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An Ecological Theory of Motion Sickness and Postural Instability

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In this article we present a new theory of motion sickness. In the sensory conflict theory, changes in stimulation of perceptual systems are believed to be responsible for motion sickness. We discuss the fact that these changes in stimulation are not independent of the animal-environment interaction, but are determined by corresponding changes in the constraints operating on the control of action. Thus, provocative situations may be characterized by novel demands on the control of action as well as by novel patterns of stimulation. Our hypothesis is that animals become sick in situations in which they do not possess (or have not yet learned) strategies that are effective for the maintenance of postural stability. We identify a broad range of situations over which the occurrence of motion sickness is related to factors that should influence postural stability. This allows us to establish a logical link between motion sickness and postural stability. Our analysis implies that an understanding of stability should be an important part of the agenda in research on perception and action in general. We suggest that postural instability could be related to the concept of dynamical disease which has been developed in the literature on nonlinear physiological control systems. We conclude with suggestions for research based on the new approach.

Motion sickness has been with us through the ages. Twenty-five centuries ago it was a problem for the ancient Greeks (Lawther & Griffin, 1986). It is a problem still. Despite this, explanations of motion sickness have remained fundamentally unchanged for over 100 years (e.g., Irwin, 1881). The most widely known

account of motion sickness is the sensory conflict theory. We have argued that this theory cannot account for the phenomena of motion sickness (Stoffregen & Riccio, 1991). In this article we present a new approach to the problem of motion sickness which differs from existing approaches in fundamental ways. These differences lead to new challenges for the study of motion sickness.

Sensory conflict is believed to interfere with the inductive inferences that animals make about their interaction with the world. Motion sickness is believed to be a byproduct of this interference. Following J. J. Gibson's (1966, 1979/1986) ecological analysis, we question the assumptions that underlie the role of inference in perception. We present a new theory of motion sickness that does not rely on these assumptions. Our hypothesis is that motion sickness results from prolonged instability in the control of posture. This is a claim about behavior rather than about sensory stimulation: Sensory conflict theory does not motivate hypotheses about postural instability. This is because generated sensory conflict is neutral with respect to the animal's state of stability or instability. We evaluate both approaches in terms of the available data, and identify specific situations in which they make contrasting predictions. Finally, we discuss new research directions that are motivated by the new approach.

Our theory is developed from an ecological approach to the perception and control of orientation and self-motion (E. J. Gibson et al., 1987; Owen & Lee, 1986; Riccio & Stoffregen, 1988, 1990; Stoffregen & Riccio, 1986, 1988, 1990). However, we believe that it has important implications for the study of perception and action in general; these are made explicit where appropriate. For instance, the concept of conflict between sensory reference frames underlies much of the sensory adaptation literature (e.g., Held & Mikaelian, 1964), yet we argue that sensory conflict may not exist. For this reason we refer, when appropriate, to works outside the motion-sickness literature.

Motion-sickness situations are characterized by their unfamiliarity to the animal. In conflict theory, unfamiliarity is construed to mean that current stimulation does not match stored templates or expectations. We have rejected this approach (as has Lackner, 1981). It is important to note that our rejection of conflict theory does not require us to deny that there are changes in stimulation in provocative situations (Stoffregen & Riccio, 1991). Such changes exist. The question is whether altered stimulation is the only relevant difference between provocative and nonprovocative situations. We believe that it is not. We discuss other differences that may underlie motion sickness.

In sensory conflict theory (as in all inference-based theories of perception) the relationship of sensory stimulation to the real world is indeterminate or probabilistic. We argue that patterns of stimulation of perceptual systems (J. J. Gibson, 1966) are lawfully related to properties of the animal-environment system and, hence, that they provide veridical information about it. We use the term *animal-environment system* because we view the interaction between the animal and the environment as a closed-loop system. That is, the behavior of the

animal affects its relationship to the environment, and the relationship of the animal to the environment affects the animal's behavior (J. J. Gibson, 1979/1986; Riccio & Stoffregen, 1988).

Patterns of intermodal stimulation make available information about properties of the environment that influence the control of behavior. In addition, the control of action is influenced by the goals of the animal. We have argued that environmental dynamics and the goals of behavior interact to constrain the control of posture (Riccio & Stoffregen, 1988). We believe that a theory of motion sickness must take into account these constraints on behavior.

We begin by examining, and rejecting, the hypothesis that stimulation of perceptual systems is ambiguous with respect to the world. We argue that changes in sensory stimulation do not cause motion sickness. This leads us to consider a new approach to motion sickness; one that concentrates on the control of action.¹ Our approach to the control of action is influenced by theories of behavior in adaptive nonlinear systems (Kugler, Kelso, & Turvey, 1980, 1982; Kugler & Turvey, 1987; Saltzman & Kelso, 1987). Many of the concepts and terms in our analysis are unrelated to those of inference-based theories of perception. Our terminology is discussed at length by Riccio and Stoffregen (1988).

SENSORY CONFLICT DOES NOT EXIST

We have emphasized that the existence of sensory conflict is hypothetical; it is an interpretation of facts, rather than a fact itself (Stoffregen & Riccio, 1991). The concept of sensory conflict derives from the assumption that stimulation of perceptual systems is ambiguous or nonspecific with respect to physical reality. In the traditional view, the separate sense organs are believed to be sensitive to independent frames of reference; it is further believed that there is a competition among reference frames in that they often suggest incompatible states of the animal or the environment (e.g., Nashner & McCollum, 1985; D. E. Parker & K. L. Parker, 1990). It is these incompatibilities that are believed to cause conflict. We have argued that animals are not sensitive to competing reference frames (Stoffregen & Riccio, 1988). The stimulation of a single sense organ can be ambiguous with respect to relative motions of the animal and the environment. However, the pattern of stimulation across sense organs may not be ambiguous with respect to such motions.² This suggests that nonredundant

¹The possibility of an alternative to the conflict hypothesis vitiates claims that the existence of motion sickness constitutes evidence for the computation or existence of sensory conflict (e.g., Oman, 1982, pp. 21, 22).

²In our analysis we concentrate on information that is available as an emergent property (Stoffregen & Riccio, 1988) in patterns of stimulation across different perceptual systems. However, information about the animal-environment system may also be available in the stimulation of

patterns of multimodal stimulation can be viewed as complementary rather than as conflicting.

We have presented explicit examples (Riccio & Stoffregen, 1988; Stoffregen & Riccio, 1988, 1991) showing that patterns of intermodal stimulation provide veridical information about these relative motions (cf. J. J. Gibson, 1966). These include the perception of orientation and motion on a variety of natural surfaces, within vehicles such as aircraft, and in weightlessness. We have stressed that the information in these patterns is different from that available to individual perceptual systems (it is an emergent property). We have further argued that these intermodal nonredundancies are objective properties of stimulation that are determined by the dynamics of the animal-environmental system (Riccio & Stoffregen, 1988; Stoffregen & Riccio, 1988, 1991; cf. J. J. Gibson, 1979/1986). Finally, we have reviewed data indicating that changes in environmental dynamics that give rise to nonredundant patterns of intermodal stimulation result in adaptive changes in behaviors such as standing, walking, and running (Riccio & Stoffregen, 1988; Stoffregen & Riccio, 1991).

This discussion should not be taken as implying that some intermodal patterns can be complementary whereas others are conflicting (such a suggestion might be advanced to account for the existence of nonredundancy in both nonnauseogenic and nauseogenic situations, or to discriminate between natural and laboratory situations). There is no principled basis for permitting the conclusion that some nonredundant patterns are conflicting whereas others are complementary. The hypothesis of intermodal specificity is incompatible with the traditional assumption of ambiguity in intermodal stimulation: Patterns of stimulation must be either always specific to their source or always ambiguous with respect to their source. We have argued that the total pattern of stimulation across perceptual systems is always specific to the actual animal-environment interaction (Stoffregen & Riccio, 1988; cf. J. J. Gibson, 1966; Stoffregen, 1990); this implies that intermodal specificity exists in provocative as well as nonprovocative situations. If intermodal specificity exists, then variations in stimulation across systems do not entail conflict that must be "resolved"; instead they constitute veridical information about the world. Within the epistemology of direct perception, no meaningful concept of sensory conflict exists.

The preceding analysis serves to shift attention away from sensory inputs in

individual perceptual systems. In the ecological approach to perception and action, the distinction between unimodal, multimodal, and intermodal availability of information is secondary. What is primary is the information itself, that is, specificity in the various patterns of energy to which the animal is sensitive (J. J. Gibson, 1966). We emphasize emergent properties in intermodal stimulation because this kind of information is largely neglected in other treatments of motion sickness. Comparisons between stimulation of different perceptual systems are common in the motion sickness and spatial orientation literatures, but these comparisons do not address emergent properties in the relations between stimulation of different systems. For example, Howard (1982, p. 444) explicitly excluded emergent properties from his discussion of "intersensory judgments."

discussions of motion sickness. Sensory conflict theory implies that there is something wrong with sensory stimulation in provocative situations. Our analysis implies that the accuracy or utility of stimulation is no different in provocative situations than it is in nonprovocative situations. The locus of the "problem" in motion sickness must be sought elsewhere. In the ecological approach to perception and action, the interaction between the animal and the environment is the fundamental unit of analysis; neither can be examined separately. In the following sections we argue that changes in stimulation in provocative situations are accompanied—in fact determined—by corresponding changes in the ways in which the environment constrains the control of posture. We begin by discussing general constraints on postural control.

MOTION SICKNESS AND THE CONTROL OF ACTION

Constraints on the Control of Posture

Many factors influence the outcome of our interactions with the environment. Although most of these are related to specific environments or behaviors (i.e., reading rate, running speed, etc.) one factor has a universal influence on animal-environment interactions. This is the control of posture: "behavior depends on posture and is inseparable from it" (J. J. Gibson, 1975, cited in Reed & Jones, 1982, p. 389; cf. Belen'kii, Gurfinkel', & Pal'tsev, 1967). In general, perturbation of any single body segment will induce perturbations in all contiguous segments (exceptions, such as rigid restraint, are discussed later). Postural control is thus fundamental to all other action. The extent to which a perturbation will be transmitted across body segments is influenced by the relative mass of the segments. Perturbations of low-mass segments (e.g., fingers) will have relatively small effects on high-mass segments such as the trunk, whereas uncontrolled motion of the trunk will have large effects on body segments of lower mass. This means that control of the torso will have general effects on behavior.

We define *posture* as the overall configuration of the body and its segments (cf. Norkin & Levangie, 1983) and *postural control* as the coordinated stabilization of all body segments (Riccio & Stoffregen, 1988). Control of the body and its segments across perturbations serves to maintain desired (i.e., goal-specific) configurations. In addition, control serves to minimize motions that degrade or interfere with perception and action. What factors influence the control of posture? We have argued that the goals of perception and action set the criteria for the outcome of all control actions, that is, that postural control is evaluated in terms of its consequences for other behaviors (Riccio & Stoffregen, 1988). This assumption has profound implications for theories about posture, from sensorimotor control to primate phylogenesis. For example, different static and

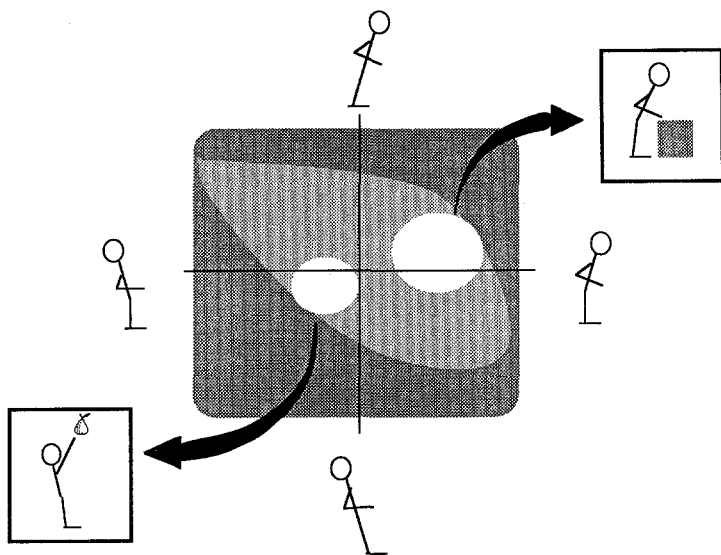


FIGURE 1 A configuration space that represents the relation between postural control and interactions with the environment (cf. Nashner & McCollum, 1985; Riccio & Stoffregen, 1988). The darkly shaded area represents hip-ankle configurations for which bipedal stance is not possible. The lightly shaded area represents configurations for which stance is possible but for which neither of the two goals (depicted in the insets) are achievable. The unshaded areas represent the configurations for which each goal is achievable.

dynamic body configurations are optimal for different behaviors or goals (Figure 1; cf. Dainoff & Mark, 1989; Riccio & Stoffregen, 1988). Moreover, the *raison d'être* for the postural capabilities of various species (e.g., primate bipedalism) may be the behaviors that different postures afford (Iwamoto, 1985; Morbeck, 1979; Robinson, 1972; Rose, 1979; Tobias, 1982; Tuttle & Watts, 1985).

The control of posture (and of perception and action in general) will also be constrained by the dynamic and static-structural properties of the environment (McCollum & Leen, 1989; Riccio & Stoffregen, 1988; Stoffregen & Riccio, 1988; cf. Horak & Nashner, 1986; Zacharkow, 1988).³ Different environments will constrain action in different ways. In the general case this should be obvious. We stand differently on ice than we do on concrete. Variation in friction of the surface of support influences the control of stance (and of other behaviors, such as walking and throwing). Changes in control on icy surfaces are adaptive: If we attempt to stand on ice in the same manner in which we do on concrete we may fall down. Another relevant contrast is between environ-

³A third class of constraints on the control of action arises from the dynamic properties of the animal's own body (Kugler & Turvey, 1987; cf. Riccio & Stoffregen, 1988).

ments that are stationary and those that are not. On stationary surfaces, muscular action at the ankle joint is effective for the control of body sway (provided that the surface is rigid and extensive; Stoffregen & Riccio, 1988). One effect of muscular action at the ankles is to stiffen the ankle joints. This stiffening can be disadvantageous when the surface of support is moving with respect to the animal (e.g., when standing on a heaving ship). In such a situation, ankle stiffness will tend to promote transmission of ship motions to the body. As a result, changes in the orientation of the ship will give rise to changes in orientation of the body. This induced body-tilt can be reduced by reducing stiffness at the ankle joint, that is, by relaxing the muscles that act on this joint. This will necessitate a different strategy for the control of body sway, such as muscular action at the hips, or stepping, staggering, and so on. (For a fuller discussion of the ways in which environmental dynamics constrain the control of action, see Riccio & Stoffregen, 1988; Stoffregen & Riccio, 1988.)

In the example of the heaving ship, the role of environmental dynamics in constraining the control of posture is explicit. Implicit in this example is the goal of maintaining upright stance. The simultaneous influence of goals and environmental dynamics is made more explicit in the following example. Consider a situation in which a vehicle is tilted with respect to the gravito-inertial force vector (e.g., in automobiles during turns on unbanked roads, or in aircraft during wind buffeting or sideslip, or when banked turns are improperly controlled). In general, occupants of the vehicle will attempt to maintain the torso in alignment with the gravito-inertial force vector rather than with the vehicle; this minimizes the effort required to control orientation. Occupants may also attempt to maintain orientation with respect to an object of regard (e.g., a dashboard or cockpit instrument); this maximizes monitoring performance. The net effect will be a tilt of the body with respect to the vehicle, and a simultaneous tilt of the head with respect to the body. The head and body tilts will be in opposite directions. This "opposite tilt" strategy is consistent with two goals; it maximizes monitoring performance while minimizing effort.⁴ If an occupant were not looking at anything (if the eyes were closed), head orientation would not be constrained by the requirements of visual stabilization. Control would be constrained only by the minimization of effort. Such a person could use a different strategy; both the head and body would be aligned with the gravito-inertial force vector (Sesek & Riccio, 1989). It follows that postural control strategies must take into account both changing environmental condi-

⁴We use the term *strategy* to describe a pattern of coordination and control of body segments that has as its end the facilitation of perception and action. In relating the means to the end, a control strategy relies on the coordinated pickup of information by various perceptual systems, that is, on intermodal relationships that specify the states of the animal-environment system. See Riccio and Stoffregen (1988) for details. Control strategies are not equivalent to templates or expected patterns of sensory stimulation. Neither are they equivalent to "scripts," "schemata," or other constructs in cognitive psychology.

tions and the goals of behavior (Riccio & Stoffregen, 1988; cf. McCollum & Leen, 1989).

Postural Stability and Instability

Posture is useful only to the extent that it is stable (J. J. Gibson, 1966). We have defined postural stability as the state in which uncontrolled movements of the perception and action systems are minimized (Riccio & Stoffregen, 1988). Actions that minimize uncontrolled movements require effort, such that in the absence of effort many postures are unstable. However, animals actively resist disturbances so as to maintain a given posture; they are dynamically stable. We assume that animals attempt to maximize efficiency in controlling postures, that is, that they strive to achieve a control strategy in which minimum energy is expended in the achievement of a stable body configuration that is consistent with the goals of perception and action (Figure 1).

Animals succeed in controlling their posture in a wide variety of situations. In addition, they can often adapt almost immediately to changes in environmental conditions that give rise to temporary instability and a decrement in perception-action performance. The adaptation should be reflected in an asymptotic approach or return to a level of perception-action performance that is consistent with the animal's goals (Figure 2a). In our view, the improvement in performance (learning) is characterized by increasing perceptual differentiation of the novel dynamics. It is noteworthy that this is consistent with recent developments in systems engineering which reveal that exponential convergence on a veridical model of system dynamics is a fundamental requirement for the robustness of adaptive control algorithms (Canudas de Wit, 1988; Chalam, 1987). In adaptive control theory, exponential convergence requires persistent excitation (i.e., wide-bandwidth activity) that aids system identification rather than immediate control of the system's states (Canudas de Wit, 1988; Chalam, 1987). Similarly, animals may exploit instability (uncontrolled movement) that results from a change in the dynamics of the animal-environment system to identify the new dynamics, and to reestablish an appropriate control strategy (cf. Newell, Kugler, van Emmerik, & McDonald, 1989; Riccio & Stoffregen, 1988).

When changes in dynamics are large or abrupt, or when we attempt a behavior for which we lack control strategies, we may lose control entirely (Figure 2b). When this occurs, behavior ceases; we fall down, fall off a bicycle, and so on. This kind of instability is brief and self-limiting. That is, there is a transition from a state of passive instability, in which control is required (e.g., standing on ice skates) to a state of passive stability, in which control is not required (e.g., lying down; Figure 2b). It is possible for postural stability to be degraded rather than lost outright. Until adaptive control (i.e., exponential convergence) is achieved, the animal will be in a state of postural instability

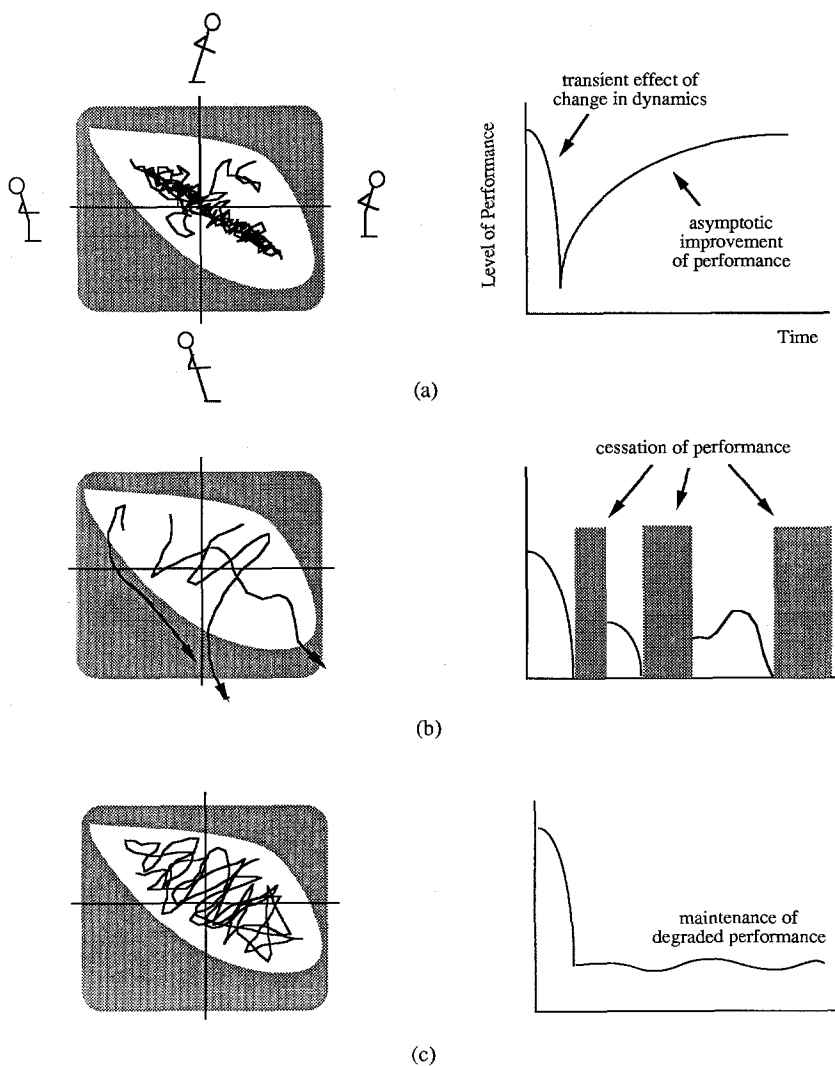


FIGURE 2 Adaptive control of posture represented in an hip-ankle configuration space and an associated performance time-history. (In this case, performance might be described in terms of the magnitude of perturbations for which stance can be maintained.) Performance drops after a change in the dynamics of interaction with the environment. (a) The original performance level is approached asymptotically as the animal discovers the control actions appropriate for the new dynamics. (b) Performance may be terminated if adaptation is not quick enough (in this case, cessation of performance results in a fall). (c) Performance may be maintained at a degraded level (i.e., without adaptation). In our view, this is the requisite condition for motion sickness.

(Figure 2c). In this condition, the animal is functionally insensitive to the relation between the new dynamics and its own performance. That is, the dynamics are not perceived in terms of their consequences for performance. Despite this, the animal may be sensitive to the boundary conditions for performance, in which case control might be characterized by gross movements such as ballistic avoidance of these boundaries (Figure 2c; cf. Martin, 1990).

We have argued that there are frequent changes in environmental dynamics and that altered dynamics dictate changes in the control of posture. Until situation-specific control is achieved, the animal will be in a state of postural instability. When adaptation is not rapid, we often simply terminate behaviors that are affected by the instability, which in turn terminates the instability itself. Alternately, we may lose control of a suprapostural task without falling over (goals are nested, such that failure to achieve superordinate goals may not lead to failure with respect to subordinate goals; Figure 3a). Frank loss of control generally reduces demands on postural control; in such cases stability is regained but true adaptation does not take place. For some behaviors, such as reading and surgery, demands on the precision of postural control are high; accordingly, postural instability can be induced by relatively small perturbations. The demands on postural control are less stringent for other behaviors. To the extent that an animal can vary the goals of behavior, then, these instabilities are under its own control. Thus, to maintain stability in a novel environment we may choose to relax our goals (Figure 3b), or we may choose to change our goals qualitatively by terminating the behavior (Figure 3c). In both cases instability will be brief.⁵

We are sometimes unwilling to terminate certain behaviors (e.g., trying to operate instruments in orbit, where the cost of each person-hour exceeds \$100,000.00, or struggling to maintain control of a high performance aircraft, where survival is at stake). In many more common situations (e.g., vehicular travel, amusement park rides, or the workplace) we are unwilling or unable to terminate our interactions with the environment, even when the dynamics of these interactions are disturbingly unfamiliar. In such situations there is not an outright loss of postural control, yet the unadapted animal is unable to terminate a state of instability. This can occur if we fail to perceive the new dynamics or if we are unable to assemble and execute the control actions that are appropriate for the new dynamics. In such situations we maintain performance at a degraded level, and we are exposed to a prolonged instability that we normally would not tolerate (Figure 2c). Another reason that we may tolerate instability, particularly if it is subtle, is that it may provide information about the underlying dynamics of our interaction with the environment. Thus instability can be both a tool for adaptive control (e.g., persistent excitation) and an indication of failure in adaptive control (e.g., lack of exponential convergence).

⁵This suggests that animals may be able to perceive the presence of instability. We argue later that there are patterns of stimulation that specify the presence of postural instabilities.

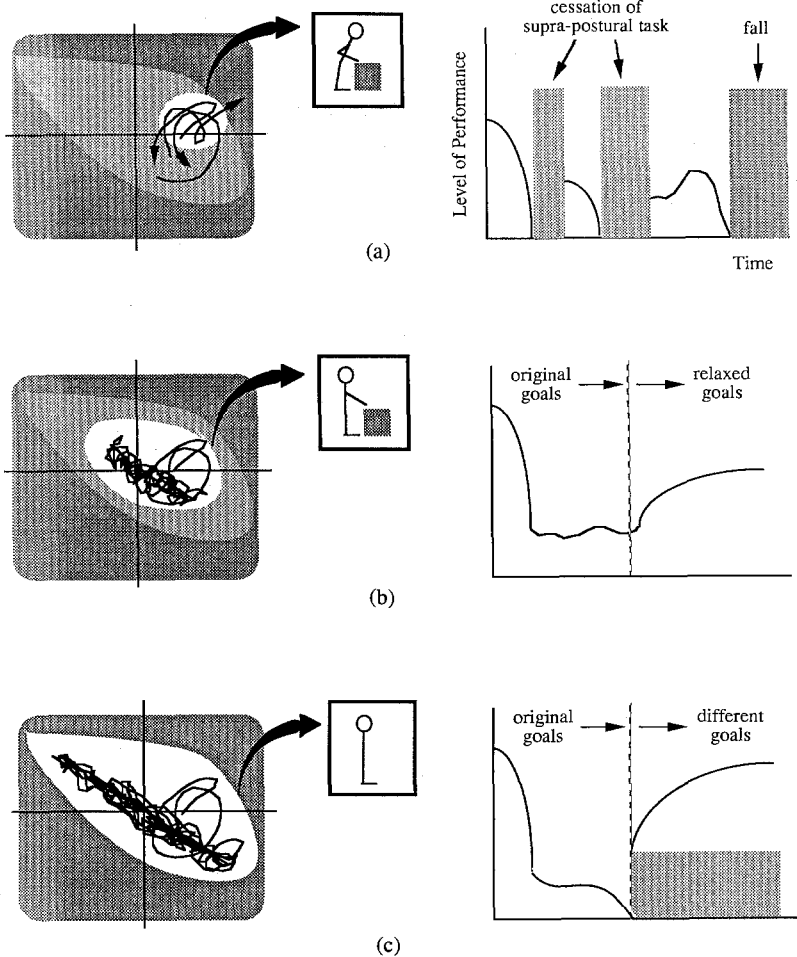


FIGURE 3 Effects of postural instability on interactions with the environment (cf. Figure 2). (a) The animal may be incapable of maintaining the configuration and stability necessary for the task. Attempted performance on the task may have deleterious consequences for performance on a subordinate task (e.g., maintaining balance). (b) The animal may accept a reduced level of performance that is within its capabilities for postural control. (c) If performance on a task is impossible without the risk of additional instability, the animal may cease performance on the task while maintaining performance on a subordinate task. The shaded area is the region in which control would have been lost if goals had not been altered.

The Cause of Motion Sickness

We believe that prolonged postural instability is the cause of motion-sickness symptoms. That is to say, we believe that postural instability precedes the symptoms of motion sickness, and that it is necessary to produce symptoms. The

data suggest to us that the severity of motion sickness will scale directly to the duration of postural instability: The longer you are unstable, the greater the likelihood and intensity of symptoms. Symptoms may also scale directly to the magnitude of instability (if it is possible to develop a metric for the magnitude of instability). Our claims relating symptoms to postural instability are data based. Oman (1982) took a similar position in relating sensory conflict to the production of symptoms. We do not know why the symptoms of motion sickness are what they are. Our theory accounts for the existence of symptoms, but not for their nature.

As already noted, instabilities of the trunk will tend to have a greater destabilizing effect on posture than instabilities of less massive body segments. Uncontrolled eye movements (gaze instability) are empirically related to motion sickness, but obviously do not have this mechanical linkage. Rather, this relationship results from an informational linkage. Overall body posture is strongly influenced by optical stimulation (Lee & Lishman, 1975). Uncontrolled eye movements interfere with pickup of the relevant information, and so can induce instabilities in body posture. If postural instability were precluded (e.g., through passive restraint of the body) we would expect that uncontrolled eye movements would not be associated with motion sickness.

We do not become sick when control is lost outright (i.e., when we fall down) because the event is brief. Similarly, instability will be brief (and of low magnitude) when it is under the animal's own control, that is to say, when the animal can either exit the destabilizing environment (e.g., by stepping back off an icy surface) or can terminate behaviors that are affected by ongoing instability (e.g., reading in an automobile). However, the instability that obtains in these cases is not qualitatively different from that found in actual motion-sickness situations. This suggests that animals should be able to make themselves sick (in otherwise nonprovocative environments) by voluntarily entering and maintaining states of postural instability. This is consistent with the fact that we can make ourselves dizzy—for example, when dancing, or through vigorous head movements. It further suggests that motion-sickness symptoms form a continuum rather than being an all-or-none phenomenon.

We noted earlier that reductions in demands on postural control should reduce the incidence or severity of motion sickness. Examples are closing the eyes, resting the head, and lying down. By contrast, Benson (1984) reported that susceptibility is reduced when participants are required to perform some tasks. However, the nature of the tasks was not reported. Tasks such as mental arithmetic, which do not involve any perception-action interaction with the environment, do not make demands on postural control, and so should not induce sickness. Such tasks may actually reduce susceptibility if they curtail other behavior. By contrast, tasks that make demands on perception-action interactions with the environment, such as visual search, often increase susceptibility (Benson & Guedry, 1971; Guedry, Benson, & Moore, 1982).

Demands on control can also be reduced through passive stabilization (through the use of seat-belts, head-restraints, etc.). The limiting case of postural control would be the complete elimination of demands on perception and action, that is, the abandonment of all goals. It should be obvious that this will be rare, especially in imposed motion environments, where physical safety depends on control of body motion. Short of death, demands on control will be eliminated entirely only when passive stabilization is complete. This is discussed in a later section of this article.

We have argued that postural instability will be present in many situations that are commonly believed to give rise to sensory conflict. For this reason, it may seem that our use of *postural instability* is not importantly different from the traditional use of *sensory conflict*. However, there are crucial differences between the two terms. Nonredundant stimulation (which is believed to give rise to sensory conflict) is no more common when animals are unstable than when they are stable. In addition, there are many nonprovocative situations in which stable animals are exposed to stimulation that should give rise to conflict. We have discussed some of these (Stoffregen & Riccio, 1991), such as static discrepancies between reference frames, and the experiments of Fox, Daunton, and Coleman (1982) and Graybiel (1980); others are discussed later. In general, mismatch between current inputs and stored expectations (the central assumption of the conflict theory) can occur when a system is passively stabilized. Hence, such mismatch is distinct from postural instability.

In addition, we have argued (Stoffregen & Riccio, 1991) that expectations that are the referent for the calculation of conflict are, in principle, unmeasurable. Insofar as this is true, the sensory conflict theory of motion sickness is not scientifically falsifiable. By contrast, we argue that postural instability is an objective, measurable phenomenon. Finally, and most important for us, the concepts of postural instability and sensory conflict are based on fundamentally different epistemologies, these being direct and mediated perception, respectively (cf. J. J. Gibson, 1979/1986; Stoffregen & Riccio, 1988).

PROVOCATIVE ENVIRONMENTS

We have claimed that prolonged postural instability is the cause of motion sickness. We argued that such instability is absent in nonprovocative situations. In this section, we argue that prolonged instability is present in known motion-sickness situations. We have divided these into classes that we believe reflect different sources of postural instability (cf. Oman, Lichtenberg, Money, & McCoy, 1986). By contrast, previous classifications of the provocative stimulus have focused on "categories of motion cue mismatch" (Benson, 1984), such as visual-vestibular and canal-otolith conflict. Our classification of instability

sources makes it possible for us to make predictions about susceptibility across situations and about the transfer of adaptation across situations. These are discussed in a later section of this article.

Low-Frequency Vibration

Body sway provides information about the efficacy of postural control strategies. Common strategies for the control of human standing posture result in concentration of power below 1.0 Hz (Dichgans & Brandt, 1978). Imposed motions in this frequency range may result in (a) impoverished feedback about postural control or (b) entrainment of postural control actions (to the imposed motions). These effects could lead to postural instability. Instability will persist until a new (adaptive) strategy is learned. Consequently, we predict that imposed motions of this kind should be nauseogenic. Data from laboratory experiments (Guignard & McCauley, 1982, 1990; O'Hanlon & McCauley, 1974) and sea travel (Lawther & Griffin, 1986) are consistent with this hypothesis. High-frequency vibration will have a smaller disruptive effect on postural control. In general, the degree of disruption will be a function of the degree of similarity between the ranges of imposed and natural motion. The nauseogenic properties of a given imposed motion should vary accordingly (Boff & Lincoln, 1988, sect. 10.4; cf. National Aeronautics and Space Administration [NASA], 1987, sect. 5.5).

Imposed motion along any axis will produce torques on various segments of the body. This is because of nonalignment between or among the centers of mass and the bases of support of the various body segments. Varying the axis of imposed motion will produce different patterns of torque. Some patterns of torque may be more likely than others to produce instability. In principle, biomechanical models could be used to make specific predictions about the nauseogenic properties of different axes of imposed motion. A study of seasickness by Lawther and Griffin (1986) suggested that motion in the vertical (z -axis) is especially provocative. However, interpretation of these correlational data is not straightforward because the axes of the imposed motion were not experimentally controlled.

Bipedal locomotion is characterized by low-frequency oscillation of the head and body. This oscillation is generated by the animal and is normally under its control. However, the patterns of stimulation to which this motion gives rise can be separated or decoupled from the physical oscillation, at least in part. This could be done, for instance, if a stationary participant watched a videotape that had been made by a camera attached to the head or torso of a walking person. The optical oscillations in the videotape, while natural in and of themselves, would not be related to the viewer's behavior, and so postural adjustments in response to them would tend to be destabilizing. Such videotapes might thus be expected to be nauseogenic.

It is important to note that nauseogenic frequencies correspond to the

frequencies of postural control, rather than to the resonant frequencies of body segments. The resonant frequencies of the body and its major segments are an order of magnitude higher (NASA, 1987, sect. 5.5). This underscores our argument that it is disruption of control that is relevant to motion sickness.

We believe that low-frequency vibration is the central cause of motion sickness in fixed- and rotary-wing aircraft, and in terrestrial and nautical vehicles (cars and ships). Low frequency vibration is present and persistent in all these vehicles (Boff & Lincoln, 1988, sect. 10.4).

Weightlessness

Motion sickness has been conspicuous in orbital flight, that is, in weightlessness (Matsnev et al., 1983; Oman et al., 1986). In weightlessness, the body is not subjected to externally imposed motions. This has led some researchers to question whether orbital symptoms reflect true motion sickness (cf. Oman et al., 1986). We believe that orbital symptoms stem from postural instability, and therefore that they do reflect true motion sickness. We further believe that the nauseogenic properties of weightlessness can be traced to the dynamics of the weightless state. In weightlessness, there is no sustained force relation between animals and surfaces. This means that the control of posture (and of behavior in general) will be qualitatively different in weightlessness from what it is under terrestrial conditions. On earth, self-generated forces on body segments are resisted by the surface of support. In space, self-generated forces are not resisted.⁶ They tend to propagate through the body until they are damped by muscle tension and/or joint viscosity. Because of this, postural movements that are stabilizing on earth will be destabilizing in weightlessness. It is well known that in space even a simple head turn can cause motion of the entire body. For unadapted animals these body motions will be uncontrolled, that is, unstable. An immediate means of coping with this is simply to reduce the amount of motion; this has been observed in astronauts (Oman et al., 1986). Reestablishing the stability of motion will depend on the development of qualitatively different control strategies—the grossest example being that in weightlessness body posture and orientation must be controlled with the hands rather than the feet.⁷ Some techniques for control of gross body motion in weightlessness are reviewed in Boff and Lincoln (1988, sect. 10.1001; cf. Homick, Reschke, & E. Miller, 1977; Lestienne & Gurfinkel, 1988).

⁶In small spacecraft (e.g., Mercury, Vostok) astronauts are generally restrained (i.e., pressed against the spacecraft). This means that their self-generated forces are resisted by the spacecraft. This may account for the fact that motion sickness in such craft is much less common than in spacecraft in which astronauts are unrestrained.

⁷The alteration in control strategies that this mandates is reflected in an increase in the mass of arm muscles relative to leg muscles in astronauts on long flights (Nicogossian & J. F. Parker, 1982, p. 190).

Simultaneous rotation in two different axes gives rise to coriolis forces in a third axis of rotation (and to neural cross-coupling). For example, a person that executes a head movement in pitch during rotation around the z -axis experiences simultaneous torque in both pitch and roll axes. Motions involving coriolis forces are known to be highly nauseogenic under terrestrial conditions. On earth, an unrestrained animal must actively balance its head. Under the influence of coriolis forces control strategies that normally produce stable pitch movements will throw the head into instability in the roll axis, and vice versa. Postural instabilities, and hence motion sickness, should not be surprising. The destabilizing effect of coriolis motions will be greatly reduced in weightlessness where the head and body do not need to be maintained in a state of balance. This may account for the observed immunity of adapted astronauts to extreme coriolis motions (Graybiel, 1980).

Changing Relationships Between the Gravito inertial Force Vector and the Surface of Support

Sustained changes in the magnitude of the gravito inertial force vector are rare. Much more common are situations in which there is a changing relationship between the direction of this vector and the surface of support. This occurs to some extent during any locomotor or vehicular acceleration (e.g., starting or stopping a car or train); these changes are typically brief. However, some vehicles, maneuvers, and laboratory devices are characterized by a rapidly changing relationship between the gravito inertial force vector and the surface of support. Examples are roller coasters, slow-rotating rooms, and certain flight maneuvers, such as rolls in high-performance aircraft, or parabolic flight.⁸ We believe that such changes are veridically specified in changing patterns of stimulation (cf. J. J. Gibson, 1966). In addition, the changing dynamics of such situations will give rise to changing constraints on the control of action. For instance, in a slow-rotation room (Graybiel, Clark, & Zarriello, 1960) the tangential velocity varies as a function of the distance from the axis of rotation. A person walking outward from this axis will be subjected to a continuously increasing tangential velocity. In essence, a slightly different control strategy will be needed for each step in such a walk. Different constraints will also operate on motion in different planes within a single position. It is therefore not surprising that adaptation to movements in such rooms can be "direction-specific" (Graybiel & Knepton, 1972).

⁸At the apex of the parabolic maneuver there is a period of weightlessness. For this reason, parabolic flight is sometimes referred to in discussions of motion sickness as a "zero gravity maneuver" (e.g., Kellogg, Kennedy, & Graybiel, 1965). This characterization assumes that the nonweightless portions of the maneuver are irrelevant to motion sickness. We reject this assumption.

Altered Specificity

In the ecological approach, linking perception and action is fundamental to behavior (in this respect our approach is similar to control-theoretic aspects of the conflict theory; e.g., Oman, 1982). We have argued that patterns of stimulation that are relevant to the control of posture are wholly determined by the dynamics of the animal–environment system. We have discussed numerous examples in which changes in such patterns result solely from changes in the dynamics of the environment. Altered patterns of stimulation can also arise from changes in the responsiveness of perceptual systems, or from other changes in stimulation that are not related to environmental dynamics. This occurs, for example, when prisms or lenses are placed before the eyes. It might be argued that such changes result in the loss of specificity between patterns of stimulation and the dynamics of the animal–environment system (a loss of specificity might give rise to conflict; Stoffregen & Riccio, 1991). We believe that there is a change in specificity rather than a loss. That is, we believe that the veridical specification of the system is preserved across such changes. In these situations some animal–environment interactions will be specified by different patterns of stimulation than previously. Similarly, some patterns of stimulation will be specific to new animal–environment interactions. A pattern of coordinated control that was linked to a given pattern of stimulation may be inappropriate given the change in specificity. Accordingly, unstable control may result until new patterns of specificity are detected.

Not all transformations will be equally disruptive of control. The greatest disruptions will occur when patterns of stimulation for which the animal already has control strategies no longer correspond to situations for which those strategies are appropriate (adaptive). Reversing prisms drastically alter the directions of change in optical stimulation that result from applied forces. This is a simple yet fundamental change that can quickly drive a system into instability, because it produces situations in which a visually guided controller would do the exact opposite of what he or she should be doing. It is thus not surprising that the wearing of such prisms is highly nauseogenic. The fact that such nausea diminishes, and performance recovers, over time (Dolezal, 1982) indicates that the optical transformation alters but does not destroy specificity of stimulation.

In fixed-base simulators, there are optically specified accelerations and rotations that are unrelated to constraints on control of the body. Consequently, postural control strategies that are linked to these optically specified events will be inappropriate. For example, one may exert muscular effort to resist an optically specified acceleration or tilt. Because the relationship of the body to the gravito-inertial force vector has not actually changed, this effort will give rise to an unintended and uncontrolled divergence of the body from the state of balance. We would expect that the greatest disturbances in postural control would be engendered by optically specified motions in the range of postural

control frequencies. Motion sickness has been reported in "moving rooms," which are specifically designed to induce perturbations in standing posture (Lestienne, Soechting, & Berthoz, 1977; Lishman & Lee, 1973; Stoffregen, 1985). We believe that this results from altered specificity in a manner similar to that found in flight simulators. In moving rooms, global optical motion is uncorrelated with movements of the body relative to the direction of balance. Accordingly, postural adjustments based on the optical stimulation will be inappropriate, and will tend to induce instability.

It could be argued that altered specificity constitutes sensory conflict. However, our account of motion sickness in these situations does not depend on the existence of any expectations within the animal, such as are required for the existence of conflict (Stoffregen & Riccio, 1991). Postural instability will result whenever an animal links its control to patterns of stimulation that have ceased to be specific to those environmental conditions for which the control is appropriate.

THE CONSEQUENCES OF INSTABILITY

We have argued that prolonged postural instability is the cause of motion sickness. This claim is data based. We have stressed the consequences of postural stability for perception and action in general (Riccio & Stoffregen, 1988). These consequences, called affordances (J. J. Gibson, 1979/1986), are what are ultimately relevant to the success or failure of an animal's interactions with the environment. Accordingly, the perception of affordances, and their exploitation by the animal, is of paramount importance.⁹ Thus, there exists a logical link between our theory of motion sickness and our theory of postural control. For this reason, we believe that motion sickness reflects perception of the consequences of instability for perceiving and acting, that is, the perception of affordances of instability (cf. Gibson, 1979/1986). We have argued that the instabilities that are relevant to motion sickness are those relating to the control of posture (Riccio & Stoffregen, 1988; cf. J. J. Gibson, 1966).

Certain combinations of environmental, organismic, and task constraints can lead to postural instability. Instability can be a consequence of a particular postural control strategy, yet a given situation may also lead to stable posture, provided that other strategies are available. The detection of instability should lead the animal to seek out opportunities for stable posture in a given situation. In this section, we discuss the existence of information about postural instability, and its pickup by animals.

⁹An existing instability has consequences for possible behaviors that might be engaged in by the animal. Perception is based on an existing state (instability), but the perception is of what is possible in the future given the existing state.

Information Available in Patterns of Postural Motion

Changes in the dynamics of the animal–environment system have consequences for control. These consequences should be detected by the animal. If they are not, control will become unstable (if it is not lost entirely). We view instability as a fault in the system that the animal needs to detect and correct. In this and the following section, we discuss the detection of instability. A later section discusses correction (adaptation). Detection depends on the existence of lawful relations between characteristics of a system's behavior and the stimulation of perceptual systems; that is, detection depends on the existence of patterns of stimulation that are uniquely related to dynamic properties of the animal–environment system. We believe that such lawful relations exist for stability/instability; that is, we believe that there is information about the stability or instability of posture. This is consistent with our argument that intermodal patterns of stimulation are always specific to the dynamics of the animal–environment interaction. We have argued that intermodal patterns of stimulation provide information about stable postural activity (Riccio & Stoffregen, 1988). The absence of such patterns should not be construed as implying the absence of information about postural activity. There is always some pattern of intermodal stimulation at any given moment. Insofar as all patterns are determined by the dynamics of the animal–environment interaction, any pattern that does not specify some form of postural stability must, of necessity, be specific to (informative about) some form of instability.

The utility of information about instability cannot depend on comparison of current behavior with expectations. Such a comparison would assume that the animal already has accurate knowledge of system dynamics. Yet it is ignorance of these dynamics that often leads to instability. Because they were based on ignorance (i.e., failure to pick up the available information), mismatch with such expectations would not be related to stability in any simple fashion. This means that an unexpected behavior would not necessarily be unstable. What follows is a speculative list of possible sources of information for instability. The list is speculative because, in general, instability in adaptive nonlinear systems is not yet well understood (Canudas de Wit, 1988; Chalam, 1987; Szebehely, 1984). It is critically important to note that the sources of information discussed here are equally available to the animal and to the experimenter. This means that it is possible, in principle, to objectively measure postural instabilities. This could be done, for example, through the use of body-mounted accelerometers, or with video technology that permits direct analysis of body kinematics.

There may be general characteristics of instability that obtain across a variety of dynamical systems, and hence could be said to constitute "signatures" of instability. The existence of such characteristics would permit perception of instability without need for, or reference to, any desired or expected pattern of feedback (i.e., templates).

1. One possibility is an increase in gross body motion (wobble) when one is trying to minimize motions (Figure 4). This is a common approach to the measurement of postural stability. However, there is not a consensus about which parameters of motion are relevant to stability (Goldie, Bach, & Evans, 1989). Martin (1990) suggested that the relevant parameter is one that references body motion to the boundaries of the region within which the motion can be maintained (cf. Riccio & Stoffregen, 1988).

2. Another possibility would be an hyperbolic sinusoid, a pattern of increasing acceleration that is characteristic of falling (as mentioned earlier, and in Stoffregen & Riccio, 1988). For example, over small angles, acceleration is proportional to tilt or lean (Figure 5); the rate of falling is also determined by the dynamics of the body. This may account for the nauseogenic properties of uncontrolled low-frequency sinusoidal motion. Presumably, high-frequency sinusoids are not as provocative because the pattern of accelerations in them is not specific to uncontrolled falling; the changes are more rapid than those of falling.

3. Instability could be specified by a reduced coherence between postural motions and movements of the arms, for example, of the surface of support, or in the optic array (Figure 6). This could indicate a reduced sensitivity of the postural-control system to perturbations (cf. Johansson, Magnusson, & Akesson, 1988; Maki, 1986).

4. Instability could be indicated in higher order moments of the amplitude distribution of postural motion (Figure 7; cf. Newell & Hancock, 1985). One example is skewness, or asymmetries in sway (especially asymmetries that

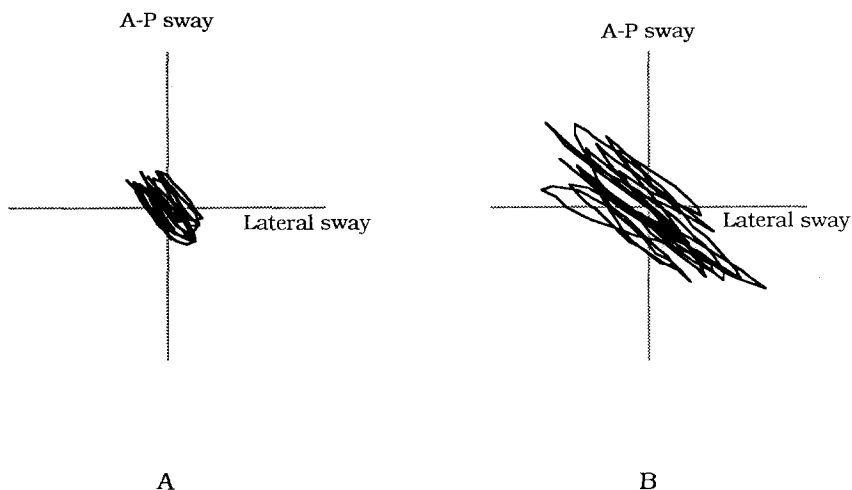


FIGURE 4 Hypothetical path of the center of mass in the horizontal plane (anterior-posterior, A-P, sway and lateral sway). In some situations, stability is related to the area covered by the center of mass. Stability is greater in (A) than in (B) if the goal is to minimize movements of the center of mass.

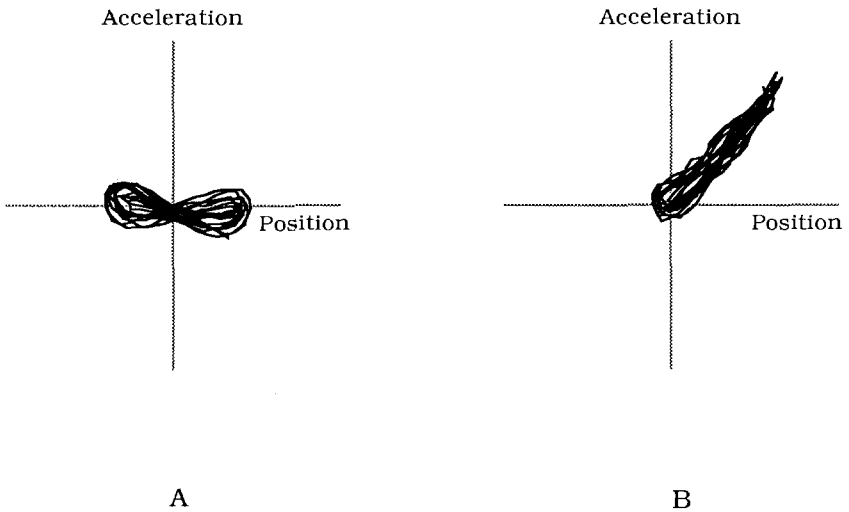


FIGURE 5 Hypothetical relation between acceleration and position of the center of mass. (A) Stable posture is characterized by a particular pattern of covariation in these parameters. (B) Unstable posture may exhibit a pattern that is characteristic of a passive inverted pendulum (i.e., falling over).

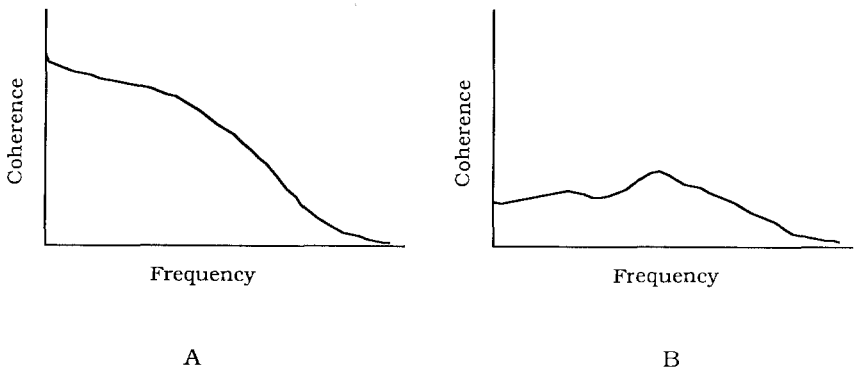


FIGURE 6 Hypothetical correlation between potential postural disturbances (i.e., variation in the body or the environment) and movements of the center of mass as a function of frequency. The shape of this coherence spectrum is determined by the observability of postural disturbances and by the controllability of the body. (A) Stable posture is characterized by higher coherence at the lower frequencies where controllability is greater. (B) Coherence at these frequencies is relatively low when inappropriate control actions lead to unstable posture.

increase over time). Another is kurtosis, the flatness or peakedness of the distribution, with flat distributions containing relatively more large-amplitude (emergency) motions. High concentrations of large-amplitude motions would also give rise to multi peaked distributions.

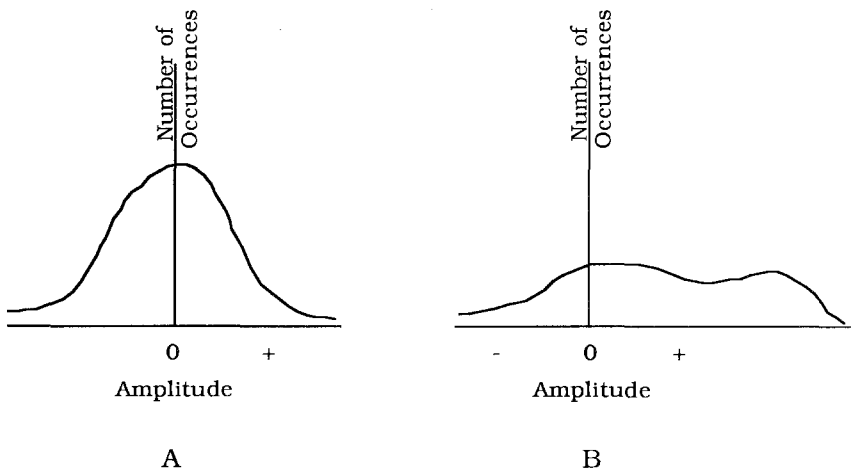


FIGURE 7 Hypothetical distribution (histogram) of movement amplitudes. (A) Stable posture is characterized by an approximately Gaussian distribution. (B) Unstable posture includes more large-amplitude movements and more movements in one direction (+) than the other (-).

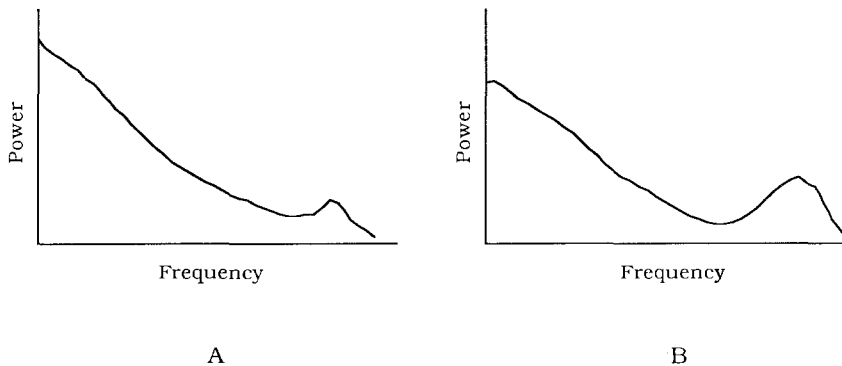


FIGURE 8 Hypothetical power spectrum for movements of the center of mass. (A) Stable posture is characterized by a concentration of activity at low frequencies; however, *physiological tremor* can reveal itself in a narrow band of higher frequencies of movement (e.g., at 8 to 12 Hz). (B) *Physiological tremor* may be enhanced during unstable posture.

5. Prolonged instability and the effortful attempt to overcome it could lead to systematic changes in the amplitude or frequency of physiological tremor (Figure 8; cf. Akamatsu, Hannaford, & Stark, 1986; Stein & Oguztoreli, 1978; Young, 1984).

Other signatures for instability could derive from the fact that postural control involves the coordination of multiple degrees of freedom, such as joints, axes, or derivatives of motion.

6. We noted earlier that there is a tendency of instability to spread across joints. Spreading instability will reduce coordination among the degrees of freedom involved in movements (i.e., among body segments). This would mean that more parameters or dimensions would be needed to describe unstable postural motion (e.g., the movement of the head may not be correlated with movement of the torso). Thus instability should be reflected in measures of dimensionality, such as the fractal dimension (cf. Kay, 1988; J. B. Myklebust & B. M. Myklebust, 1989; J. B. Mykelbust, Prieto, B. M. Myklebust, & Lang, 1990). Increased dimensionality gives rise to characteristic patterns in low-dimensional relationships to which the animal may be sensitive (Figure 9:) Stable postural control is characterized by a high degree of coordination (low degrees of freedom).

7. Instability might be revealed in the covariation among motions in multiple degrees of freedom. For example, paths or trajectories of the center of mass in the horizontal plane may be different when posture is unstable (Figure 10; cf. van Emmerik, 1990; Tokita, Miyata, Matsuoka, Taguchi, & Shimada, 1976).

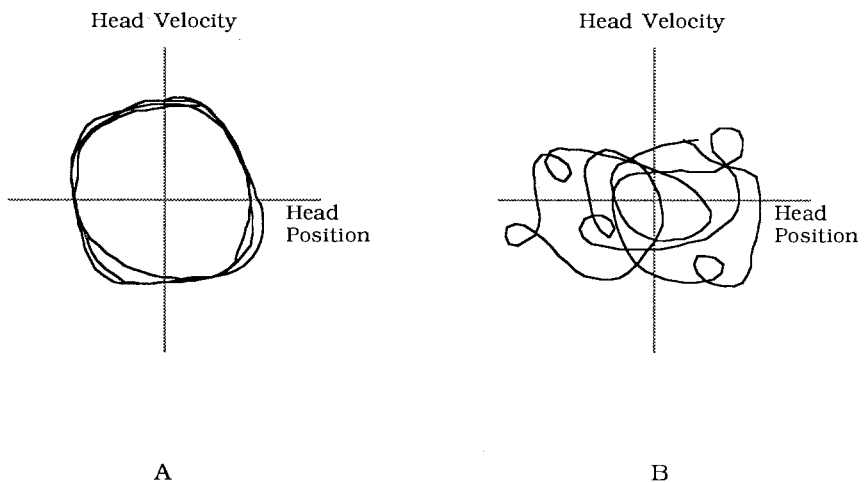


FIGURE 9 Hypothetical relation between position and velocity of the head (i.e., phase plane for head movements). (A) Stable posture is characterized by a low-dimensional pattern (e.g., a limit cycle) in which phase-plane trajectories do not overlap in any single cycle. (B) A higher dimensional pattern of overlapping trajectories and nested limit cycles may be revealed for unstable posture if movements of the head, torso, and legs are not coordinated.

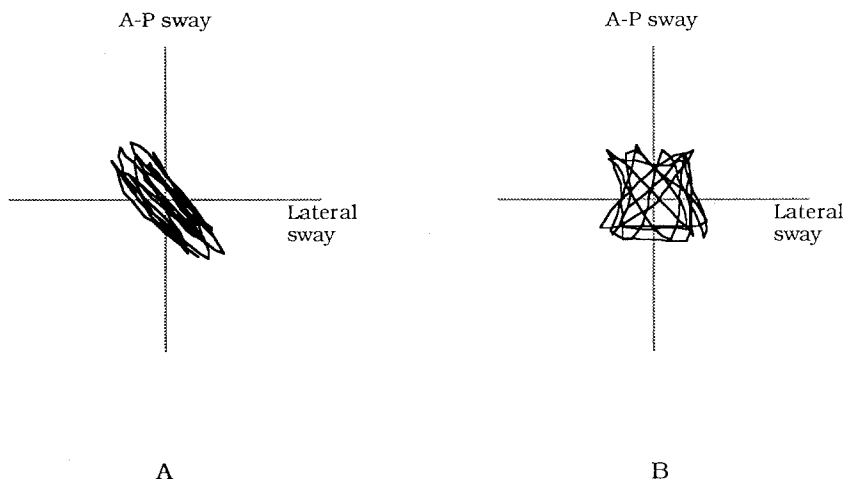


FIGURE 10 Hypothetical relation between movements in different axes. (A) Stable posture is characterized by particular paths of the center of mass in the horizontal plane (i.e., predominant orientations of line segments or trajectories). (B) Orientation of trajectories may be more variable, or simply different, during unstable posture.

8. Systems are less stable at the boundaries of patterns of coordination (Schoner & Kelso, 1988). Instability is indicated by increasing variability in the phase relation among the various degrees of freedom involved in movement. The relation between ankle and hip motions, for example, may become more variable as posture becomes unstable (Figure 11; Ko, Riccio, & Newell, 1990).

9. Finally, postural instability could be specified by the way in which the postural control system resists or responds to perturbations (Figure 12). This information might be available in the amount of time or action required to reverse the effect of a perturbation, that is, in the relaxational characteristics of the system (Schoner & Kelso, 1988).

Our list of sources of information for postural instability is speculative. It should be noted, however, that the speculative nature of the list does not diminish the validity of the logical connection that we have established between motion sickness and postural instability. We have identified a broad range of situations over which the occurrence of motion sickness appears to be related to factors that should influence postural stability. This allows us to establish a logical link despite the current lack of consensus on the definition and measurement of postural stability.

The Pickup of Information for Postural Control

We have argued that prolonged postural instability is a necessary condition for motion sickness. Implicit in our analysis is that detection of prolonged instability

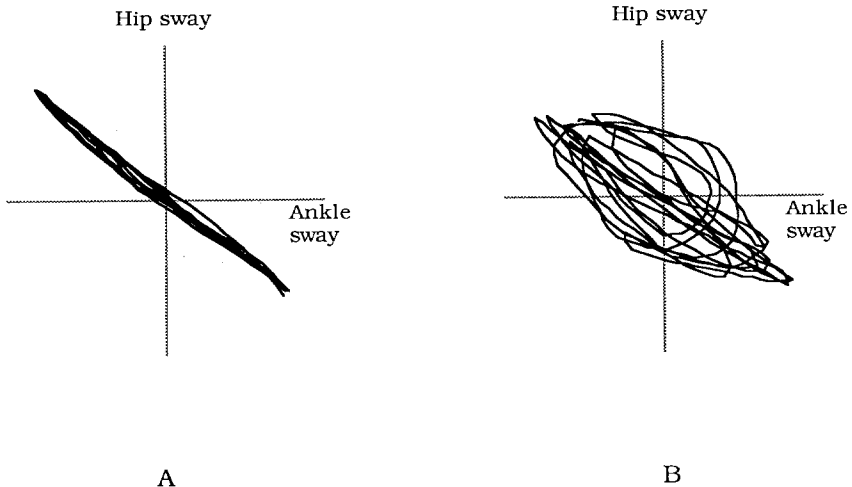


FIGURE 11 Hypothetical relation between movements at different body joints. (A) Stable posture is characterized by a consistent phase linearity, that is, a linear relation between the amplitudes of two movements because of a consistent phase relation. (B) The relation between the amplitudes of postural movements will vary if the phase relation varies; phase variability may be indicative of a breakdown or change in the pattern of coordination.

is both a necessary and sufficient condition for motion sickness. That is, an animal will become sick if and only if it picks up information about prolonged postural instability. However, we believe that it would be virtually impossible to create a situation in which instability could be prolonged without pickup of information about the instability. This is because instability can be prolonged only if it can be maintained within bounds that are consistent with the behavioral demands of the animal. Failure to pick up information about instability should lead to a complete loss of control and a cessation of the behavior. Stated in control-theoretic terminology, instability is controllable only to the extent that it is observable; furthermore, observability and controllability are required for a system's behavior to be bounded. As already mentioned, an animal may not be able to minimize (i.e., completely control) instability even though it has the instability under partial control. Complete control implies that the animal can adapt to (achieve stability over) changing conditions by picking up information about the change in conditions (i.e., information about the dynamics of its interaction with the environment). Thus prolonged instability generally will indicate that information about instability has been picked up by the animal, but also that information about the dynamics of the interaction with the environment has not been picked up.

Postural instability is useful only to the extent that it provides information

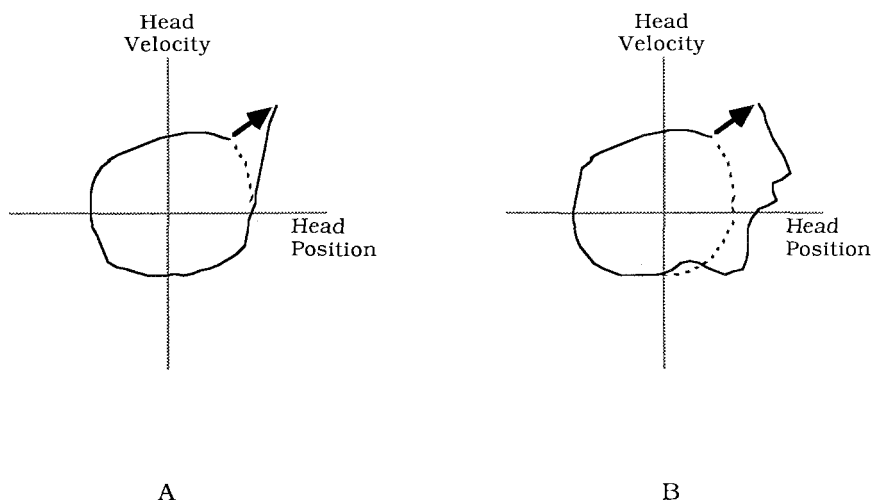


FIGURE 12 Hypothetical responses to perturbation represented in the phase plane for head movements. The position and velocity of postural movements can be changed by self-produced or imposed forces (represented by arrow in figures). (A) Stable posture is characterized by a quick return to the original pattern of movement. (B) Responses to perturbations may not be efficient or expedient during unstable posture.

that is relevant to postural control, for example, information about the dynamics of the animal's interaction with the environment. In this section, we discuss two ways in which animals may fail to pick up information for postural control. One of these concerns situations that have been designed to be misperceived. The other concerns the general role of the vestibular system in the pickup of information about postural activity.

The fact that specificity exists in stimulation does not necessarily mean that it will be detected by the animal (J. J. Gibson, 1979/1986; Neisser, 1976; cf. Becklen & Cervone, 1983). This is particularly true in situations that have been designed to be perceived in a nonveridical manner, such as simulators. Yet intermodal stimulation may still be specific to the simulator as such, rather than to the simulated vehicle. From the point of view of the designer, the success of the simulation will depend on the extent to which the operator fails to pick up the information that specifies the simulator as such, that is to say, the extent to which the operator controls the simulator as if it were the real vehicle. However, the properties of the environment that constrain control of the operator's body are those of the simulator (including the gravito-inertial force vector), not of the simulated vehicle. Accordingly, effective control of the body (detection and minimization of postural instability) in simulators will depend on detection of the constraints imposed by the forces and surfaces in the simulator.

A person in a simulator is thus confronted with two independent tasks; he or

she must control the simulator as if it were the actual vehicle (i.e., control it with respect to the simulated force environment), but the person must control his or her own body with respect to the actual force environment. In the latter task, the person needs to ignore or "see through" the simulation, whereas for the former he or she must perceive it as such (i.e., perceive and respond to that-which-is-simulated). Stimulation specifying the simulator as such will be made available through the operator's attempts to control his or her body. The likelihood that this information will be picked up can be reduced by reducing its relevance to the person. Passive restraint (for example) reduces the need for control (stabilization) of the body and so reduces the relevance to the person of information for the simulator as such. Hence passive restraint of the operator should increase the fidelity of the simulator with respect to vehicle control, but it may decrease fidelity with respect to control of the body within the vehicle. This may influence transfer between the simulator and the real vehicle (cf. Brown, Cardullo, Sinacori, & Riccio, *in press*).

It is commonly believed that an intact vestibular system is a prerequisite for susceptibility to motion sickness. This is because it is difficult or impossible to induce symptoms in labyrinthine-defective (LD) animals in many of the situations in which labyrinthine-normal animals do display symptoms. The apparent immunity of LDs does not fit comfortably into extant explanations of motion sickness. It is sometimes hypothesized to stem from a privileged connection between the vestibular organs and "vomiting centers" elsewhere in the nervous system (Oman et al., 1986; but cf. A. D. Miller & Wilson, 1983). The data on LDs are compelling. However, in our view they are not definitive. We reserve judgement because data on patterns of movement are not reported in studies of LDs. Such data are important because of the possibility that LDs may remain stable in situations in which intact participants become unstable. The vestibular system plays an important role in the control of movement; this is consistent with the reduced motor-control capabilities of LDs (Fregly, 1974). Adaptation to these limitations should lead LDs to avoid behaviors or movement strategies that they are no longer able to control. This could mean that LDs behave differently from normals in provocative situations (this need not imply that they move less). It would be premature to assign a definitive role to the vestibular system until this possibility has been evaluated empirically.

We have taken a conservative course in drawing conclusions about the centrality of the vestibular system for motion sickness. Despite this, there are reasons to believe that the vestibular system may play an important role in the detection of instability. The vestibular system is exquisitely sensitive to patterns of linear acceleration and angular motion. It should therefore be sensitive to many of the subtle patterns of motion referred to in the previous section. In particular, the relations between canal and otolith stimulation would be ideal for picking up information about coordinated movements around multiple body joints. This is because the relationship between angular and linear motions is

determined by the distance of the sensor from the axes (joints) of rotation. Hence stimulation of the vestibular system is specific to motions of different body joints (when such motions influence motion of the head) and to their effect on stability of the head.¹⁰ This will be the case for movements of the neck, torso, and legs when a person is in contact with a surface of support (i.e., under terrestrial conditions). This information is also available to the visual system. Unfortunately, data on visual sensitivity to axes of body rotation (i.e., the joints about which the body rotates) are not available. Unlike the vestibular system, the visual system does not have readily identifiable transducers that are specially suited to pickup of this important information. It should be noted that feedback to the vestibular system (and the visual system) about bodily movements will be dramatically altered in weightlessness. This will compromise control of the body in unadapted animals. It is also important to note that LDs do not exhibit multiaxis control of stance (coordinated bending at the ankles and hips) under conditions in which such coordination is observed in intact individuals (Black, Shupert, Horak, & Nashner, 1988). Instead, they confine their control to one axis of rotation (the ankles) even when this results in their falling over.

Information for instability may also be available intermodally, as emergent properties in patterns of stimulation across perceptual systems. This follows from our belief that intermodal stimulation is important in the coordinated control of movement in general (Riccio & Stoffregen, 1988). The importance of intermodal stimulation would not necessarily preclude a central role for the vestibular system in motion sickness. This could occur if vestibular stimulation were part of the intermodal patterns that were specific to instability.

Postural Control and Passive Restraint

Our analysis of the data suggests that motion sickness in truly passive animals is rare (cf. Daunton, 1990). This is consistent with our claim that prolonged postural instability is required for motion sickness. In this section, we discuss the relationship between the information for postural instability and the consequences of that information for actual control by animals.

Perception is goal directed; animals pick up information that is relevant to the control of behavior (that has consequences for the activities in which they are engaged). We have argued that the control of posture is fundamental to all behavior, that is, to all perception-control interactions with the environment. Accordingly, information for postural instability will be continuously relevant. The only exceptions to this rule would be situations in which postural stability

¹⁰From an ecological point of view, coordinated patterns of linear and angular motion are more fundamental than each considered separately. For this reason we regard as unfortunate the fact that the vast majority of vestibular research has considered these motions independently. For an exception, see Parker, Reschke, Arrott, Homick, and Lichtenberg (1985).

did not depend on the animal's own activity, that is, if the animal were passively stable. Such passive stability can be achieved by complete relaxation, but only when there is no relative motion between the animal and the environment. When there is relative motion, passive stability can be achieved only through full restraint (or through water immersion, which is discussed later). It is possible to present fully restrained animals with information for postural instabilities (e.g., in optical flow patterns, or by moving the restraining device). It might be argued that such presentations should lead to motion sickness. However, in this situation the information for instability would no longer have any relevance to the animal's behavior; a fully restrained animal is incapable of control. This situation would therefore constitute a breaking of the fundamental link between perception and action. In such situations information for postural instability might be available, but we predict that it would not be picked up by the animal—that the animal would not perceive itself to be unstable. Accordingly, we predict that motion sickness cannot be induced under conditions of full passive restraint.

In the real world, complete restraint of most animals is impractical or impossible; the fleshy parts of the body prohibit rigid restraint. This means that some body mobility will always be present. The range of such mobility will be very small, but it may be large enough to lead to skeletal strain (principally of the spine) under conditions of high acceleration. These strains are nontrivial; they can give rise to discomfort or damage. They can be minimized by the animal's own muscular effort, such as the Valsalva maneuver (Norkin & Levangie, 1983), or co-contraction of flexors and extensors of the neck (if this does not give rise to easily observable motions, it may be necessary to use electromyography to detect the attempted control). Because the animal is able to exert some control over its body, information specifying this type of body motion will be relevant. This suggests that it may be possible to produce motion sickness in not-quite-fully restrained animals. However, it is not clear whether instabilities of this kind would be sufficient to produce motion sickness.

In our view the "stimulus" for such sickness will be different from that in unrestrained animals. The instabilities that are possible in these conditions are quite different from those found in unrestrained animals. One difference is in the frequencies at which the motions are concentrated. The instabilities of restrained humans will be in the range of the resonant frequencies of various body segments (4 to 8 Hz; Boff & Lincoln, 1988, sect. 10.4). As noted earlier, these resonant frequencies are much higher than those of postural control in unrestrained humans. This allows us to predict that vibration-induced motion sickness in restrained persons, if it is possible at all, should be found only with vibrations in this higher range. By contrast, all versions of conflict theory would have to predict that a participant restrained in a device would become sick if the participant produced a low-frequency oscillation (< 1.0 Hz) of the device (through manual control). In experiments in which participants produced

motions of this type we have observed no incidence of motion sickness (Riccio, Martin, & Stoffregen, 1991).

The vestibulo-ocular system can be disrupted following extreme vestibular stimulation. For example, after prolonged high-velocity rotation, the eyes often move spontaneously in a pattern that is referred to as postrotary nystagmus (PRN). This eye movement is not perceived as such; the failure to pick up information about eye movements can result in an inappropriate use of optical stimulation for the control of posture. Disrupted postural control following rotation is well known. We believe that this postural instability is responsible for motion sickness in these situations. In other words, we believe that vestibulo-ocular instability is not a sufficient condition for motion sickness: Motion sickness should result only if vestibulo-ocular instability leads to instability of body posture. This could be tested by inducing vestibulo-ocular instability in persons who were under maximum restraint. When the body is restrained, the vestibulo-ocular and postural systems are decoupled; accordingly, vestibulo-ocular instability would have no consequences for postural stability.¹¹

INFLUENCES ON STABILITY

In general, stability will be determined by the characteristics of the environment and the control skills of the animal (Riccio & Stoffregen, 1988). In this section, we discuss those characteristics of environments that promote stability. We also discuss characteristics of adaptive control systems that promote the detection and exploitation of postural control strategies that promote stability.

Stabilizing Environments

Environments differ with respect to their consequences for postural stability. For example, a person is more stable when seated in a chair than when seated on a stool. The degrees of freedom of movement are reduced by leaning against the back of the chair. The degrees of freedom can be further reduced by strapping the torso to the chair back. Increasing restraint could be added, up to the point where the person was completely immobilized. As mentioned in the previous section, we believe it would be difficult, if not impossible, to induce motion sickness under such conditions. However, complete immobilization is not a satisfactory prophylactic measure for most operational situations, in which the person must be able to move.

Stabilization need not be achieved at the expense of freedom of movement. For example, stability should be increased by performing tasks while lying down.

¹¹We have informally observed that the dizziness associated with PRN is reduced if one is quickly immersed in water (attains neutral buoyancy) after rotation.

For this reason, we predict that simulator sickness will be reduced or prevented if the cockpit of the simulator is oriented so that the operator (pilot) is lying on his or her back.

During water immersion, each body segment is directly supported by the water's buoyant forces. This is because the body is naturally close to a state of neutral equilibrium with respect to water. In addition, motions of the body and its segments are damped by the viscosity of water.¹² For these reasons, posture requires minimal active stabilization in water, and hence motion sickness under water should be extremely rare. This is consistent with the fact that people can be very active under water without incurring motion sickness.¹³ Passive stabilization under water is complete when the body is at neutral equilibrium. In principle, water immersion could be used as a prophylactic measure in a wide variety of provocative situations, such as orbital flight (we realize that water-filled space vehicles would be prohibitively expensive). By contrast, the absence of motion sickness under water should be a serious problem for the sensory conflict theory, as we have argued elsewhere (Stoffregen & Riccio, 1991).

Behavior in Provocative Situations

We have argued that posture, and hence postural stability, are fundamental to all behavior. In adapted animals, postural stability is directed toward facilitating other behaviors in which the animal is engaged; stable posture affords such behaviors (Riccio & Stoffregen, 1988). Postural instability is characteristic of the unadapted state. The fundamental influence of posture on all behavior means that suprapostural behavior will be degraded by instabilities in posture. Instability can be reduced by "relaxing" into a postural control strategy that is more stable. Such alternate strategies may be incompatible with particular suprapostural performance goals. In such cases, instability will be reduced at the expense of other goals. For example, astronauts have been observed to wedge themselves into corners; this stabilizes the torso at the expense of mobility. A pilot may stiffen his or her body in a simulator; this maintains postural stability, but it may reduce capabilities for looking around, reaching, and so on. LDs may

¹²In this respect, the dynamics of water differ dramatically from the dynamics of weightlessness. In neutral buoyancy under water, the body is always passively stable. In weightlessness, passive stability obtains only when there is no relative movement among body segments. We believe that this accounts for the differing nauseogenic properties of weightlessness and water immersion. Stiff pressure suits, such as those worn outside spacecraft, can also damp body motions, thereby increasing passive stability. We are not aware of any reports of motion sickness during extravehicular activity, even when EVA occurred soon after entry into orbit (e.g., Skylab II).

¹³Motion sickness might be possible under water if an animal attempted tasks that made high demands on the positioning and timing of high-amplitude high-velocity movements (an example might be synchronized swimming; I. Rovegno, personal communication, September 1990). In such cases, the viscosity of water might not be sufficient to stabilize the body.

lie down rather than be thrown around on a heaving ship. Finally, after prolonged rotation a participant may close his or her eyes to eliminate the destabilizing effects of PRN; this obviously compromises visual activity. In general, people at risk for motion sickness often experience a desire to "stop what they're doing." Motion sickness is attenuated or absent when this is permitted.

An alternative is to pursue performance at the expense of postural stability (examples of this were given earlier), to engage in behaviors for which posture is unstable. Motion sickness occurs under these conditions. Such conditions are also problematic in other ways. The fundamental dependence of behavior on posture means that performance will be degraded when posture is unstable. This implies that there will be decrements, though not necessarily cessation, in performance on suprapostural tasks. Successful completion of tasks may take longer, for instance, or involve greater error rates. Improvements in performance will occur only when the animal learns a new pattern of coordination for which posture is stable. This implies that while instability is a sufficient cause for susceptibility it may not be a sufficient cause for adaptation, because instability can be reduced simply by reducing demands on performance. Adaptation occurs only when there are demands on control, because it is only under such circumstances that new control strategies are necessary.

We have suggested that the utility of control strategies is influenced by dynamics of the animal-environment system. Accordingly, the reestablishment of stability will depend on detection of the ways in which control is influenced by novel dynamics. Exploration of the altered environment is an important part of this learning process. Exploration involves probing the animal-environment state space for novel characteristics, that is, discovering the consequences of both old and new patterns of coordinated movement (Riccio & Stoffregen, 1988; cf. Bingham, Schmidt, & Rosenblum, 1989; E. J. Gibson, 1987; Newell et al., 1989). This exploratory activity may reveal stable regimes in the state space that have been created by changes in the dynamics of the animal-environment system. Exploration can be more or less systematic, and more or less intentional. In this context, postural instability may actually serve a useful role by "moving" the animal around in the state space. Thus, instability serves to generate new patterns of movement among body segments. By doing so, it can make information available to the animal. This scheme for "systems identification" does not depend on comparisons of current inputs with expectations (Kugler & Lintern, in press).

In most cases, exploration will reveal new patterns of movement that can achieve given goals (rare exceptions to this are discussed next).¹⁴ One example of

¹⁴Two additional outcomes are possible. A given goal can still be achieved using a previously effective pattern of movement, in which case no adaptation is necessary for that goal. More interesting, there will be cases in which new goals become possible, in which patterns of movement (and hence the goals that they subserve) that were previously impossible become possible. Astronauts have discovered new and useful movements that are possible only in weightlessness (Cooper, 1976).

this is the acquisition of "sea legs" by mariners, as discussed earlier. Another is learning new coordinated patterns of eye, head, and (possibly) body movement to facilitate looking around: In space one may learn to avoid high-velocity head movements that would perturb the body, and hence the direction of gaze. Strategies involve not only coordinated patterns of movement but also the pickup of information (Riccio & Stoffregen, 1988). Earlier, we discussed the fact that the operator of a flight simulator must learn that "movements" of the simulated vehicle do not have consequences for postural control. For example, optically specified vehicular accelerations do not have consequences for body balance. The operator must learn to decouple postural control strategies from vehicular control strategies.

A person that has adapted to a flight simulator will have learned that optically specified (for example) motions do not have consequences for postural control. This may give rise to postural instabilities when the person leaves the simulator and reenters the world in which such motions do have postural consequences (Hettinger, Berbaum, Kennedy, Dunlap, & Nolan, 1990), for instance, during the drive home. Similar problems are sometimes observed in other cases in which adapted persons have returned to previously nonprovocative situations, such as *mal de débarquement* following sea or space voyages. These "aftereffects" indicate that adaptation to provocative situations can have consequences for behavior which transcend the symptoms of motion sickness. Adaptation solves problems in the provocative situation, but can create problems for return to the original environment.

It is well known that the operators of vehicles are less susceptible to motion sickness than passengers. This is true despite the fact that both operator and passenger are subjected to the same motions of the support surface (the vehicle). Some of these motions are the product of the operator's control. Because the operator is generating the motions, he or she can anticipate their perturbing effects on posture and can coordinate postural control with respect to them (coordination is advantageous because postural instability can also degrade the operator's ability to control the vehicle). These motions cannot be anticipated by passengers. Accordingly, they will tend to induce postural instabilities in the passengers. Any uncontrolled motion of the vehicle will perturb the posture of its occupants; for passengers, all movements of the vehicle are uncontrolled, whereas for the operator only a subset of vehicle motions are uncontrolled.

Situations in Which Adaptation May Be Impossible

There may be situations in which stabilizing control strategies are not available to the animal. In some situations, a task can place constraints on posture that exceed the animal's ability for coordinated control (within a given environment). It may be that such tasks require a degree of postural stability that simply is not possible given the environmental constraints (e.g., imposed motion or

insufficient support). In such cases, attempts at task performance will exceed the limitations of the animal-environment system. This will inevitably lead to postural instability, and may lead to positive feedback, such that control actions magnify the instability rather than reducing it. This is a logical implication of our analysis for which data are not currently available. One situation that may fit into this category is "workstation sickness" (Morrissey & Bittner, 1986). Poorly designed workstations may force users to exceed their postural control capabilities. This may result from the person's being forced by the workstation into an inherently unstable body configuration. Alternately, the chair may provide insufficient support. Another possible example is attempting to read while riding in a car. Anecdotal reports suggest that adaptation in this situation is difficult, and may be impossible. Sensory conflict theory has not generated any hypotheses about situations in which animals would be unable to adapt to motion sickness. It is not clear how the conflict theory would account for such situations.

Susceptibility Across Situations and Individuals

Our analysis allows us to suggest principles for predicting susceptibility or adaptation across situations. Susceptibility should be related to the similarity of dynamic constraints across situations. This includes the way in which the environment resists forces imposed on or generated by the animal, but it also includes the characteristics of the body. That is, both environmental and body dynamics must be considered. In addition, our analysis of behavior in provocative situations indicates that one must take into account specific postural demands. This suggests that there will be an interaction between the dynamics of the animal-environment system and the goals of behavior. For example, there may some transfer of adaptation between cars and airliners, two low-frequency vibration regimes in which people assume a seated posture. We would expect less transfer between cars and ships. Both of these are low-frequency vibration regimes, but different behaviors are observed; in cars we sit, whereas on ships we frequently stand and walk. Although such gross postural differences may have a measurable influence, a more powerful influence may be the degree to which similar postural demands are made by different suprapostural tasks. For example, adaptation to being a passenger in an aircraft would not necessarily transfer to being a crew member (e.g., a navigator), insofar as these different roles lead to different demands on postural coordination.

The dynamics of the animal-environment interaction may be less important in situations of altered specificity. Alterations in specificity do not alter the actual dynamics of the animal-environment system. Consequently, adaptation in such situations may be independent of these dynamics; that is, it may generalize across different dynamical regimes. Consider the case of flight simulation. We noted previously that operators of flight simulators must learn that

information in optical displays is not useful for maintaining balance. In principle, this could be learned in situations outside a specific simulator. This might happen in other (less expensive or more accessible) vehicle simulations, or in any device in which the optical surround is moved independently of postural sway (e.g., Stoffregen, 1985).

Schemes for "preadaptation" to orbital flight are based on the assumption that weightlessness gives rise to altered specificity (D. E. