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Sensory and Motor Interdependence in Postural Adjustments

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The sensory reafference from a movement depends upon the movement, and the movement chosen depends upon the available senses, as demonstrated by vestibular patients who abandon certain movements. Often, one variable is assumed to be dependent whereas the other is independent; however, sensory and motor dynamics in posture are interdependent as conditions upon each other. This paper applies conditional dynamics to characterize the global structure of interdependence between sensory states and motor strategies in fast postural adjustments. The mathematical formalism incorporates rich but disparate experimental, clinical, and theoretical results about sensory and motor control of posture.

The control structures presented include relatively stable anatomical, physiological, and functional structures, both continuous and discrete, leading to a composite functional logic for the coordination of these structures in sensorimotor control. Results include sensorimotor control structures for postural adjustments for healthy subjects and certain types of vestibular patients. The sensorimotor control structures for patients with absent vestibular function suggest implications for management of the deficit.

Keywords: Control, mathematical, sensorimotor, vestibular

1. Introduction

The intricate sensorimotor system that keeps us humans upright on two relatively small feet can be probed by observing subjects on a moveable platform. The movement by which an individual regains upright stance following an abrupt movement of the platform is a "fast postural adjustment".

Postural behavior – both movements and use of senses – can be altered by a change in sensory registration. For example, when somatosensation was temporarily excluded from subjects' feet in experiments by means of pressure cuffs around the ankle and the subjects closed their eyes, their posture changed to include more hip movement, an effective way to exert shear forces on the floor that stabilize posture (Fig. 1A) [15]. Similarly, patients with vestibular disorders but no specific motor disorder may change their movement patterns to eliminate certain movement types. Both healthy subjects and vestibular patients make many complex movement decisions, from choosing a stepping pattern to eliminating a movement type, unconsciously and smoothly, without conflict or hesitation.

Patients with absent vestibular function but intact vision and somatosensation cease to use hip movements for postural stabilization, even though vision plus somatosensation afford enough physical information to initiate a hip movement [26]. These patients use only the ankle movement, a rotation about the ankle depending upon the exertion of ankle torque against the floor (Fig. 1B), even in circumstances for which it is not mechanically effective for lack of reaction forces from the floor [26,62]. Why would a sensory deficit cause loss of a movement strategy, when the patient has physically enough sensory information to initiate the movement? An hypothesis motivating this study is that a movement strategy may be eliminated from the movement repertoire when necessary in order to maintain completeness, consistency and lack of ambiguity in the global sensorimotor control system.

Early investigations of hip and ankle movements made it clear that there are both continuous and discrete aspects in the motor control of postural adjustments and that individuals' control structures differ [41]. How-

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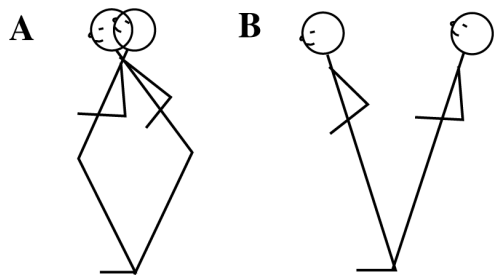

Fig. 1. Postural adjustment movements. A. The hip movement. B. The ankle movement.

ever, a lack of mathematical framework for unifying discrete with continuous aspects of sensorimotor control affected both experimental and theoretical research. For experimental research, one had no formal language for reporting certain observed phenomena; theoretical research lacked a mathematical framework for manipulating both continuous and discrete objects and relations in a meaningful way. Continuous mathematics, usually equations of Newtonian mechanics, are standardly used to analyze quantitative experimental data on movement. For example, the hip and ankle movements (Fig. 1) are both well described by equations of Newtonian mechanics. Furthermore, some subjects produce a range of intermediate movements, well described by a mechanical continum (Fig. 2A).

However, other subjects localize their postural movements into either the hip or the ankle bundle of trajectories (Fig. 2B), and make discrete transitions between the hip and ankle movements in response to discrete changes in the support surface [25,41]. At the time these observations were made, there was no mathematical framework available to us for analyzing and synthesizing discrete changes of behavior or control systems that combined continuous variation with discrete transitions. Even though mathematical methods have long analyzed discrete relations and systems (especially abstract algebra and logic), these methods were not combined with Newtonian mechanics (which uses mathematical analysis).

Treating the hip and ankle movements as discretely different does not require ignoring continuous variations within each movement. Nor does it require ignoring the possibility to produce a continuum of intermediate movements. Rather, it requires the recognition that behavior is often controlled over a range of outcomes, not a particular trajectory.

In a previous paper [44] sensory transition structures were constructed that were consistent both with observation and within themselves, as control structures that allow unambiguous transitions among sensory states, each of which can be entered and exited. In that study, modelling assumptions assured the completeness and internal consistency of each control structure. Experimental data narrowed the choice of control structure to a few structures. Just as individuals may be left- or right-handed or choose to part their hair on the left or right, individuals may have different control structures, as long as they obey certain functional criteria. The control structure then governs the particular sensory state, depending on external and internal conditions. The results of the previous paper [44] on sensory state transition structures are extended in the present paper to interdependent sensory and motor state transitions, using similar methods, in which experimental data and modelling assumptions are used together to construct control structures.

The purpose of this paper is to examine the functional logic of sensorimotor postural adjustment control systems, expecially the dependence of sensory and motor dynamics as conditions on each other. Conditional dynamics [24,34–40,57,58] will be used to model sensorimotor control systems for postural behavior.

The following section will briefly present modelling assumptions and their applications in conditional dynamics. Section 3 will present experimental observations and previous theoretical results upon which the sensorimotor control systems will be based (plus some of the lacks). Section 4 will present sensorimotor control systems, both in general form and specific to the vestibular-absent case.

2. Theoretical methods

In this paper, conditional dynamics will be used to represent a control system in which the discrete structure is salient; the continuous aspects are secondary here. Conditional dynamics allows mathematical reasoning about discrete transitions, while incorporating mechanical analyses. Data provide localizations of behavior, determined by various standard experimental techniques. Control systems are constructed using both observational data and modelling assumptions, so that data support certain orderings and relationships, rather than being simply portrayed by lines in diagrams.

A major impetus for developing conditional dynamics came from the effort to unify sensory with motor behavior in posture. The geometric representation of postural movements led to the exploration of a model in which sensory and motor aspects of postural adjust-

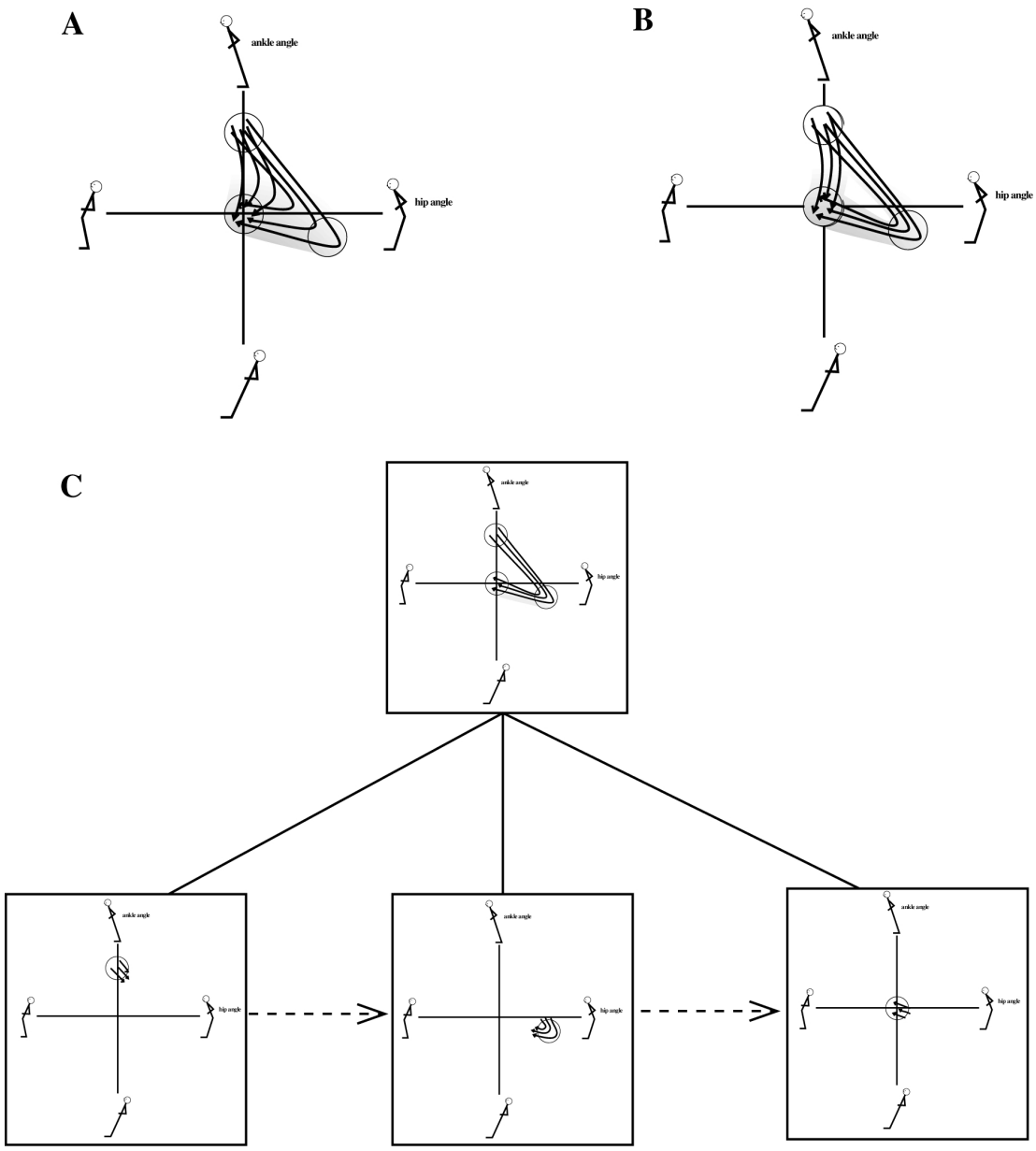

Fig. 2. Postural adjustment regions as mechanical flows in joint angle space. A. A continuum of trajectories including both hip and ankle movements. B. Separate ankle and hip regions, each consisting of a bundle of trajectories. C. The hip movement analyzed into an overall governing dynamics (top), including three sequential regions: initial, turning, and final. A d-space such as this is to be read as a mathematical expression, like an equation, and is not intended as an illustration (such as the stick figures in Fig. 1).

ment are geometrically coherent – related by continuous mathematics [43]. However, in experiments later that year, vestibular patients with clearly abnormal sensory performance had completely normal ankle movements, showing that the idea of geometrical coherence was wrong. Instead, sensory and motor performance are logically independent [4,51]. A discrete model of sensory transitions was developed [44], but it did not encompass the continuous aspects of sensory and motor behavior. Conditional dynamics allows the simultaneous analysis of continuous and discrete sensory and motor behaviors.

