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Spatial symmetry groups as sensorimotor guidelines

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Abstract. While some aspects of neuroanatomical organization are related to packing and access rather than to function, other aspects of anatomical/physiological organization are directly related to function. The mathematics of symmetry groups can be used to determine logical structure in projections and to relate it to function. This paper reviews two studies of the symmetry groups of vestibular projections that are related to the spatial functions of the vestibular complex, including gaze, posture, and movement. These logical structures have been determined by finding symmetry groups of two vestibular projections directly from physiological and anatomical data. Logical structures in vestibular projections are distinct from mapping properties such as the ability to maintain two- and three-dimensional coordinate systems; rather, they provide anatomical/physiological foundations for these mapping properties. The symmetry group of the direct projection from the semicircular canal primary afferents to neck motor neurons is that of the cube (O, the octahedral group), which can serve as a discrete skeleton for coordinate systems in three-dimensional space. The symmetry group of the canal projection from the secondary vestibular afferents to the inferior olive and thence to the cerebellar uvula-nodulus is that of the square (D8), which can support coordinates for the horizontal plane. While the mathematical relationship between these symmetry groups and functions of the vestibular complex are clear, these studies open a larger question: what is the causal logic by which neural centers and their intrinsic organization affect each other and behavior? The relationship of vestibular projection symmetry groups to spatial function make them ideal projections for investigating this causal logic. The symmetry group results are discussed in relationship to possible ways they communicate spatial structure to other neural centers and format spatial functions such as body movements. These two projection symmetry groups suggest that all vestibular projections may have symmetry groups significantly related to function, perhaps all to spatial function.

Keywords: Mathematical, symmetry, group, vestibular, projection

1. Introduction

Physical space forms the stage for functions of the vestibular complex such as standing balance, visual fixation, and smooth pursuit. The semicircular canals are shaped and placed in the head so that they register angular motions in three dimensions of physical space. However, this shaping and placement is insufficient for the nervous system to receive geometrically meaningful information about angular motion. Rather, the geometrically meaning is maintained by the organization, with respect to the vestibular endorgans and to the target cells, of the pathways that carry canal activity. The

synaptic and projection patterns of the vestibular complex are organized to communicate effectively to other neural centers the information they need about angular motion. These synaptic and projection patterns format the vestibular information as it is carried to other neural centers. In particular, the canal projection from the vestibular nuclei via the inferior olive to the uvula-nodulus of the cerebellum arranges the four vertical canals according to canal planes – a major geometric simplification over arranging them in homologous pairs of two anterior and two posterior canals – and gives them the symmetry group of a square, the necessary discrete skeleton of a continuous plane. The

disynaptic projection from the canal primary afferents to neck motor neurons is organized with the symmetry group of a cube, the necessary discrete skeleton for a three-dimensional coordinate system. This review presents these two projection patterns and their symmetry groups, without repeating the original determination of the symmetry groups. The purpose of this review is to present the synthesis of functions of the vestibular complex suggested by the projections' symmetry groups.

1.1. Intrinsic logic in neural systems

The crucial geometrical formatting provided by the disynaptic semicircular canal-neck projection and the canal vestibulo-olivo-nodular projection suggests that geometrical formatting is a major function of the vestibular complex. These two neural projections, like many biological systems, have an intrinsic organization. This organization gives them an intrinsic logic.

The intrinsic logic of a pattern encompasses an array of relationships, predictive in itself and often leading to particular predictions. Before delving into the specifics of the logical structures found in the vestibular projections, consider a familiar example of predictive arrays of relationships: the periodic table of the elements presents a logical structure that unifies a set of chemical elements. As the periodic table was assembled, its logical structure was used to predict atomic weights that turned out to be more accurate than current measurements, along with the existence of gallium, scandium, and germanium. The periodic table continues to be displayed on the walls of chemistry classrooms not because of these predictions but because of the logical structure.

The logical structure of a neural system may be inscrutable from experimental results. Mathematics provides many languages for determining, expressing, and analyzing the intrinsic logic of biological systems. One such language is the mathematics of symmetry groups.

1.2. Symmetry groups

Mathematically, a symmetry of an object is a transformation that returns the object to its original form [39]. For example, a 90° rotation returns a square or cube to its original form (Fig. 1A). Another symmetry transformation of a square or cube is a reflection through a bisecting line or plane (Fig. 1B). A square has two reflection symmetries through lines bisecting its sides; a cube has three through planes bisecting its

Fig. 1. Symmetry transformations of the square and the cube. A. Rotation and reflection symmetries. In the left-hand column are shown the original forms of the square and cube. The 90° rotations (middle column) and right-left reflections (right-hand column) non-trivially return the square and cube to their original forms, so they are symmetry transformations. B. Some of the reflection lines of the square and reflection planes of the cube. Those shown bisect opposite edges of the square and faces of the cube. (Those not shown are through opposite vertices of the square and vertices or edges of the cube.) There are two reflection symmetries through lines bisecting opposite edges of the square, in contrast to the three reflection symmetries through planes bisecting opposite faces of the cube.

sides. The set of all symmetry transformations, along with their compositions (performing one after the other) form the symmetry group. (For more formal definitions, see the Appendix.)

The array of relationships among the symmetry transformations provides a logical structure for the projection. For example, a projection with only right-left reflection symmetry has a less elaborate logical structure than one in which rotation symmetry can also be identified. The relevance of identifying reflection, rotation, and other symmetries in neural systems is that they relate intrinsic neural organization to function. In the case of the vestibular projection symmetries presented here, the symmetry groups characterize the physical space in which the functions of perception and movement occur.

1.3. Symmetry groups and function

Rotation symmetry in a projection of the vestibular nuclei echoes the perceptual and motor abilities to

function regardless of direction. For example, saccadic eye movements are made to an array of positions which seems to be a continuum. A discrete rotational symmetry in a projection may serve as the foundation for a coordinate frame for this continuous rotational symmetry. Furthermore, physical conservation laws are often expressed in terms of symmetry. When the physical equations of motion have a symmetry such as rotational symmetry, it corresponds to a conserved quantity such as angular momentum. Inanimate objects have no choices in following physical laws. Animals must also follow them, but can choose to move in such a way that physical laws work to their advantage. For example, a standing turn is simplest when the turn is about a vertical axis, so that gravitation does not break rotational symmetry. On the other hand, if a reaching movement is intended during the turn, the arm can be extended in such a way as to ride out on the angular momentum developed by the body. In these ways, an attention to geometry can be crucial in guiding dynamics to be most favorable to intended function.

These points are crucial to development, when young animals learn to substitute active for passive motion. Neural organization with an intrinsic structure related to physical laws, especially the conservation of angular and linear momentum and of energy, provides guidelines in which to frame active movement. Neural organization related to the conservation of angular momentum corresponds to the ability to pivot accurately and without falling; intrinsic logic related to the conservation of linear momentum corresponds to the ability to locomote in a straight line; a sense for the conservation of energy corresponds to the ability to accurately estimate the acceleration of a body that exchanges kinetic and potential energy as it rises or falls. Having symmetry groups that are related to physical space and physical laws inscribed in vestibular projections may serve as a deep foundation providing coordinate frames and guidelines for optimizing movement.

The two studies reviewed here show that such a deep foundation exists in vestibular projections. The following two sections present the background and results of those studies. Section 4 presents the picture that emerges from these studies and questions that arise.

2. The disynaptic projection from semicircular canal nerves to neck motor neurons

The semicircular canals register three-dimensional rotation information because of their orientations, near-

ly perpendicular to each other. These orientations are external to the nervous system. To maintain the geometric relations that make primary afferent activity most meaningful requires judicious convergence within the vestibular nuclei and beyond. At the extreme, convergence of activity from all endorgans would expunge all three-dimensional geometry. Communication of geometrically significant angular motion information requires an intermediate convergence pattern. In fact, the activity arriving from canal nerves is projected to neck motor neurons in a patterned way, as demonstrated by experimental studies [50–52,54] summarized in §2.1. The patterns found by the experimental studies did not, however, bring to light their geometric significance, as found by the mathematical analysis that determined their symmetry group [40]; the mathematical methods used are briefly discussed in §2.2. This analysis displays a logical structure necessary to maintain a coordinate frame. Interpretation and relationship to other experiments is discussed in §2.3.

2.1. Experimental background

Using anaesthetized cats, Wilson and Maeda [54] found that stimulation of either anterior canal nerve (ACN) produced excitatory post-synaptic potentials (EPSP's) in biventer cervicis and complexus motor neurons, stimulation of the contralateral lateral CN (LCN) also produced an EPSP, stimulation of either posterior CN (PCN) produced an inhibitory PSP (IPSP), and stimulation of the ipsilateral LCN produced an IPSP (Table 1; Fig. 2). Shinoda et al. [52] replicated these results; in addition, they recorded from rectus capitis posterior and cervical multifidus motor neurons with similar results [51]. Individual ampullary nerves were stimulated separately, with negligible current spread. Essentially all of the motor neurons supplying neck extensors displayed the same pattern of EPSP's and IPSP's.

Similar experiments were performed, recording from the motor neurons of obliquus capitis inferior [51], longus capitis, sternocleido [50], obliquus capitis superior, splenius, and longissimus [52]. Individual ampullary nerves were stimulated with 0.2 ms-negative constant current pulses. Threshold currents for evoking PSP's were 23–30 μ A; stimulation at 2–5 times threshold was usually used for analysis. Virtually all of the motor neurons received afference from all six canal nerves. Shinoda et al. [50–52] determined that most of the PSP's were disynaptic; the trisynaptic results are not considered in the following. The disynap-

Table 1
EPSP's and IPSP's recorded from neck motor neurons upon stimulation of canal nerves. Each column displays a response pattern observed among the motor neurons of certain muscles, as listed in the text [50–52,54]

Innervation Pattern: Canal Nerve:	Pattern 1. Extensors	Pattern 2. Flexors	Pattern 3.	Pattern 4.
Ipsilateral ACN	EPSP	IPSP	IPSP	EPSP
Ipsilateral LCN	IPSP	IPSP	IPSP	IPSP
Ipsilateral PCN	IPSP	EPSP	IPSP	EPSP
Contralateral ACN	EPSP	IPSP	EPSP	IPSP
Contralateral LCN	EPSP	EPSP	EPSP	EPSP
Contralateral PCN	IPSP	EPSP	EPSP	IPSP

Fig. 2. Innervation pattern found for right neck extensor motor neurons. A. Schematically-drawn excitatory and inhibitory responses recorded in right extensor motor neurons are shown for each canal stimulated [50–52,54]. The muscle is indicated in the center; the canals are drawn from the above back, exaggerated in size, around the muscle. B. The same data – the innervation pattern – summarized as an asterisk diagram. Excitatory responses are indicated by dashed lines; inhibitory, by solid lines.

tic innervation patterns fell into four classes, with the extensor motor neurons displaying Pattern 1, longus capitis motor neurons displaying Pattern 2, obliquus capitis superior, splenius, longissimus, and sternocleidomastoid motor neurons displaying Pattern 3, and obliquus capitis inferior motor neurons displaying Pattern 4 [50] (Table 1). These innervation patterns also divide neck muscles into eight classes, four on each side, R1–4 and L1–4 (Fig. 3).

These results were considered clear enough in aggregate to determine the symmetry group directly from the innervation patterns as presented in the experimental results [50,52]. For example, for rectus capitis posterior motor neurons, ipsilateral ACN stimulation resulted in an EPSP for 70/72 neurons tested, with one neuron showing an IPSP and one showing no effect [51]. After presenting the mathematical methods, we will discuss the small variations in the light of the symmetry group and its significance.

Pattern 1 (Extensor Motor neurons): rectus capitis posterior, cervical multifidus, biventer cervicis, and complexus
Pattern 2 (Flexor Motor neurons): longus capitis muscle
Pattern 3: obliquus capitis superior, splenius, longissimus, and sternocleidomastoid
Pattern 4: obliquus capitis inferior muscle

Fig. 3. Canal-neck projection data. The data are shown diagrammed according to muscle groupings, as determined by Shinoda et al. [50, 52]. The data are shown from above, as is the cat's head in the center. The semicircular canals in the cat's head are exaggerated in size to indicate directions. Each "asterisk" diagrams the inhibition (solid) or excitation (dashed) contributed by each of the six canals to each motor neuron. (Diagram based on [40].)

2.2. Determination of the symmetry group

The eight innervation patterns – four on each side – found in the disynaptic projection from the semicircular canal nerves to neck motor neurons [50–52,54] each display excitatory-inhibitory pairing on the three canal planes: horizontal, right anterior and left posterior (RALP) and left anterior and right posterior (LARP). There are exactly eight = 2^3 possible innervation patterns of this type [40]. Thus, the patterns found experimentally form a combinatorially complete set, which speaks for the robustness of the experimental result.

The existence and form of the innervation patterns were established according to experimental standards [50–52,54]. For the mathematical analysis, mathematical standards come into play. First, we diagrammed the experimental results so that the patterns were clear and the effects of transformations would show easily (Fig. 3).

We serially tested transformations to find their effect on the innervation patterns of the projection (Fig. 3). The requirements that a group include compositions of transformations and have inverse transformations guided us in completing the transformation group. (See Appendix for more detail about mathematical groups.) From the transformation group, we identified the symmetry transformations of the projection. We demonstrated that the projection data have the rotation and reflection symmetries of the cube, the octahedral group O [40].

Based on our result, Golubitsky et al. [28] have given a more transparent demonstration of the cubical symmetry of the projection (Fig. 4). In their presentation, the eight muscle innervation types are placed on the eight vertices of a cube in such a way that the four vertices of each face are inhibited by one canal. Because each canal inhibits four of the muscle types and excites the other four, it is sufficient to show which are inhibited by placing each canal on the face whose vertices are inhibited. This figure is cubically symmetric by inspection; it can be reflected or rotated to return to the same configuration, exactly as can a cube.

Figure 4 summarizes the data [50–52,54] in such a way as to display plainly the cubical organization found by McCollum & Boyle 2004 [28]. It does not, however, emphasize the rotation properties in the same way as the original depiction of the projection's organization did [40]. Presented either way, the projection itself embeds fundamentally in the nervous system a three-dimensional logical structure that both preserves logical properties of the physical space in which the canal pairs register angular motion and provides useful logical structure for sensorimotor behavior in physical space [40].

2.3. Functional interpretation of the cubic symmetry in the disynaptic canal-neck projection

Perception and movement in three dimensions requires the nervous system to embed the geometry of three dimensions. A fundamental part of that geometry is its symmetry group. The finding that the disynaptic canal-neck projection has the symmetry group of the cube shows that the organization of neural connections themselves provide a framework for maintaining three-dimensional coordinate systems.

The head rotates on the neck in any plane in three-space. The muscle activation required for a head rotation depends not only on the intended rotation but also on the initial position of the head. A system of this

Fig. 4. Cubic display of canal-neck projection data. Innervation patterns are labelled as in Fig. 3 and placed (in squares) at the vertices of a cube. On each face is the canal (in circle) that inhibits the four motor neuron types represented at the face's four vertices. For example, the left anterior canal inhibits motor neurons of innervation patterns L2, L3, R2, and R4 and excites motor neurons of patterns L1, L4, R1, and R3. Excitation is omitted, because each canal nerve stimulation excited all those motor neuron types it did not inhibit [50–52,54]. Dashes are used to show that a line is behind the front faces of the cube. The label L3 obscures the canal label rh, and the canal label lh obscures the innervation pattern label R3. l – left; r – right; h – horizontal; a – anterior; p – posterior (Cubic symmetry due to McCollum and Boyle [40]; diagram modified from Golubitsky et al. [28], with permission).

complexity is expected not to have a rigid projection pattern, but a flexible one based on a simple system. The maintenance of cubic symmetry might serve as such a system. If it does, the innervation patterns as we move our heads voluntarily would shift according to head position. In that context, it is not clear what the projection patterns in anaesthetized cats would mean; it is perhaps surprising that they vary as little as they do. On the other hand, the anaesthetized case may be a default position because of the absence of voluntary movement; the cube may rotate from that default position.

Because the intermediate synapse of this disynaptic canal-neck projection occurs presumably in the vestibular nuclei, the cubic symmetry group is apparently established there, supported by convergence patterns and commissural connections. It would be plausible for the vestibular nuclei to contain convergence patterns that maintain the cubic symmetry group with head turning,

just as they shift center of reference with voluntary movement [19,41].

3. The vestibulo-olivo-nodular projection

Perhaps even more fundamental in establishing sensorimotor geometry is the projection that leaves the vestibular nuclei and passes via the inferior olive to deliver climbing fibers to the uvula-nodulus of the cerebellum. The vestibular system interacts closely with the cerebellum, and the uvula-nodulus is the midline, caudal portion of the vestibulo-cerebellum. The uvula-nodulus receives climbing fibers that carry vestibular information regarding angular motion about two horizontal axes and optokinetic information regarding motion about a vertical axis [5]. (We do not address linear, otolith information here.) While it is clear that all sensorimotor behavior takes place in three-dimensional physical space, our focus in this paper is on the spaces constructed within the nervous system to shape and predict behavior. Thus, not every neural space is required to be the same. Instead, neural spaces may complement each other and function in different aspects of behavior. This is likely to be true of the two projections reviewed in this section and the previous (§2).

3.1. Experimental background

The pathways from the vestibular nuclei to the uvula-nodulus have been investigated both anatomically and physiologically. Within the rabbit uvula-nodulus, zones specific to particular semicircular canal planes have been physiologically identified by recording from Purkinje cells while using natural stimulation consisting of sinusoidal roll-tilt about graded axis orientations [10,24]. This result demonstrates that the cerebellar zonal organization categorizes the vertical canals according to canal planes, rather than individual semicircular canals or homologous pairs (right and left anterior; right and left posterior). The pathways have been traced from the vestibular endorgans to the uvula-nodulus by making similar recordings in the vestibular nuclei and inferior olive under natural stimulation [5,7,9,12].

These climbing fiber pathways have also been traced anatomically. GABAergic connections from the parabrachial nucleus of the vestibular nuclei to the β -nucleus and dorsomedial cell column (DMCC) of the inferior olive have been demonstrated by immunohistochemically labelling with an antibody to glutamic acid de-

carboxylase (GAD) and by injecting retrograde tracers directly into olivary sub-nuclei [4,6,8,44]. A complementary, glutamatergic pathway connects the γ -group of the vestibular nuclei to the same areas of the inferior olive, which send climbing fibers to the contralateral uvula-nodulus [11].

Separate visual pathways arrive in the uvula-nodulus from the retina via the nucleus of the optic tract (NOT) and the inferior olive [2,5,6,53]. These pathways have been traced physiologically using optokinetic stimuli and investigated anatomically as part of the accessory optic system [5,6,25,53]. Horizontal optokinetic information is relayed through the NOT onto neurons in the caudal dorsal cap of the inferior olive (DC). The DC, in turn, projects onto a small strip of Purkinje cells in the ventral nodulus. Vertical optokinetic information, represented in more rostral regions of the DC, does not project to the uvula or nodulus. Conversely, horizontal vestibular information is not projected onto the uvula-nodulus.

3.2. Symmetry group

Our first question was whether these pathways, carrying three degrees of freedom of angular motion, together had three-dimensional symmetry. Although the uvula-nodulus itself may weave three-dimensional symmetry, the visual pathway breaks symmetry with the vestibular ones in both midline crossings and excitatory and inhibitory connections. The visual pathways cross the midline twice, once from the retina to the NOT and again from the inferior olive to the uvula-nodulus [2,5,6,53]. All of the connections are excitatory, and the right and left pathways are separate. Therefore, the visual pathways do not participate in the symmetry of the projection.

In contrast, the vestibular pathways form two interconnecting pairs according to canal planes (Fig. 5). There are canal-specific, ipsilateral, inhibitory connections from the vestibular nuclei to the inferior olive and contralateral, excitatory ones from the γ -group [5]. Under the physiological transformations we consider, exchange of canal planes φ and exchange of excitatory and inhibitory response σ , the vestibular pathways transform into each other [23].

The left anterior (LA) and right posterior (RP) pathways form the interconnecting LARP pair, as the right anterior (RA) and left posterior (LP) pathways form the interconnecting RALP pair. Each pathway pair can be reversed by exchange of excitatory and inhibitory responses, just as the canal pairs can [23].

Fig. 5. Summary diagram of anatomical and physiological data on pathways from the vertical semicircular canals to zones in the uvula-nodulus. A. Along each side of the square is the sequence of neural centers from the canal (L-left, R-right, A-anterior, P-posterior) to the parasolotarius (Psol) to the β -nucleus to zone 1 (Z1) or zone 2 (Z2) of the nodulus. Across the square are shown the connections from the canals to the y-group to the b-nucleus. Within each neural center, the directions of maximum response (left box – left ear down; right box – right ear down) are labelled with dashed (excitatory) or solid (inhibitory) lines, forward-leaning for the right-anterior-left-posterior plane and backward-leaning for the left-anterior-right-posterior plane. Within each pathway, the canal plane of response does not change. Excitation or inhibition changes in a predictable way within the pathway. Arrows separate out the response chosen to exemplify the pathway. B. Diagram representing the innervation pattern in the data. The diagram is made up of the four representative physiological responses, in their places in the square.

In order to clearly understand how the pathways use physiological symmetries to embed those of physical space, we separated the transformations tested on the data into two types: those of physical space, which could be performed on any physical object, and physiological transformations, which were specific to the physiological system. In particular, the exchange of canal planes φ is specific to an organism with two canal planes. So are the exchanges of excitatory and inhibitory response σ_L in the LARP plane and σ_R in the RALP plane. Each of these physiological transformations is of order two, meaning that repeating the transformation returns the object to its original configuration. For example, using the transformation φ on the summary diagram of the data (Fig. 5A) reverses the canal plane on each side of the square, as shown in Fig. 6A in the top row; the resulting configuration is shown to the right of the arrow. Performing the transformation φ on this result returns the pathways to the original configuration, that of the data.

The two transformations φ and σ_R do not commute, as shown in Fig. 6B [23]. This point is crucial in understanding the symmetry group, which consists of phys-

ical/physiological pairs. The physical rotation ρ of a square by 90° is a transformation of order four, because it takes four applications of ρ to return the square to its original position. None of the simple physiological transformations φ , σ_L , and σ_R can correspond to ρ , because they are each of order two. Nevertheless, because φ and σ_R do not commute, their composition is of order four, as shown in Fig. 6C. It is this composition that corresponds to a physical rotation of the square.

3.3. Functional interpretation of the square symmetry in the vestibulo-olivo-nodular projection

The symmetry group of the square provides the skeleton of a planar coordinate system. The symmetry group leaves the horizontal plane invariant. Like three-dimensional space, the horizontal plane strongly formats both movement and perception. Locating the horizontal plane in three-dimensional space is essential for many movements, for example, for the rotations discussed in the Introduction (§1.3). For this reason, it makes sense that the nervous system would embed the symmetry group of the square. Furthermore, the

Fig. 6. Properties of physiological transformations. The pathway square shown in Fig. 5A is abbreviated to the simpler diagram shown in Fig. 5B for ease of depiction of the effects of the transformations. Arrows indicate the effects of a transformation. Each arrow is labelled with a particular transformation, which may be a composition of transformations. A. Actions of φ , the exchange of canal planes, and of σ_R , the exchange of excitatory and inhibitory responses in the RALP plane. Double arrows indicate that the transformation goes both ways. B. Non-commutativity of φ and σ_R . The first transformation shows the composition with σ_R performed first (where a composition is written with the first transformation to be performed written on the right), and the second transformation shows the composition with φ performed first. C. Physiological analogues of physical rotation. Because φ and σ_R do not commute, their composition is of order four.

Fig. 7. Two patterns of differing significance. A. The Big Dipper tells us little about the compositions of the stars or their positions in space, except from the earth. B. The hexagonal symmetry of a snowflake relates to the structure of the water molecules that compose it and therefore to the behavior of water in all its forms.

plane is crucial to both the postural and the visual systems, each of which is served by the uvula-nodulus. Although a full investigation of the organization of the uvula-nodulus would require determination of the symmetry groups of the mossy fiber and otolith projections, along with other projections and their interaction within the uvula-nodulus, the canal vestibulo-olivo-nodular projection symmetry results appear to be pivotal for explaining lesion results. For example, removal of the uvula-nodulus affects the spatial properties of the ver-

tical but not of the horizontal angular vestibulo-ocular reflex (AVOR) [3].

Perhaps more basic than the square symmetry is the pairing of semicircular canals according to canal planes. It is possible that the vestibulo-olivo-nodular projection is the first place where evolution made this geometric simplification [23].

More telling in terms of the ability of the projection symmetry group to produce a rotation (§3.2, Fig. 6) is the function of the uvula-nodulus in illusory rollvection. In an imaging study, the uvula-nodulus was activated during illusory rollvection; it was the only brain area more active during perceived self-motion [37]. It is likely therefore to be involved in thevection illusions caused by a tilted rotating disk [21,32,33]. These illusions depend on the establishment of a shared visual and postural horizontal plane. The uvula-nodulus is in a pivotal position for coordinating eye movements with posture in such a way.

4. Discussion

The results reviewed here demonstrate that projections from the vestibular nuclei have physiological organization with symmetry groups that are crucial for sensorimotor behavior in physical space [23,40]. Although both projections that have been analyzed originate in the semicircular canals, the symmetry groups and the anatomy and physiology over which they hold differ markedly. These contrasts, along with the functional relevance of the symmetry groups, suggests that vestibular projections broadly may have functionally-relevant symmetry groups. An obvious subject for further research is to determine the symmetry groups of other vestibular projections, particularly otolith projections and combined otolith and canal projections. A deeper question is how the symmetry group of a projection is expressed functionally over multiple systemic levels: what is the causal logic by which significant organizations have functional effect in nervous systems? We will begin with a discussion of the context and synthesis of the two symmetry group results (§4.1). Because behavioral outcomes for the canal-neck symmetry have been suggested [28], we will discuss the way vestibulospinal projections contact the spinal cord and its different systemic levels (§4.2). Finally, we will discuss approaches to the causal logic holding among multiple systemic levels (§4.3).

4.1. Context and synthesis

The vestibular complex includes a rich array of projections – commissural, vestibulo-cerebellar, vestibulo-oculomotor, vestibulo-spinal, and vestibulo-thalamic, among others. These projections serve to convey head movement information gained from the vestibular endorgans, both otoliths and semicircular canals. In addition, they serve as links in sensorimotor integration processes. In both capacities, organization is important for carrying out their function. The two results reviewed here address two key projections, the canal-neck projection, an important vestibulo-spinal projection, and the vestibulo-olivo-nodular, a major vestibulo-cerebellar projection.

As a vestibulo-cerebellar projection, the vestibulo-olivo-nodular projection participates in a complex of interweaving vestibulo-cerebellar and cerebello-vestibular projections linking the two sensorimotor integration centers, the vestibular nuclei and the cerebellum. By passing via the inferior olive, the vestibulo-olivo-nodular projection contacts the cerebellar cortex as climbing fibers. Within the uvula-nodular cortex, the vestibular afference is joined with optokinetic information via the NOT. The vestibulo-olivo-nodular projection organizes the semicircular canals according to canal planes, and its symmetry group supplies the the cerebellar system and vestibulo-cerebellar complex with the fundamental geometry of the plane.

In contrast, the disynaptic canal-neck projection implicates the vestibular nuclei themselves in maintaining the symmetry of the cube, which is the necessary skeleton of a three-dimensional coordinate system. Although the intermediate synapse was not identified in the experiments that determined the innervation patterns [50–52,54], the supposition that it is in the vestibular nuclei is consistent with known physiology (reviewed in more detail in the following subsection, §4.2). What functional advantage would be conferred by the vestibular nuclei maintaining the symmetry of a cube? Maintaining simple guidelines, like those of the three-dimensional symmetries of the cube, is functionally advantageous. Head movements must be quick and accurate, despite the multiplicity of neck muscles, the differences in function depending on position along the neck and rotation axis, and the variation of a muscle's function depending on head position. Because of these complications, correspondences to particular canal planes would be unrealistic. Thus, epitomizing the requirements of head movement in three-dimensional space in terms of the symmetries of a cube

is a simple way to functionally organize neck muscles for head movement.

Each of these projections, the vestibulo-olivo-nodular and the canal-neck projection, not only conveys activity from the semicircular canals, but also formats that information in a way that can serve as a set of guidelines for sensorimotor behavior in physical space for other neural centers. This brings us up against a conceptual question: how might such guidelines be conveyed and used through multiple systemic levels? In the next section, we review specifics of vestibulospinal projections and the spinal cord. In the final section (§4.3) we address questions of the causal logic by which effects communicate through multiple systemic levels more generally.

4.2. Vestibulospinal projections and the spinal cord

How does the canal-neck projection, with its cubic symmetry, affect the spinal cord? Morphological studies, also in cats, show secondary vestibulo-spinal neurons in contact with neck motor neurons [48,49]. Morphological techniques combined with antidromic activation have demonstrated that medial vestibulospinal tract (MVST) neurons differ in the way they contact the cervical spinal cord. Vestibulo-oculo-collic (VOC) neurons, which have both ascending and descending branches, carry single-canal activity to more diffuse targets, whereas vestibulo-collic (VC) neurons, only descending to the spinal cord, carry convergent information to more focussed targets [45,46]. A variety of contact patterns are found also in squirrel monkeys [13]. These data are consistent with the conclusion that the canal-neck projection classifies motor neurons and therefore muscles according to a set of eight innervation patterns (§3).

With great versatility in terms of following variables relevant to a particular movement, motor neurons in the spinal cord focus force, as experienced by pushing on something and as demonstrated in detail by studies of spinal vector fields [20,26,34,42,43]. The mechanism by which motor neurons exert force is by contacting muscles. However, knowledge of this mechanism does not answer the deeper question: how the spinal cord is organized so that it can focus force.

The spinal cord also generates dynamic movement, including oscillations. As with focussing force, the generation of dynamic movement requires an intricate, intrinsic organization of motor neurons, descending pathways, and interneurons. Movement dynamics can be mathematically formalized in a number of ways.

One way is to write equations, typically Lagrangian or Hamiltonian [27,47]. Another is to depict the dynamical landscape on the basis of equations and other known properties of the system [1,40,47]. Although the body certainly follows the laws of classical mechanics, its composition and configuration assure that small changes in force often result in distinctly different functional outcomes. For this reason, it often provides more insight into motor behavior to consult the dynamical landscape than particular numerical trajectories. For example, each quadruped species has a typical set of gaits, despite the fact that specific leg movements within the gait vary enormously depending on the size and age of the individual, the terrain, and other factors. The dynamical landscape provides a cogent description of the gaits in which these variations are irrelevant. Furthermore, it has a symmetry group that allows the overall organization of quadruped central pattern generators (CPG's) to be predicted [29,30].

The dynamical landscape of body movements depends on the geometry of the body and properties of the nervous system, especially its organization. For example, the properties of CPG's in the spinal cord are likely to be predictable, using symmetry techniques, from the experimentally determined anatomical organization and physiology of spinal neurons [17,31,36]. Like other neural centers, these lumbar and sacral spinal areas have intrinsic organization, which is expressed in the way its ongoing activity incorporates afferent activity. The activity reaching the cervical spinal cord via the canal-neck projection brings with it the symmetry group of the cube, which likely affects the dynamical landscape of the cervical cord.

4.3. Systemic levels

The spinal cord and the canal-neck projection with its innervation patterns are but one example of multiple systemic levels. A pattern can be of little global significance, like the Big Dipper, or it can have deep significance for the system in which it occurs, like the symmetry of a snowflake (Fig. 7). The form of the snowflake reflects the 120° angle of the water molecule and is therefore of deep significance in displaying fundamental properties of all forms of water. Fundamental properties of water are retained in all circumstances in which this molecular form is maintained, such as differing temperatures, pressures, and states of matter. We know this by the laws of physics. It is plausible that the symmetry groups occurring in both vestibular projections are of major significance for sensorimotor

behavior. Indeed, a significant relationship has been found in the visual system, between neural symmetries in the visual cortex and the forms of hallucinations [14–16]. We have clear logical structures that unify one systemic level, that of a projection from the vestibular nuclei, either the disynaptic canal-neck projection or the vestibulo-olivo-nodular projection [23,40]. However, we lack a compelling conceptual basis for relating multiple systemic levels to each other, including the level of projections and that of sensorimotor behavior.

An experiment that relates the activity of a neuron to the behavior of the animal assumes only one systemic level. If there is only one systemic level – that is, if the disynaptic canal-neck projection is the immediate and sole influence on neck motor neurons – then the symmetries of the disynaptic canal-neck projection translate immediately into a set of preferred head movements. One more assumption is necessary: that movements are described by ordinary differential equations. On this basis, Golubitsky et al. [28] have identified a set of periodic head movements, most of which are common, such as a right-left shake “no”. This approach depends on the dynamical landscape implied by the symmetry group. It is plausible that the projection does induce these symmetries and movements in some circumstances and in species in which this disynaptic projection is dominant.

However, there are multiple projections from the vestibular system and other brain centers to the cervical spinal cord, connecting diverse systemic levels. Thus, the canal-neck projection, with its symmetry group, is one projection among many. Then the oscillations conferred by the symmetry group [28] belong to the projection itself. Like a plucked string, the projection favors certain oscillations in this view. A similar conclusion would apply to the vestibulo-olivo-nodular projection and any projection with symmetries. Thus, the projections converging on cervical motor neurons would compete or cooperate, like an orchestra playing dissonant or harmonious notes.

A different approach to the relationships among multiple systemic levels is to divide projections into separate connections and model nervous systems as digital computers or as electrical circuits. Since Turing raised the question whether a nervous system is a universal computational device – a Turing machine – there have been efforts to simulate nervous systems by means of computers. In the case of the vestibular system, there have been particularly careful computational simulations, including the bilaterality of the vestibular system (for example [18,38]). Computations can,

to some extent, use the particular topology of the nervous system, including patterns of reciprocal connections, rather than just the collection of connections [35]. However, when a nervous system is conceived of connection by connection, it bypasses the issue of specifying systemic levels and their relationships to each other.

Elsasser [22] has proposed that a fundamental property of biological systems is ordered heterogeneity and the ability to reconstruct an inherent organization given disparate materials. Applying his concepts to the question of causal logic among systemic levels suggests that each systemic level reconstructs an inherent organization, incorporating afferent activity. For example, the spinal vector fields discussed above would be affected, perhaps transformed, by vestibulospinal activity, but they would retain their inherent nature as vector fields. This ability to reconstitute inherent structures would confer autopoietic (self-creating) stability that is clear over the lifetime of an individual and of a species. To understand the way each systemic level reconstitutes inherent structures would require a thorough understanding of its physiology and the intrinsic logic of its organization. We have experimental and mathematical methods for specifying these systemic levels and their intrinsic organization, such as the clearly organized vestibular projections reviewed here, and for determining their relationships to each other; we can use them to investigate and formalize an autopoietic causal logic for the effect of one systemic level on another, from neurons to behavior.

Behaviors are formatted by the same symmetry groups as are embedded in the two vestibular projections reviewed here: three-dimensional space and the horizontal plane. Are there relationships that link the symmetry groups of these two systemic levels, as the form of the water molecule links the symmetries of the snowflake to other properties of water? There is no vestibular “molecule” making up these behaviors. Another analogy may be more helpful: the round, snow igloo. As the first ring of snow or ice blocks is placed, each is held up by the forces of its internal properties. One block on top of another is similarly held in place by forces down through the blocks. As the dome is completed, however, three-dimensional relationships among the forces confer additional stability not enjoyed by a straight wall. It is plausible that the intrinsic organizations of particular systemic levels, such as the symmetries found in vestibular projections, confer stability on sensorimotor subsystems that is communicated all the way to organism sensorimotor behavior.

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Appendix

Mathematics is based on definitions that specify logical structure as a list of properties. A group has three properties:

A group is a set of elements G together with a binary operation $G \times G \rightarrow G$ such that 1) this operation is associative, so that $a(bc) = (ab)c$, 2) there is an identity element $e \in G$ with $ea = a = ae$ for all $a \in G$, and 3) for this element e , there is to each element $a \in G$ an inverse element $a' \in G$ with $aa' = e = a'a$. A group is complete in the sense that all products of the elements of the group are included in the group. Anything with these three properties is a group; anything that lacks even one of them is not a group.

A symmetry is a transformation that non-trivially returns an object to its original configuration. Which transformations are symmetry transformations depends on the object. For example, a 120° rotation returns a perfect snowflake to its original configuration, but not a cube. This difference in symmetry transformations characterizes the difference in form between the snowflake and the cube. The symmetries of a natural object such as a snowflake or physiological projection are found empirically, by testing each transformation either physically or indirectly.

The elements of an object's symmetry group are its symmetry transformations. The operation of a symmetry group is composition ab : performing b then a . The composition of any two symmetries is also a symmetry. For example, if the 90° rotation ρ is a symmetry of an object, then so is ρ^2 , a 180° rotation. However, the composition of symmetries may not be distinct. For example, $\rho^5 = \rho$. By taking compositions and identifying all distinct compositions, we find the complete symmetry group of an object.

A projection and a behavior with the same group share clear, mathematically-specifiable characteristics. Group theory provides one mathematical formalism for investigating the themes and relationships that unite a nervous system.

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