditional dynamics. Conditional dynamics accommodates the characterization of natural movement sequences, besides the mathematical analysis of sensorimotor control systems [27,31]. Like group theory and dynamics, conditional dynamics is a mathematical method that accommodates but does not provide the specification of intrinsic physiological organization. Conditional dynamics and studies of movements on earth provide a framework for investigations of the way astronauts eliminate expectations of gravitational cues as they adapt to freefall and incorporate, instead, conditions encountered in space. This approach provides a way to characterize the difference between earth and space sensorimotor adaptation states.

The results presented in Section 6 are applicable to the adaptation period. This section presents logical structures, especially the dyad, that have expressed the organization of sensorimotor behavior on earth. These structures have not yet been applied to the evaluation of behaviors in space. An ambiguous condition for transition was found to be related to motion sickness. When astronauts lose gravitational horizontal and vertical, habitual conditions for movement transition become ambiguous. Motion and motion onset are related to space sickness [16]. As the natural movements in freefall are investigated, an awareness of ambiguous conditions for movement transition may suggest ways to reduce space sickness.

The techniques presented in this review can be used to extend previous studies of natural movements in space [45–47]. Such movements may use conditions for transition that are not used on earth. Because of the ubiquity of intrinsic organization in physiological systems, it is expected that further investigation of conditional control structures will reveal novel mathematical structures. A combination of mathematical and experimental approaches are advantageous, because they complement each other in their treatment of biological variation in the performance of similar tasks. Experimental techniques are often designed to establish a certain uniformity. Variability that would be unwelcome in such an experiment may allow a theorist to demonstrate that disparate performances arise from mathematically similar organizational structure. Astronauts, especially, carry terrestrial physiological organization into space and revise it for freefall conditions. Awareness of the intrinsic physiological organization of sensorimotor behavior, expressed in mathematical languages, provides a precise, formal means for understanding, comparing, and perhaps assisting performance by different individuals and in different circumstances.

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