Observations by Shupert et al. [63] have since posed a new problem: Why does vestibular loss with no mo-

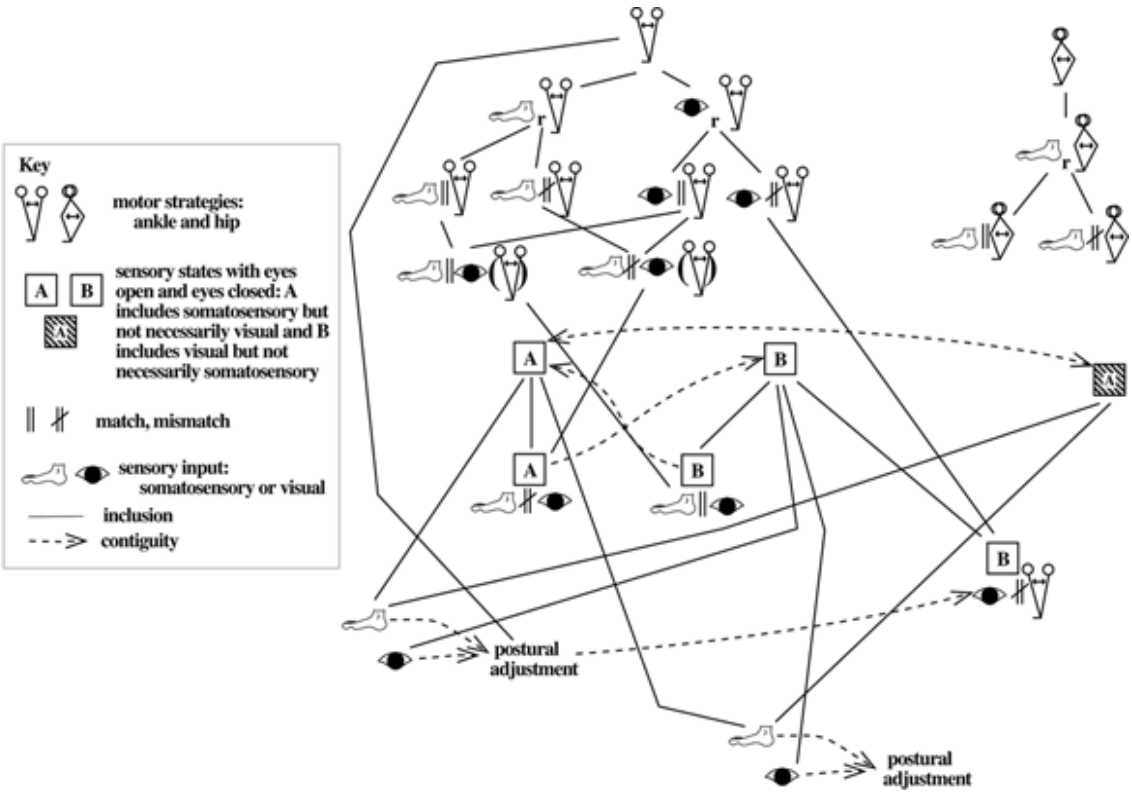

Fig. 3. Sensorimotor postural adjustment d-space of a vestibular-absent subject, assuming that vision can not be used to monitor the hip movement. Sensory states are represented by boxes; motor strategies are represented by stick figures. (The letters in boxes are sensory states from McCollum, et al. [44]. Hatch marks indicate sensory states with eyes closed. See Key.) Regions included in each sensory state or motor strategy (underneath and connected by a solid line) specify the state of the system more narrowly. *Note that neither sensory states nor motor strategies include each other.* That is, they are logically independent and are chosen independently. However, *the selection mechanism is governed by both the sensory state and the motor strategy.* For example, the region directly below sensory state A with eyes open, which triggers a transition to sensory state B, is governed by both sensory state A and the ankle movement. Normally contiguities connect the parts of the d-space involving ankle and hip movements – the figure shows regions that are not connected and would normally be omitted for that reason. In the vestibular-absent case, the hip movement is separated from the d-space and is *not accessible*.

tor loss lead to a specific failure to use the hip movement? How can a sensory deficit cause a particular motor deficit to which it is not directly linked? Using conditional dynamics, we have produced a model showing the circumstances in which the hip movement is no longer accessible to a vestibular-absent patient (Fig. 3). (Figure 3 is the main result. It is shown at this point to orient the reader to the type of formalism and notation used here. Figure 3 will be clarified in following sections.) The results are compatible with more than one type of behavior by vestibular-absent patients.

Postural control is a complex combination of sensory and motor dynamics. However, it is modular: for example, sensory dynamics can be distinguished from motor dynamics. Furthermore, different forms of sensory dynamics, or "states", can be distinguished from each other [44], just as the hip and ankle movements can be distinguished from each other. (The word "state" is used here in the sense of a *mode*, as in the energy state of an electron, rather than in the engineering sense of the *value* of a continuous variable.) However, different forms of sensory and motor dynamics are interdependent, acting as conditions governing each other or allowing each other to arise.

Conditional dynamics is the analysis of the conditions that allow each form of dynamics to arise, and the hierarchy in which dynamical controls govern each other. The analysis depends upon two algebraic relations between different dynamical controls.

All mathematics is based on simple relationships. The simple relationships can be elaborated to complex structures because the relationships are understood to have perfect precision. For example, analytic mechan-

ics is based on the relationships between variation in time and variation in space. When these relationships are precise, the equations of mechanics can be written, manipulated, and applied to mechanical systems in general.

Similarly, algebraic relations such as inclusion can lead to complex structures if they are used with precision. (Lines and boxes are often used to mean a sequence of operations, with no other requirements. That is not how lines and boxes are used in this paper.) Even though continuous mathematics may be used to specify almost-discrete objects such as square waves, continuous mathematics is not designed to specify the discrete relations between them, much less to construct complex structures of discrete objects and relations.

2.1. Abstract mathematics of conditional dynamics

In order to express the conditional dynamics of a control system with mathematical rigor, we require a mathematical object, analogous to a dynamical space described by an equation [24,34–36,40,57,58]. (For the most complete and formal presentation, see [36].) Such a mathematical object ties together the modular dynamics, such as the hip and ankle movements, which are localizations of movements to ranges of trajectories (Fig. 2B). Such localizations of dynamics, whether sensory, motor, or neural, are called *regions*. An important step in analyzing the conditional dynamics of a particular behavior is to identify the natural regions of the behavior. Some regions occur in a fixed sequence, for example, in the hip movement, there is an initial region, a turning region, and a final region, in that order, each arising from the previous region in the overall dynamics of the hip movement (Fig. 2C). The overall dynamics of the hip movement is a range of trajectories that together governs the movement, and is in that sense an *invariant* of the motion. The diagram in Fig. 2C is called a *d-space* ("d" for discrete and dynamics and several other words). It shows that the overall dynamics of the hip movement governs the movement from the initial to the turning to the final region. A d-space (such as Figs. 2C and 3) is to be read as a mathematical expression, like an equation, and is not intended as an illustration (such as the stick figures in Fig. 1).

Formally, *a d-space is a set of regions on which there are two relations, inclusion and contiguity.* Some regions allow some concept of movement, typically expressed as a range of trajectories or *flow*. Other neural regions involve discrete aspects such as thresholds and discrete transitions. *Inclusion* is standard in mathematics and will be denoted in the standard way in figures: by connection with a solid line (for example, Fig. 3). The concept of inclusion used must be the same throughout. Here, it is *set inclusion*. A d-space may be understood as a *poset* (*p*artially *o*rdered *set*) on which there is an additional relation, contiguity. *Contiguity* is a binary relation denoting an opportunity to transition from one region to another. Contiguity may be directed (denoted by a dashed arrow as in Fig. 3) or undirected (denoted by a dashed line or double arrow). The two relations, inclusion and contiguity, express two different kinds of dependence, "constrained by" and "arising from". Thus, in the hip d-space of Fig. 2C, the overall hip dynamics is represented as including or governing the smaller three regions, which are connected by contiguity (dashed arrows) to show one arising from the other.

Conditional dynamics, as represented by a d-space, generalizes vector spaces and topological dynamics by introducing algebraic relations. It also segments continuous spaces in order to serve empirical applications in which control is specific to only a segment of a space – as is usually the case for sensorimotor applications. The segmentation of a space may be mechanically determined, as in strategies for rising from sitting [56] and Collins and Stewart's model of gaits [13,14]. Alternatively, the segmentation may arise for sensory, environmental, functional, stylistic, or other neural reasons. For example, environmental conditions such as the compliance of the support surface may change abruptly, requiring a change of sensorimotor dynamics.

2.2. Application of conditional dynamics to sensorimotor control

Conditional dynamics is the approach of choice for identifying postural sensorimotor control structures because:

1) The information available about sensorimotor control is rich but disparate, including various levels of analysis, from mechanics and sensory physiology to global properties of the control system. Information of various types and levels of analysis can be used in forming a d-space.

2) It is not particularly natural to distinguish independent and dependent variables in sensorimotor control. For example, the force produced by a muscle and the intended movement cause each other, as do movement and sensory reafference, in either order. Even though conditional dynamics can be used to model

input-output relationships, it is well suited to closed, cooperative control systems.

3) Sensorimotor control involves continuous and discrete conditions affecting dynamics in various combinations. A d-space can contain not only discrete relations between regions but also regions with discrete internal structures. Segments of continuous spaces occur as regions in a d-space and continuous flows on spaces may govern contiguity [36]. For example, the continuous flow consisting of a range of sit-to-stand trajectories [56] governs the contiguity of the sitting motor state to the standing motor state. Similarly, continuous neural processes may govern the contiguity between distinct neural and sensorimotor states. This inclusion of continuous flows relates the present approach to various continuous approaches, such as Kuo [30], Peterka and Benolken [52], Dijkstra et al. [16–18], and Collins and De Luca [11,12].

4) The structure of the postural control system is itself of intrinsic interest (not just its predictive capabilities), as a reflection of anatomical, physiological, and functional structures that remain moderately fixed for a time in nervous systems. For example, muscle mechanics, sensory physiology, and even habitual movement patterns are relatively fixed. The structure of a d-space is itself a mathematical object (rather than only an analytical tool), which can be used to order and synthesize what is known on various levels about the conditional dynamics of a complex control system.

The d-space control system is the global space expressing the dynamics followed by the system, along with the conditions under which each type of dynamics obtains. It is formed by the regions together with all the relations: an overall structure is formed. (A d-space is a space in the senses of Riemannian space, Hilbert space, and Greechie space – given in order of most continuous to most discrete.) If a flow is specified, it must include both ends of any contiguity it governs. Recall that inclusion is transitive: inclusion does not have to be direct to express governance. Contiguities may be optional or obligatory, depending on the flow governing them. Sensory aspects of the sensorimotor control system are based primarily upon previous investigation of a discrete sensory transition structure [44].

Contiguity links the regions the system may move between, as in the hip d-space (Fig. 2C). However, the physiological ability to change an imposed invariant can be expressed simply as a contiguity with no explicit flow. For example, in those subjects and circumstances in which there is a discrete transition between the hip and ankle movements, those states are joined by contiguity. The neurophysiological mechanisms governing the contiguity can be made explicit in the d-space when they are understood.

Zajac and Gordon [64] point out that a muscle contraction can have almost any effect, depending upon the movement of the body, activity of other muscles, and external forces. To assure a certain effect of muscle use, invariants must specify or control these other factors.

2.3. Modelling assumptions

Even though the form of sensorimotor control structure presented in this paper is more general, the specific control systems include only certain senses (vision, vestibular, and ankle proprioception) and movements (hip, ankle, and mixed). Senses are divided only according to the physical origin of the signal (i.e., whether the sense transduces light, inertial, or mechanical signals) even though the same type of physical signal is registered by more than one physiological receptor type, e.g., inertial signals are registered by motion of limbs and internal organs, semicircular canals, and otoliths, light signals are registered by peripheral and foveal vision, and mechanical signals are registered by tactile receptors, joint receptors, muscle spindles, and tendon organs. All contiguities are examined to be sure that they are allowed by a plausible flow, whether physical or physiological.

The internal structures of sensory and motor states are expected to involve both discrete and continuous aspects. However, internal structure is not focussed upon (much less specified exactly at the outset), because the internal structures of states are expected to depend upon the global structure of sensory and motor interdependence. Rather, global structure is expected to be the more tractable problem.

Global constraints on the control structures not specified by the mathematics are that the d-spaces will be complete, consistent, and unambiguous in the formal senses that:

1) All regions are accessible and may be exited. On a global level, this means that the control structure is closed and is in that sense complete. (In general, a d-space need not be complete in this sense. An example of a d-space that is not complete in this sense is in Fig. 3. The reason that it is separated into two pieces is that it can not be complete as one control d-space. Another example is the hip movement, Fig. 2C, in which the initial region can be exited but not entered and the final region can be entered but not exited.)

2) No extra flows are contained in the d-space. This ensures a more internal form of completeness.

3) All contiguities are usable. No extra contiguities are included; those that are included function in and are consistent with the rest of the control structure.

4) Invariants do not require the application of two contradictory flows at the same time. This addresses consistency and lack of ambiguity.

3. Experimental and theoretical basis

This section will briefly summarize the experimental data and theoretical results used as a basis for the conditional dynamical analysis and sensorimotor control d-spaces presented in the following sections. Some lacunae in experimental and theoretical basis will also be pointed out.

3.1. Individual differences

A sensorimotor postural adjustment d-space is not required to be unique, because it is assumed that individuals differ in the conditional dynamics that they follow. In previous research, several distinct, consistent control systems were found for transitions among sensory states [44]. Different individuals assign different roles to sensory modalities, both in the variations of posture within quiet stance [11,12] and in fast postural adjustments because of different mechanical and sensory environments and the absence or disorder of a sensory modality [4,5,44,47]. Individuals differ in motor aspects of fast postural adjustments [41,50,59].

Given all these results, it would not be surprising to find individual differences in the roles of sensory modalities in fast postural adjustments. There are almost always individual differences in region boundaries, determined by such mechanical parameters as the height and weight of the individual. However, the discrete structure of the d-space – the number of regions along with their inclusions and contiguities – may be unchanged by variations in region boundaries.

In other cases, one region may be separated into two separate regions. For example, the postural adjustment continuum (Fig. 2A) is separated in certain individuals and certain circumstances into the ankle and hip movement regions (Fig. 2B). The separation of one region into two distinct regions not only changes region boundaries but also changes the discrete structure of the d-space – the functional logic of the posture control system. A different role assignment for a sensory modality may also change the discrete structure of the d-space. Therefore, it is reasonable to have different sensorimotor control d-spaces for different types of patients and for different individuals, even though the d-spaces may share basic characteristics.

3.2. Logical independence of sensory states and motor strategies

There is no evidence that healthy individuals use or avoid certain combinations of sensory states and motor strategies. Each sensory state (among those under consideration) occurs when subjects use the ankle movement as their motor strategy [51]. The independence of motor performance from sensory state also suggests that motor strategy and sensory state are assorted independently. For these reasons, in this paper, sensory state and motor strategy will be assumed to be logically independent.

3.3. Motor

Experiments indicate that individuals bound the range of ankle to hip postural movements (Fig. 2A) into regions in different ways. Runge, et al. [59] found that some subjects had only one postural adjustment region, in which responses to perturbation consisted of the ankle synergy plus variable amounts of hip synergy, with the amount of hip synergy activation depending upon the platform velocity. This pattern is consistent with the previous observation that the abdominal muscles are often activated during the ankle synergy. Other subjects had two postural adjustment regions, one in which only the ankle synergy was used, regardless of the platform velocity, and one in which the ankle synergy was combined with variable amounts of hip synergy. Subjects change regions as the perturbation increases. With the present data, the existence of two regions can be interpreted in two different ways: control of the two regions is distinct and there is a discrete transition between them, or control of the two regions is the same and the amount of hip synergy is too small to detect in one of the regions. For the purposes of constructing d-spaces to describe motor strategies, the second interpretation makes the two-region subjects indistinguishable from single-region subjects.

There is, in addition, a hip movement region observed in certain circumstances and subjects [25,41]. The pure hip movement occurs in at least two cases. Some vestibular patients use a kinematic hip strategy to the exclusion of the ankle strategy, with at least two dif-

ferent variations of muscle burst pattern [63]. Healthy subjects standing crosswise on a beam change to the hip movement, either abruptly or gradually through a sequence of mixed strategies [41]. The mixtures of hip and ankle synergies and movements can be considered to be physically a continuum, are produced more or less as a continuum by some individuals, and perhaps can be produced as a continuum under certain conditions by all healthy subjects. However, because of the data showing individuals separating the range of mixtures into regions and because of the widespread tendency of movement continua to be discretized (e.g., into walk and run or walk and skip, as analyzed in McCollum [35]), this paper will assume that individuals can have more than one motor strategy region and can adjust the mixture within a region.

Like oil and water, the hip and ankle synergies retain their separateness when mixed [41]. They interdigitate, retaining their separate sequences without producing a cocontraction in healthy subjects. In contrast, Parkinson's patients produce simultaneous, cocontracting superimpositions of the two synergies [27]. Thus, a postural coordination function appropriately interdigitating the synergies may be interrupted by a lesion in the basal ganglia.

3.4. Amplitude determination

The data of Runge, et al. [59] suggest that the initial vestibular signal determines amplitude of the hip component in the postural response. The head movement causing the initial vestibular signal is a passive result of the platform movement, varying with its abruptness. A gentle perturbation can be corrected using the ankle synergy, the synergy of choice for most subjects. However, a very abrupt perturbation elicits an ankle-hip mixture [59].

Runge, et al. [59] found the best correlation between the magnitude of initial passive head acceleration (caused by the perturbation) and greatest trunk flexion. Even though consideration of mechanical aspects is absent from their work, data of Allum, et al. [2] can be interpreted similarly. This correlation leads to the hypothesis that head acceleration, probably registered by the vestibular system, determines the amplitude of postural adjustment muscle activity and the ratio of ankle to hip synergies (Fig. 4).

This hypothesis can be used to explain the loss of motor strategies: a patient may lose the ability to change the ratio of ankle and hip muscles. In particular, a patient with complete vestibular loss may lose the ability to change from a pure ankle movement [63]. Also, experimental subjects with temporary somatosensory loss in the feet [15] and some patients with positional nystagmus [63] may lose the ability to change from a pure hip movement. This explanation is weak because it involves an extension of the results of Runge, et al. [59]; in that study none of the healthy subjects used a pure hip movement. Also, no explanation has yet been given that connects particular vestibular disabilities with particular inabilities to use head acceleration to control postural adjustment mixture. Despite the weakness of the conclusion, it needs to be included as the most specific mechanism in the literature for changing postural adjustment mixture according to perturbation abruptness.

How can the determination of hip muscle amplitude by vestibular signals operate in subjects with two motor regions? A d-space would be ambiguous if the hip muscle amplitude were determined (perhaps at different values) both by motor strategy region and by vestibular signal. Both the particular motor strategy region and the relationship between vestibular input and hip muscle activity are invariants governing the postural adjustment. It may be that one invariant includes the other. If the motor strategy region includes the vestibular influence, the relationship between vestibular input and hip muscle activity may be shifted, depending upon the motor strategy region, as shown in Fig. 5A.

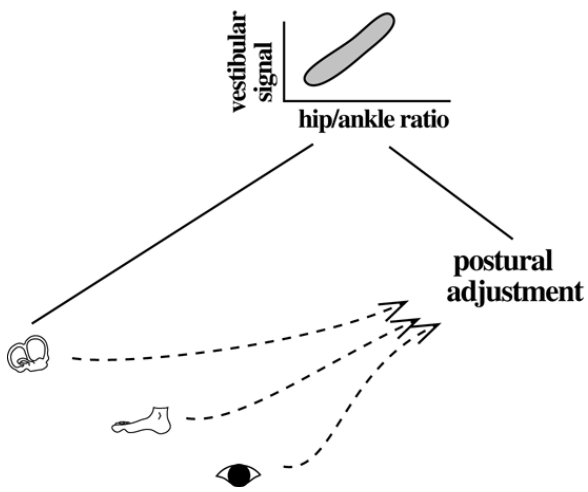

Fig. 4. d-Space relating the vestibular signal to the postural adjustment mixture, as in Runge, et al. [59]). The correlation between the vestibular signal and the hip/ankle ratio is represented as a region in which the two quantities increase together. Vestibular, somatosensory, and visual reafferences are represented as icons giving rise to the postural adjustment governed by the correlation between the vestibular signal and the hip/ankle ratio.

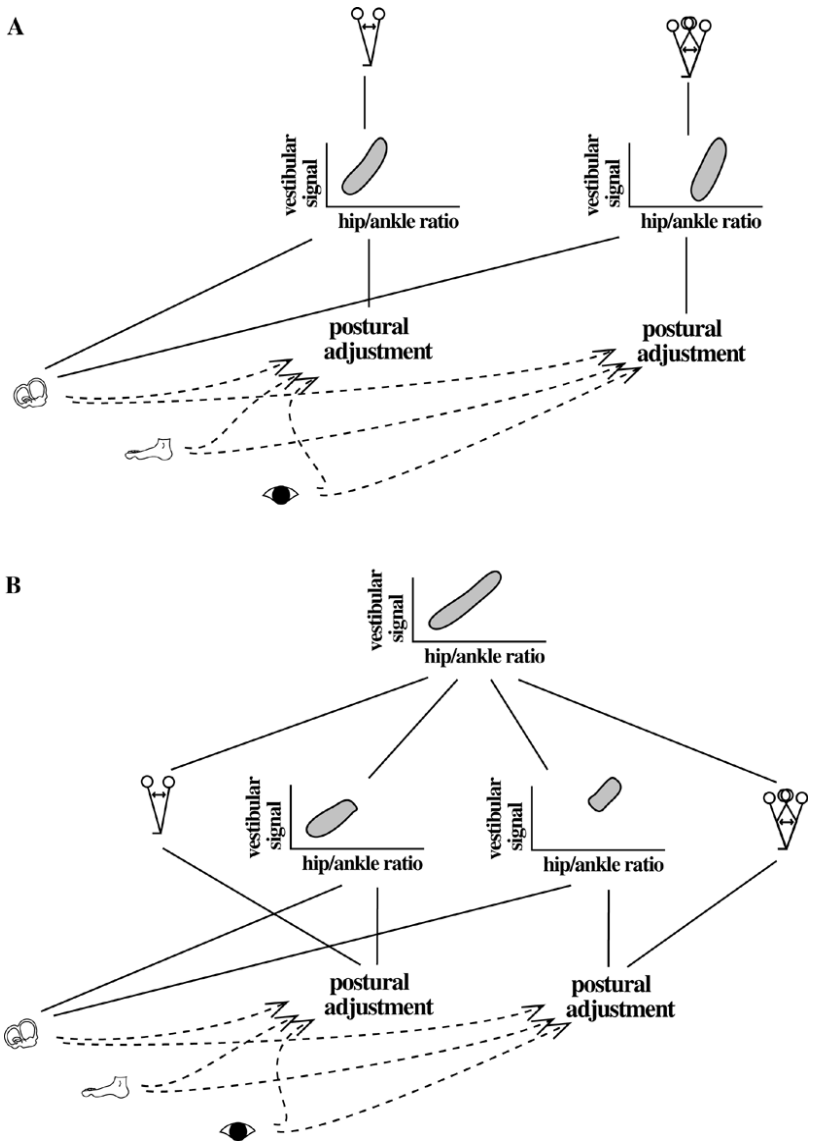

Fig. 5. Alternative d-spaces, disambiguating the dominance of vestibular influence versus motor strategy region in the mixture of ankle and hip synergies. The two motor strategy regions are an ankle strategy region and a mixed strategy region, represented by a mixed icon. A. Motor strategy regions dominate. Each motor strategy region has its own correlation between the vestibular signal and the hip/ankle ratio. The two correlation regions may be quite different, for example with different slopes. Experimental evidence favors this option. B. Vestibular influence dominates. A subset of the correlation region intersects with each motor strategy region.

Otherwise, the vestibular influence may dominate the motor strategy, so that only a subset of the correlation region is relevant to each motor strategy region and the vestibular input plays a role in determining the motor strategy (Fig. 5B). Even though it seems likely that the vestibular system does play a role in determining motor strategy, the ability of subjects to use different motor strategies in response to similar postural perturbations [25,41] argues for domination of the vestibular influence by the motor strategy (Fig. 5A). It is possible, however, that some individuals use a control structure incorporating the form shown in Fig. 5B.

Assuming that the motor strategy dominates the vestibular influence, the vestibular influence can be subsumed in the coordination of the motor strategy and omitted from the discrete structure of the d-space for the purposes of the present paper. The contiguities changing motor strategy regions in Fig. 5 have been omitted so far because they depend on both the motor strategy regions and the sensory states.

3.5. Sensory

A *sensory state* is a set of sensory role assignments, along with their implications for neural and sensorimotor coordination. Within a sensory state, a sensory modality may trigger an action, monitor another sense, modify another sense or an action discretely or according to a continuous parameter, etc. Because sensory states and transitions between them were analyzed in a previous paper [44], they are not a focus of the present paper. For this paper, sensory states will only distinguish physical divisions of senses: inertial/vestibular, light/visual, and mechanical/somatosensory. Sensory reafference arises in particular combinations, depending upon the movement performed and the sensory environment. For example, an ankle movement typically results in the visual world approaching and in ankle flexion. This sensory combination can be said to be a "match" of sensory modalities for an ankle movement, whereas visual approach without ankle flexion can be said to be a "mismatch". Matches and mismatches between sensory modalities can be used parsimoniously to explain transitions in sensory state [44].

A sensory state transition d-space repeats such contiguities for multiple states and matches and mismatches. Requirements on the sensory state transition d-space include:

1) The sensory environment includes (is above) the registration of the sensory environment and any matches or mismatches it affords.

2) The combination of state and sensory match or mismatch is included in (below) the flow region specifying sensory state transitions, the sensory state, and the registration of a sensory match or mismatch.

In a simple control structure satisfying these requirements, a flow allows a contiguity from a region on a lower level, in which the registration of a change in sensory match or mismatch is denoted, to a region on a higher level, where the sensory state is denoted (Fig. 6A) [36–39].

The sensory state transition d-space based on previous results for sensory transitions [44] is shown in Fig. 6B. The sensory states are: A, in which somatosensory information is primary and may be supplemented by vision and the vestibular system, B, in which vision is primary and may be supplemented by the somatosensory and vestibular systems, and C, in which the vestibular system is primary and may be supplemented by vision and the somatosensory system. The internal structure of each sensory state is interdependent with the sensory state transition structure and, indeed, the entire postural sensorimotor d-space. For example, which secondary senses or combinations of senses may initiate a postural adjustment in a particular sensory state is expected to depend upon the matches and mismatches leading to the sensory state. (An example is given in Section 4.) Therefore, this paper is a further step in the analysis of the internal structure of the sensory state.

The sensory state transition d-space (Fig. 6B) satisfies the requirements given above. The transitions among sensory states are governed by a flow formalized and analyzed in the previous paper [44]. The flow between sensory states only operates on condition that two invariants coincide in an intersection of a sensory state and the registration of a sensory match or mismatch. A flow that operates in an intersection can be likened to fire, because the fire behavior arises when heat, fuel, and oxygen intersect.

The sensory state does not change as a result of a change in the sensory environment; rather, the change of sensory state is a process in the nervous system that involves the nervous system registering the change in sensory environment. A likely mechanism for registering the change in sensory environment is a movement (a postural adjustment or other movement) that stimulates the relevant senses. However, each movement imposes a particular relationship between the reafference in different sensory modalities. For example, the maintenance of head-trunk motor invariants allows an individual to visually fixate a target during locomotion, and lack of the motor invariant may interfere with the combination of locomotion with visual fixation [6,7, 53,54].

4. Sensorimotor control dynamics and vestibular-absent patients

This section presents the results of conditional dynamical analysis in the form of d-spaces. The text in this section is largely intended to motivate and explain the figures showing the d-spaces. Because the d-spaces are mathematical expressions, like equations, their purpose is not primarily illustration, although their form directly indicates the sensorimotor control structure.

The initiation and adjustment of postural movements depends upon reliable sensory references. At the same time, the interpretation of orientation senses depends upon the motor strategy being used. In terms of conditional dynamics, the sensory state acts as an invariant, governing the use of senses shaping movement. At

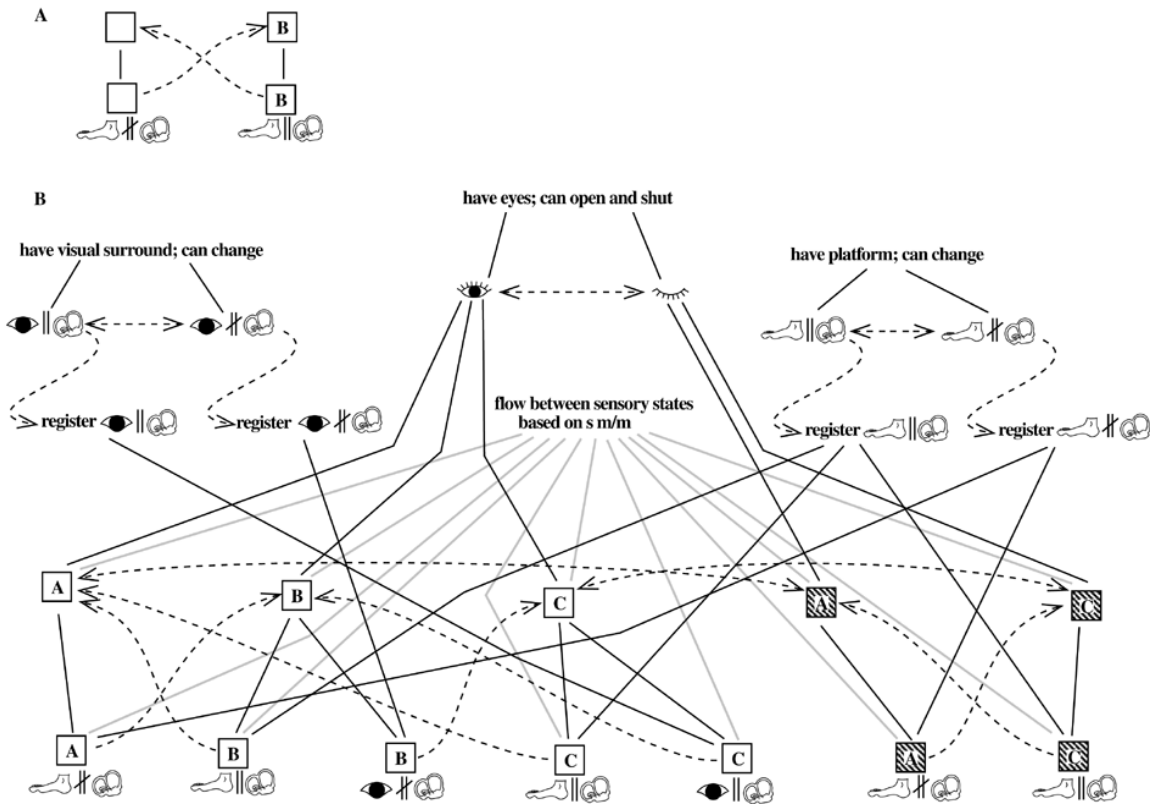

Fig. 6. Sensory state transition d-space for healthy individuals. A. Detail, showing the transitions between two sensory states. Included in each sensory state (A and B, at the top) is a trigger region in which the sensory state is combined with a particular sensory condition, a match or mismatch between somatosensory and vestibular cues. This detail is in the form of a dyad, analyzed and developed more fully in McCollum [36–38]. It appears in the lower left-hand corner of the full d-space. B. Full d-space: results from McCollum, et al. [44] rendered in d-space notation. Across the top are sensory environment manipulations. The letters in boxes are sensory states from McCollum, et al. [44]. Sensory state boxes are shaded when the eyes are closed. The matches and mismatches across the bottom use the same notation as in Fig. 3. Although no further matches or mismatches were required for the model in McCollum, et al. [44], a fuller model may include, for example, visual-proprioceptive or otolith matches and mismatches. The flow specifying sensory state transitions is called "flow between sensory states based on s m/m", where "s m/m" stands for "sensory matches and mismatches". For visual simplicity, matches and mismatches leaving the sensory state unchanged are omitted. [A better notation for sensory state transitions is found in McCollum, et al. [44]. That notation does not generalize well for the purposes of this paper.] Lines of inclusion in that flow region are in grey to reduce visual confusion.

the same time, the particular motor strategy region acts as an invariant governing the interpretation of sensory activity.

4.1. Binary sensorimotor postural adjustment d-space

Characteristics of a d-space satisfying the above requirements can be displayed in a symmetric, binary sensorimotor d-space with a minimum of two sensory states, two motor strategies, and two orientation senses (Fig. 7), even though healthy subjects have at least five sensory states, many people distinguish at least three motor strategy regions, and there are at least three orientation senses. The symmetric, binary sensorimotor d-space is presented to display basic organization, not as a prediction of any individual's sensorimotor d-space.

In order to make the structure more visible, the sensory state transitions are presented in a separate d-space diagram (Fig. 7A) from the motor strategy transitions (Fig. 7B). In the symmetric, binary sensorimotor d-space (Fig. 7), as in the sensory state transition d-space (Fig. 6B), sensory matches and mismatches ("s m/m") govern transitions between sensory states (Fig. 7A). The sensory matches and mismatches leading to sensory state transitions are included in motor strategy regions to show that sensory matches and mismatches are interpretations depending upon the motor strategy. In the case of postural movements, those dependent on motor strategy involve one modality in the head and one elsewhere, especially in the legs and feet. Matches and mismatches between the visual and

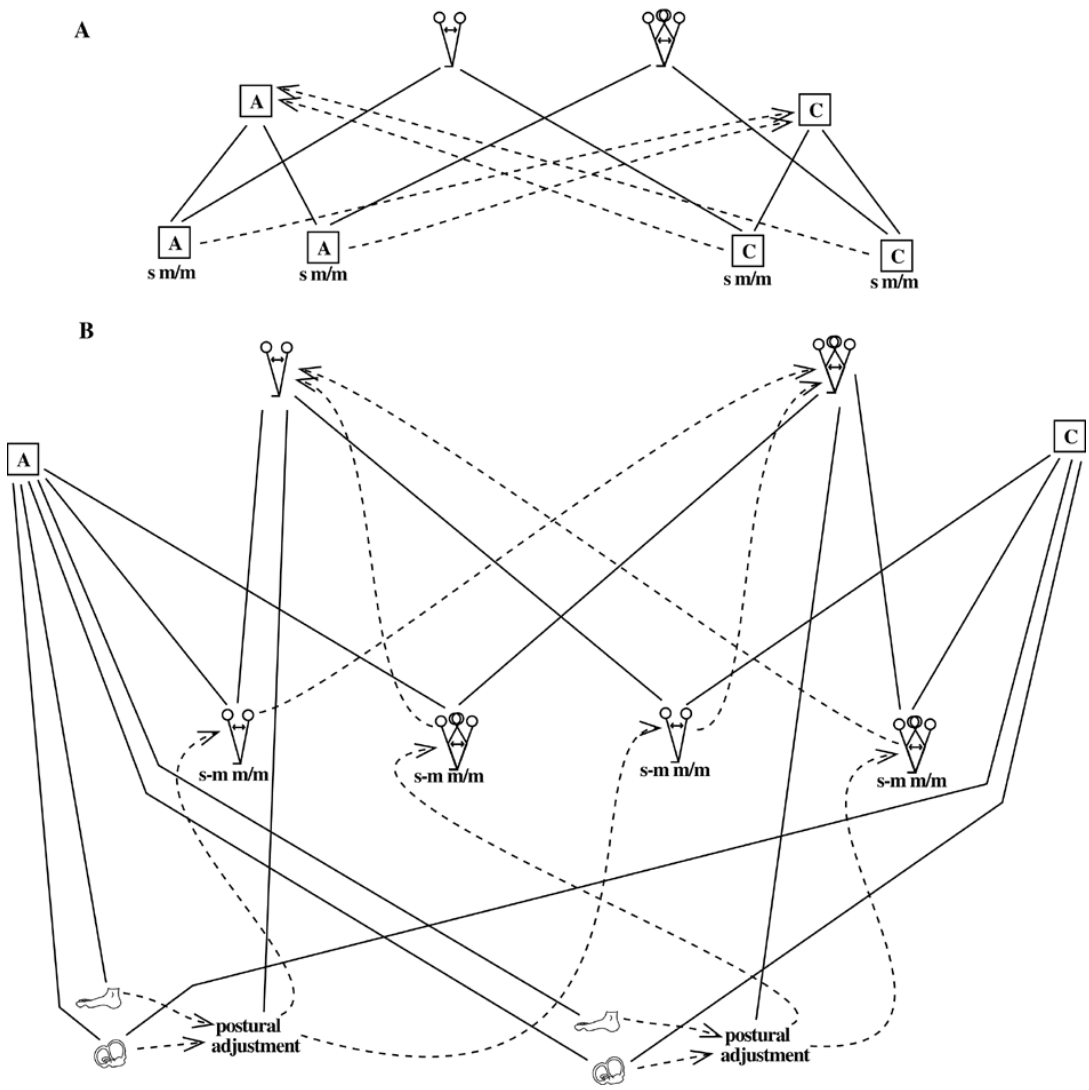

Fig. 7. Binary sensorimotor d-space, showing interdependence of sensory states and motor strategy regions. To make the structure visually clearer, exactly two are included of motor strategy regions, sensory states, and sensory initiators of postural adjustments. The two are chosen arbitrarily in each case. Also for visual clarity, the sensory state transitions are separated from the motor strategy transitions, although for full interdependence they should be thought of as being in one d-space, with the sensory states and motor strategy regions identified. A. Sensory state transitions. The sensory environment is omitted for visual simplicity. The intersections leading to a sensory state transition involve not only the sensory state and the sensory match or mismatch, but also the motor strategy region. B. Motor strategy transitions. As with sensory state transitions, motor strategy transitions involve intersections. The intersections are between the motor strategy region, the sensorimotor match or mismatch (s-m m/m), and the sensory state. The difference in form between A and B arises from the production of a postural adjustment (at the bottom of the d-space), which must occur before the motor strategy is judged by sensorimotor match or mismatch to be effective or ineffective.

vestibular modalities are not strongly dependent upon postural motor strategies, but rather upon gaze movement strategies, such as smooth pursuit versus saccadic movement. Such movements are omitted from the d-space, but may contribute experience leading to the registration of a sensory match or mismatch. Transitions of sensory state are fast, subtle, and not easily observed.

In contrast, changes of motor strategy on the basis of feedback require at least one previous postural perturbation (Fig. 7B). For simplicity, considerations of coordination and amplitude are omitted from the discrete structure. The postural adjustment leads (by an omitted physiological flow) to sensori*motor* matches and mismatches ("s-m m/m") that govern transitions between motor strategies. The sensorimotor matches and mismatches are included in both motor strategy regions and

sensory states. They may be simple matches between the movement and the range of a sensory modality. Alternatively, they may be more complex or specific to the movement, as in the head-ankle relationship in the hip movement. When the hip movement is used on ice, the slipping may be signalled by a whole body pitch rotation, leading to a transition to the ankle movement. When the ankle movement is used on a beam, the lack of ankle torque may be signalled by the flopping motion of the foot or by the lack of movement of the head toward upright. The sensorimotor matches and mismatches are left unspecified in Fig. 7B, because there are many possibilities which are not well understood.

The basic sensory modalities, visual, vestibular, and proprioceptive, used in Fig. 6B may match or fail to match the intended movement. A sensorimotor mismatch means that the sensory modality fails to register the reafference that would be caused by the intended movement. Sensorimotor matches between the intended movement and two separate sensory modalities allow a match between the two sensory modalities. Sensory matches and mismatches may govern transitions between sensory states, depending upon the individual's sensory state and sensory state transition d-space.

4.2. Vestibular-absent patients

People who have no signal from the peripheral vestibular organs to the central nervous system do not use the vestibular system for balance or for monitoring postural movements, so that the vestibular system would not appear in their set of sensorimotor matches and mismatches. Similarly, the possible sensory state transition d-spaces can be constructed by removing all vestibular states and transitions, matches, and mismatches from the possibilities for healthy people (Fig. 6B), and finding all consistent sensorimotor d-spaces using the remaining elements. Using only the three physical divisions of orientation senses, vestibular-absent patients have two possible sensorimotor transition d-spaces with three sensory states (Fig. 8). (Fewer sensory states are also possible.) When vision is available, it may be used in preference to proprioception in state B (Fig. 8A). In that case, the person would fall when the visual surround gives inappropriate information, even when the support surface is fixed, giving appropriate orientation information. In the alternative sensory state transition d-space, proprioception in state A is used when vision and proprioception disagree (Fig. 8B). In that case, the person would fall when the support surface gives inappropriate information, even when the visual surround is fixed, giving appropriate orientation information.

Failure of a motor strategy, such as continuing to fall when ankle torque is ineffective or slipping on the ice when attempting to use the hip movement, occasions a sensory mismatch relative to the intended motor strategy. Because a sensory state transition is so much faster than a motor strategy transition, the sensory state has already changed, by the time the movement is completed, to the sensory state specified by the sensory state transition flow in the case of a sensory mismatch. In the case of the vestibular-absent sensory state transition d-spaces, the default state in case of a motor strategy failure is easy to determine. If vision is used in preference to proprioception when there is a mismatch (Fig. 8A), then a failed motor strategy causes a transition to state B. In addition, a sensorimotor match or mismatch is required for a transition of motor strategy. The only sense that is trusted in state B in this sensory state transition d-space is vision, so only vision may monitor motor strategies to cause transitions (Fig. 9A). The two motor strategies shown are the ankle and hip movements because they have been salient in experimental data concerning vestibular-absent patients.

Because vestibular-absent patients do not maintain the head upright in the hip movement by neck muscle activity [62], vision may not be available to monitor the hip movement. In that case, vestibular-absent patients using the vision-preferred sensory state transition d-space could not use the hip movement, because they could not monitor it. In the d-space (Fig. 9A), the monitoring loop including a mismatch between vision and the hip movement would be absent. The d-space would be incomplete as a control system, according to the modeling assumptions, if the motor strategy could be changed to the hip strategy, but could not be changed from the hip strategy to the ankle strategy. So the entire loop is absent, making the hip movement inaccessible to the patient (Fig. 3), as is found experimentally [63].

If proprioception is used in preference to vision when there is a mismatch (Fig. 8B), then a failed motor strategy causes a transition to state A. In that case, proprioceptive monitoring is available for both the hip and the ankle movement (Fig. 9B). This result suggests that encouraging use of proprioception, in preference to vision, may be advantageous for vestibular-absent patients.

In the acute stages after vestibular loss, patients may fall when either the visual surround or the support surface is sway referenced (moves with them), failing to

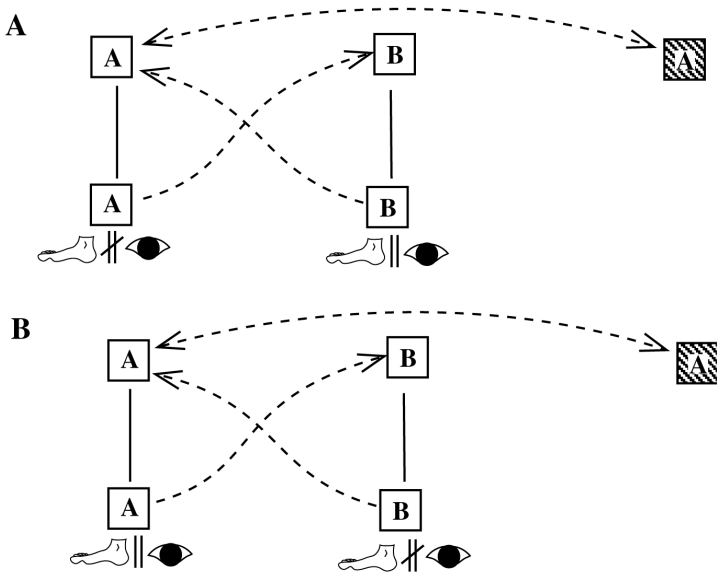

Fig. 8. Sensory state transition d-spaces not using the vestibular system, with only physical divisions of the senses. Sensory state C is omitted, for both open and closed eyes, because the vestibular system is primary in C. When the eyes are closed, only somatosensory information is available. The only available sensory matches and mismatches are between somatosensory and visual information. A. When somatosensory and visual information disagree, vision becomes primary and somatosensory information is distrusted. B. When somatosensory and visual information disagree, somatosensory information becomes primary and vision is distrusted.

give appropriate orientation information. These results are consistent with the two sensory state transition d-spaces (Fig. 8A, B).

The behavior of vestibular-absent patients is highly variable, depending upon whether the loss is unilateral or bilateral and the degree of compensation. A patient with unilateral vestibular loss is not vestibular-absent, because the other side still functions. The transition structures shown in Fig. 9 represent the movements of some vestibular-absent patients, but not all and not all of the time. Acute vestibular-absent patients may be more generally distressed and disoriented, making them unable to use visual or proprioceptive information. Well-compensated vestibular-absent patients have postural behaviors that are more variable than shown in Fig. 9, suggesting that they exploit other sources of orientation information, sources perhaps not usually attended to by healthy individuals.

Although further studies of the movements of vestibular-absent patients need to be done, present results are consistent with the hypothesis that acute vestibular-absent patients use the same physical divisions of the sensory modalities as healthy subjects, but that for vestibular-absent patients the healthy sensorimotor d-space is reduced by omitting all use of the vestibular system. Sensory state transitions (Fig. 6B) are reduced and transformed in the sensorimotor transition d-space to ones that do not use the vestibular modalities (Fig. 8) [44]. Because there are fewer sensory states in the vestibular-absent case, the motor strategy transitions are less complicated. Also, a fuller sensorimotor d-space would contain a region of mixed motor strategies (Fig. 10). It may be that healthy individuals do not use fine distinctions among sensory submodalities in making transitions among sensory states; the undivided modalities may be adequate for them. However, vestibular-absent patients may need to be more resourceful. The sensorimotor d-spaces presented here indicate that later, in the process of compensation, other sources of orientation information are tapped, perhaps by subdividing the physical sensory modalities into their physiological components.

5. Discussion

This study has presented a logical system for the interdependent distributed control of sensory states and motor strategies, in which the sensory and sensorimotor matches and mismatches initiating transitions are governed by both the sensory state and the motor strategy. The interconnectivity of a physiological system makes such interacting governance inevitable. Moreover, smooth, unhesitating motor behavior appropriate

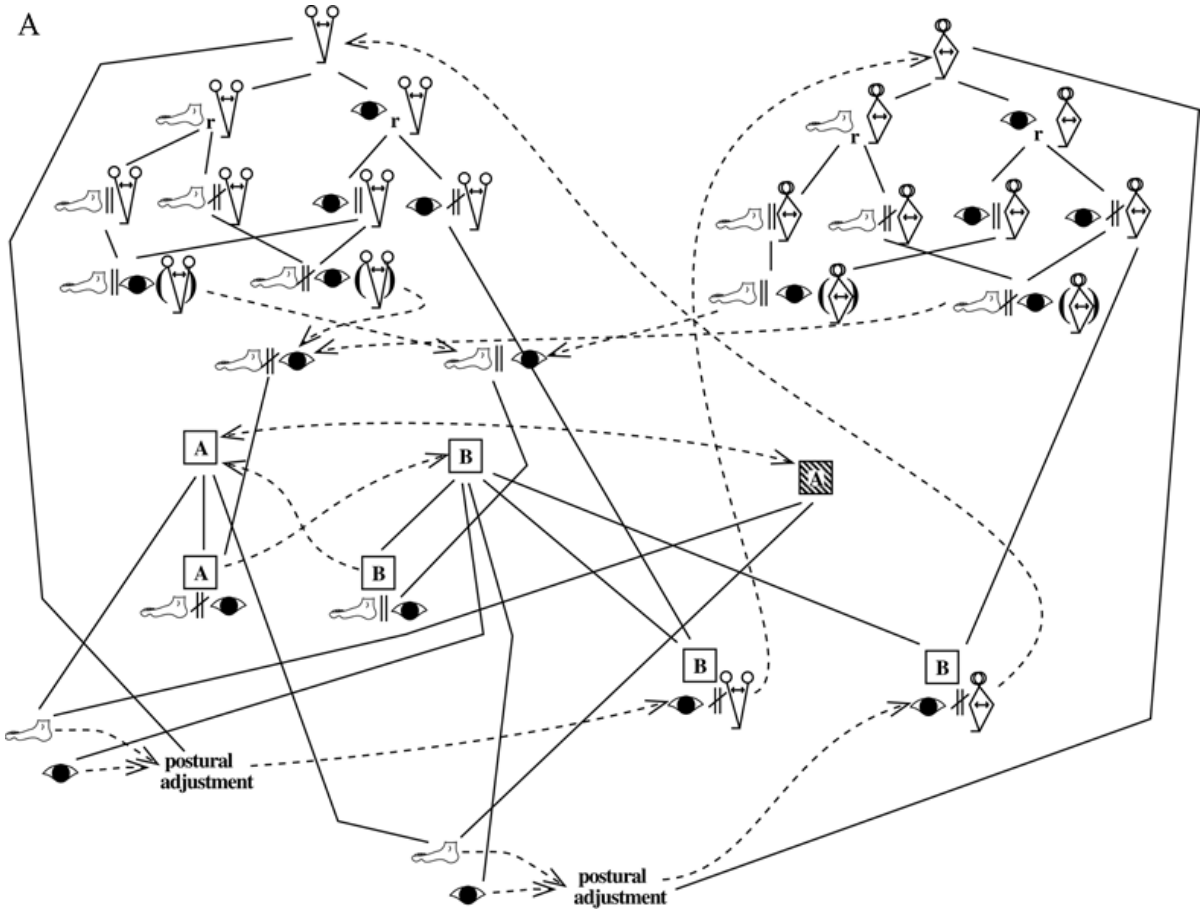

Fig. 9. Vestibular-absent sensorimotor d-spaces, showing interdependence of sensory and motor transitions. Sensory matches and mismatches relative to the ankle and hip movements are shown near the top. The sensory matches and mismatches govern the sensoty state transitions shown near the middle. Near the bottom are shown the postural adjustments, which are monitored according to the motor strategy and the sensory state. A. The sensory state transitions to B in the case of a mismatch (Fig. 8A). B. The sensory state transitions to A in the case of a mismatch (Fig. 8B). The possibility of using vision to monitor the hip movement is removed in Fig. 3, disallowing transitions between ankle and hip motor strategies. Experimental evidence indicates that the ankle movement is chosen.

to the sensory and mechanical environment requires a logic of discrete transitions among sensory and motor modes that is complete, consistent, and unambiguous.

Application of the results to the case of patients with total loss of vestibular function (1) clarifies their postural behavior during the acute period preceding compensation to the condition, including an explanation of failure to use the hip movement, and (2) identifies the period of compensation as one in which new sources of orientation information are found and the basic ones, used undivided by healthy people, are subdivided. For example, vision may be subdivided into foveal versus peripheral vision and somatosensation may be subdivided into muscle spindle, tendon organ, joint, and cutaneous inputs and may include inertial components of limb and internal organ motion.

These results suggest that subdividing the basic sensory modalities and using their logical combinations in the d-space formalism developed in this study has strong potential to clarify the motor responses of various groups of vestibular patients, especially the well-compensated vestibular-absent patients, who fail to use the hip movement. They also suggest that increasing sensitivity to proprioception as an orientation cue may be advantageous to these patients. There are two sensory state transition d-spaces not using the vestibular system, under the assumptions in this paper (Fig. 8). Patients using the one in which a sensory mismatch leads to a transition to state A (Fig. 8B) may have a satisfactory, proprioceptive monitor of the hip movement. A skillful physical therapist may be able to lead patients to change the type of sensory state transition

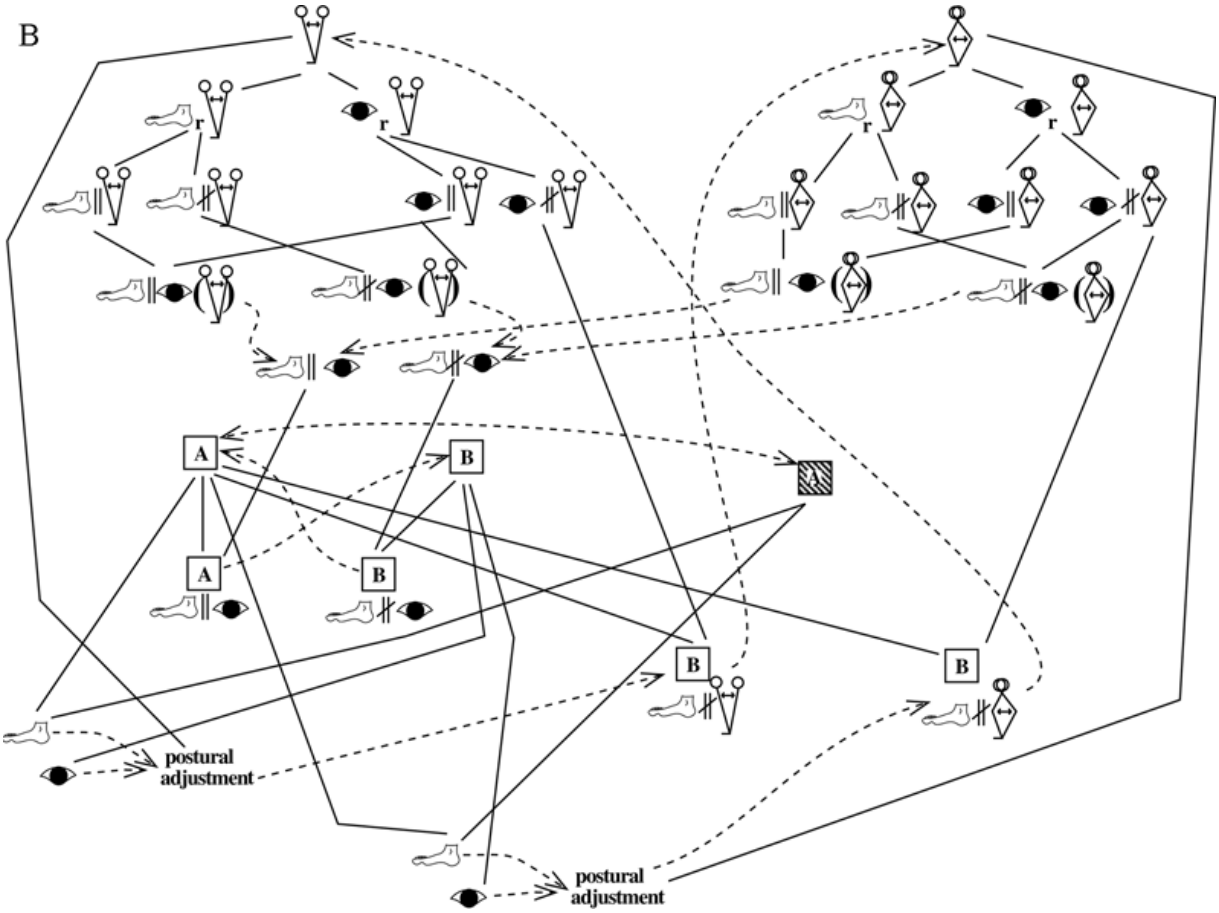

Fig. 9. continued.

d-space they use, by enhancing awareness of different sensory combinations.

Another group whose sensorimotor behavior this approach may clarify consists of those positional nystagmus patients who fail to use the ankle movement. An important question to address would be how to distinguish different groups of positional nystagmus patients. Besides vestibular patients, another group whose behavior would be clarified by such an analysis are astronauts just returning from microgravity, not yet readapted to earth conditions [49].

This study has focussed on complete, consistent, and unambiguous d-spaces. Studies of clinical d-spaces will need to include types of incompleteness, inconsistency, and/or ambiguity. For example, some vestibular patients' sensorimotor d-spaces are complete, consistent, and unambiguous on land, but not in transitions between sea and land conditions. In such a patient, adaptation to sea conditions is irreversible: the patient is motion sick indefinitely after coming back to land – such a patient is said to suffer from mal de débarquement. The sensorimotor d-space of such a patient contains states that can be entered but not exited or flows that move in one direction without corresponding flows that move in the other direction. Such a d-space is not complete according the modeling assumptions of this study.

The present study of complete, consistent, and unambiguous control structures has led to more focussed research on the dyad (Fig. 6A) [37]. Sensorimotor transition d-spaces can be considered to be products of dyads [36–39], leading to a study of the generation of biological control structures [38].

5.1. Different levels of analysis involved in patient movement hypotheses

Hypotheses on several different levels, from specific physiological mechanisms to distributed control, have been proposed to explain the loss of motor strategies by

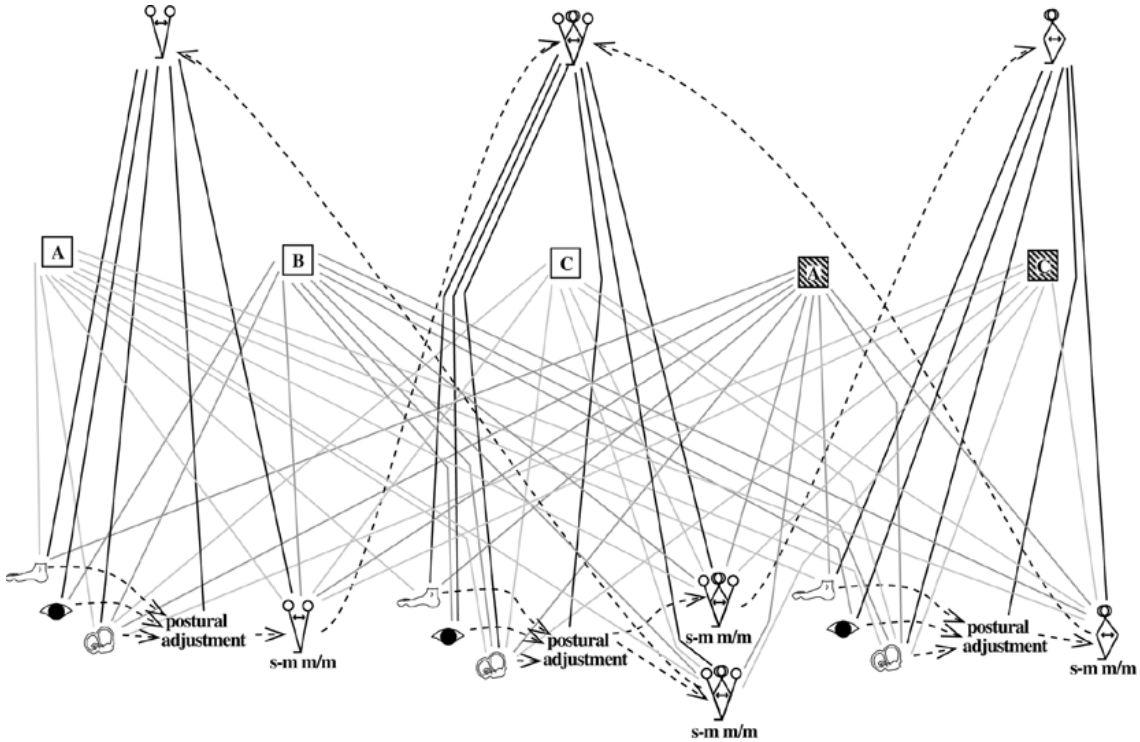

Fig. 10. Motor strategy transitions for healthy individuals with three motor strategy regions. Inclusion lines in sensory states are shown in shades of grey for visual clarity.

vestibular patients. There is no reason to expect that the hypotheses are mutually exclusive. The present study includes within a distributed control structure physiological mechanisms that have been proposed previously. The various hypotheses do not need to compete with each other; rather, understanding of the whole phenomenon requires multi-level explanation.

Nashner et al. [48] have specified the amplitude-frequency regions in which the vestibular endorgans are sensitive and in which ankle and hip movements are made. They have also shown that changes in otolith or canal thresholds affect the ability of the vestibular system to follow the different motor strategies. Although they do not address the visual and somatosensory modalities or how senses might be combined in orientation and balance, the basic point of their analysis has been incorporated into the present paper: that frequency-amplitide regions of sensory sensitivity must overlap frequency-amplitide regions of movement for the sense to follow the movement. Also, Nashner et al. [48] give important clues for separating the function of the vestibular otoliths from the canals in future studies.

Runge et al. [59] have found a correlation between the vestibular signal produced by the initial head movement and the amount of hip movement used in response to a postural perturbation. For the type of perturbations used in their studies, one might think that the mapping from initial vestibular signal to motor strategy is collapsed to the ankle end in the case of vestibular-absent patients and is collapsed to the hip end in the case of some positional nystagmus patients. Although they do not explain changes in motor strategy in response to mechanical changes in the support surface or address the mode by which vestibular-absent patients change postural adjustment amplitude, their results have been incorporated into the present study as the clearest indication of one mechanism for changing the mixture of ankle and hip movements.

Diener et al. [15] address the use of somatosensation in postural adjustments and find that temporary somatosensory loss from healthy people's feet increases their use of hip movements when vision is not available. Such results have led to the suggestion that the ankle movement is driven by sensory inputs to the feet whereas the hip movement is driven by sensory inputs to the head [29]. Positional nystagmus may interfere with processes within the vestibular nuclei that allow comparison of the position of the feet and legs to the

vestibular and visual senses of the head. A related suggestion, derived from consideration of the logic of sensory states [44] is that each motor strategy must have at least two senses, one to initiate it and another to monitor it. Although they do not give details, Horak et al. [26] conclude that the advance selection of motor strategy depends upon multi-sensory information. The present study has specified a logic for selecting both sensory state and motor strategy.

Because it is our job to understand the the postural system rather than to construct it, it makes sense to have multiple explanations, which may and may not interact with each other. Indeed, if the postural system is complex (as the nervous system certainly is), then it may be expected to require several different, complementary approaches for understanding [61]. Although evaluating the instantaneous sensorimotor coordination is also clearly relevant for understanding the postural system, this study has addressed the global functional logic first because (1) the instantaneous potential for transition depends upon the global system and (2) the global functional logic seemed the more tractable problem. It is assumed that an individual's global functional logic will be replicated in subsystems, will have consequences on many levels, and will be conserved as much as possible through changes, such as learning and injuries.

5.2. Continuous versus discrete

At each physiological level, discrete and continuous phenomena are intertwined. Each muscle is discrete, yet can be activated an amount that varies continuously, considered on the scale of whole body movements. Two separate muscles can be activated in continuously varying ratios. Each sensory receptor is anatomically distinct, yet body movements can occasion sensory registration in continuously varying ratios. Each discrete sensory receptor has at least one continuous range of transduced variables. Because of the intertwined continuous and discrete aspects of sensory and motor function, overall control of posture must take into account both continuous and discrete aspects. For example, when cats are perturbed in different directions, there is a continuous change of ratios between discrete muscles to maintain an invariant mechanical strategy, involving particular (discrete) directions of ground force [32,33].

Studies of bifurcations relate continuous spaces to discrete boundaries between different behaviors. Gaits are different behaviors in the same motor space, well described by bifurcations [13,60]. Gaits also admit a group structure [13,14]. The expression of bifurcations within d-spaces is discussed in Roberts and McCollum [57].

The present study focusses on discrete aspects of sensorimotor control. It probes the discrete postural modes necessary because of environmental requirements and specifies global structure required by these transitions in the distributed control system. Continuous aspects are included within regions, the elements of the d-space. For example, the adjustment of motor strategy mixture to the abruptness of the perturbation [59] is presented as continuous (Fig. 4).

A different approach to studying continuous and discrete aspects of the sensorimotor control of posture involves observing sway induced by the different senses [16,52]. Visually-induced sway has been studied as a mode, in a sense similar to acoustic modes, by analyzing phase dynamics and temporal stability [17, 18]. An exciting possibility would be to combine extensions of these studies with extensions of the present conditional dynamical approach.

In contrast, computational approaches tend to focus on continuous and numerical aspects. Discrete changes in strategy or goal can be made by hand, by changing certain values or cost functions [22,30]. It is essential to understand continuous aspects of body mechanics [10, 21,31,42] and sensory function in order to understand overall postural functioning. Numerical results are often desired for comparison with experiment. However, computational approaches have tended to make rather narrow assumptions about the nature of the overall system, especially the discrete structure, and the meaning of numerical results is limited by those assumptions. Also, behavior patterns are as available for comparison with observation as numerical values are.

Not all computational approaches are completely continuous. Prochazka (1996) describes control systems based on "conditional logic" using concepts of fuzzy logic. Jacobs [28] has modelled locomotion using a fuzzy logic approach. These computational approaches seem to reflect a similar intuition to that motivating the mathematical approach used here.

The combination of discrete and continuous aspects of postural function in the d-space approach used in this paper allows both the analysis of the discrete logic and the application of well-developed fields of mathematics, such as set-valued maps [3], topological dynamics [1], and formalisms of mechanics [20] and quantum mechanics [19,45]. Instead of attempting to include all variables in a many-dimensional continuous space, conditional dynamics allows each region to spec-

ify only the relevant variables. That is, the continuous spaces may be quite simple. Where appropriate, they may be linear, but the assumption is that in general they are non-linear. Conditional dynamics easily accommodates discrete transitions in the limit of extreme non-linearity.

5.3. Appropriate level of generalization

The ultimate theory of postural behavior would accommodate all the postural strategies of each individual in free, natural movements in everyday life, just as Newtonian mechanics applies to every mechanical action in a certain range of size and velocity. Individuals vary in body parameters, postural habits, details of sensory functioning, and many other ways. Environments and postural requirements can differ enormously. For example, shifting reading position in bed is much less demanding than finding the correct posture while walking over a mountain rock field while carrying a heavy pack. Even within fairly similar circumstances, each postural behavior takes place in a slightly different position and for slightly different purposes.

The challenge for a theorist is to find the appropriate level of generalization at which some statement can be made that is significant for a broad range of postural behaviors. The challenge for an experimentalist is to set up a situation in which different individuals behave in comparable ways. In the currently most accepted experimental paradigm, the behavior is specified by a number, rather than, for example, by a pattern of behavior. Experimental results are essential to empirical theory, whether the results are physical or physiological. In choosing experimental results and interpreting them formally, a theorist must take into account the experimentalist's purpose; the theorist's purpose may be quite different. Theoretical investigations include demonstrations of the overall consistency of experimental data on an already accepted level of explanation and generation of new frameworks, providing new types of explanation. New frameworks may suggest further experiments, leading to a different understanding of the overall system. Another use of new frameworks may be for diagnosis and rehabilitation in a clinical setting.

Rehabilitation and other clinical purposes are best served by individual sensorimotor d-spaces, which express the biological individuality of the patient, from body parameters and habits to sensory and motor deficits. Although experimental studies emphasize the commonalities between patients, especially given a shared pathophysiology, individual differences are often clearer than the generalizations. Individual physical and physiological parameters such as body parameters and sensory and motor deficits are important because an action can be prevented from many levels, from the receptor level to overall distributed control. Individuality of movement habits and perceptions is important in modifying a patient's behavior, because strategies easily available to the patient are also individual [24, 50].

For such clinical purposes, a d-space based on averaged experimental results is inappropriate, just as assuming right-handedness is inappropriate. Averaging handedness across a population gives handedness *between* right and left, a miscarriage of statistics which is accurate for no one.

In the present study, choices of individual d-space were allowed, while limitations on the physical situation were accepted. An individual may have any of the different consistent sensory transition d-spaces [44]. An individual may have one ankle-hip motor strategy region or two regions, one pure ankle and the other a mixture region [59]. On the other hand, movements outside the sagittal plane and aside from two-legged stance have been ignored, with the expectation that generalizing the logical considerations to freer movements will be fruitful. This is a major assumption, because even slight variations, such as light touch to a stable surface, change postural strategies [23]. Another limitation is that people are assumed to always be in a sensory state and a motor strategy set, even though that may not always be the case, for example in sleep.

As envisioned in this study, the postural adjustment system in the organism acts like a bumper in a pinball machine, designed to ricochet the body back into the balanced region. Such a bumper is advantageous to healthy functioning insofar as it keeps people from falling over. The bumper is complicated by a system of sensory alternatives. It is important to have the flexibility afforded by those complications, in order to use postural adjustments in various sensory environments. The flexibility is insufficient, however, to allow people to use their whole repertoire of motor strategies after they suffer certain vestibular damages. The logical methods used here allows an approach to such questions as: Do some postural adjustment d-spaces afford more flexibility in the face of nervous system injury? Which postural adjustment d-spaces afford the most long-term postural health? The most flexible ones? However, these questions will be best treated after a more detailed consideration of the sensory physiology.

5.4. Physiological function

Each sensory organ (eyes, vestibule, etc.) and nervous system component (vestibular nuclei, cerebellum, etc.) affords its own distinct contribution, determined by its physical transduction, internal structure, and combination of connections. Each voice is essential to the opera, yet it is equally essential that some voices drop out on cue. In the case of sensory deficits, the whole usually adjusts in order to function as well as possible.

The vestibular nuclei combine vestibular, visual, and cervical information to govern eye and head posture. The spinal cord has a similar integrative role in somatosensation for the rest of the body. Many other nervous system components also have integrative and postural roles, including the cerebellum, superior colliculus, and basal ganglia.

Discrete sensory states and motor strategy sets require discrete transitions in the physiological functioning at some level, perhaps in each individual component or perhaps in the relationships between the various components. In an example of similar underlying physiological function leading to opposite behavior, cats were found to walk backward using the same neural impulses to the leg muscles as in walking forward; the effect of the muscle contractions was reversed by the position of the pelvis [8,9]. A discrete transition in any one level, such as in motor state or in an individual component of the nervous system, is expected to be reflected in the overall logical functioning of the whole. Consistent postural functioning as formalized in a consistent d-space – which requires no external monitor for unambiguous transitions to and from each state – predicts consistent physiological transitions. The multiplicity of physiological options, including the multiplicity of sensory modalities, complicates a sensorimotor d-space, but poses no barrier to consistency.

Dividing sensory modalities into submodalities such as foveal versus peripheral vision, vestibular canals versus otoliths, and muscle spindles, tendon organs, joint receptors, and cutaneous sensors of the various parts of the somatosensory system, is expected to lead to a more complicated sensorimotor d-space which can nevertheless be consistent. It is possible, however, that the sensorimotor d-space might be simplified if submodalities are found to be effective for the whole task, so that other submodalities may be ignored. The other submodalities would remain available if required in other circumstances.

An intriguing example has been uncovered by use of pressure cuffs in experiments on healthy subjects. Cuffs applied at the ankle did not change the sensory state transitions, but did lead the subject to increase hip movement when the eyes were closed [26]. When the cuffs were applied above the knees, however, the hip movements were larger and remained even when the eyes were open [15]. Because the higher cuffs, above the knees, affected all the somatosensory inputs from the shanks and feet, especially the muscle spindle input from shank muscles, a sensorimotor d-space can be constructed by eliminating leg somatosensation (Fig. 11). Even though vestibular and visual modalities remain available for monitoring every motor strategy, experimental data indicate that the ankle movement is eliminated. Furthermore, the experiments with ankle cuffs demonstrate that the elimination of the ankle movement is not dependent upon muscle proprioception and the change in the sensory state transition d-space; rather, it is dependent upon sensory modalities intrinsic to the feet plus vision. This example argues that it would be fruitful to consider the structure of d-spaces that subdivide sensory modalities.

Examples in which multiple components cooperate, as the senses do, arise in central nervous system functioning. A vestibular disorder may be masked by cerebellar compensatory functioning. Later, if cerebellar functioning is lost or diminished, the vestibular disorder becomes apparent. These examples emphasize the integration of multiple physiological components in controlling posture.

Even though the purpose of the postural adjustment system is to return the body to stable posture in the case of a threat to balance, an important criterion for the distributed control system is that it maintain enough instability to change strategies. For example, a packing crate is more posturally stable than a standing human, but a standing human requires the instability of moving from a totally balanced position in order to walk and to make other movements. Such instability or flexibility gives our precarious upright stance an enormous movement power. Nevertheless, the instability must be managed unambiguously and with consistency, or it leads to sensory or physical misfortunes.

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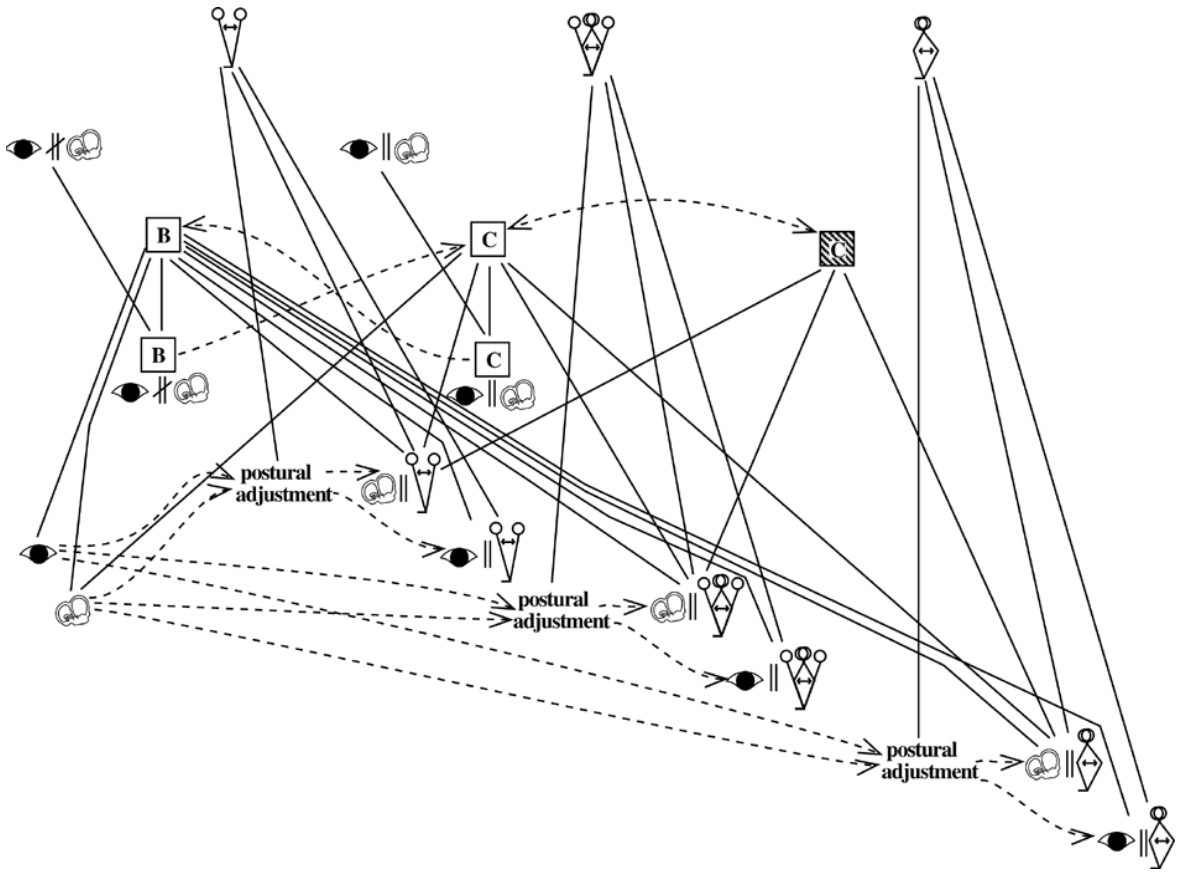

Fig. 11. Sensorimotor d-space in which somatosensory information is not used. Because sensory matches and mismatches involved in sensory state transitions only compare vision with vestibular information, postural movements are irrelevant to sensory state transitions. The opposite sensory state transition is also possible, in which vision becomes primary when there is a mismatch between vision and vestibular information.

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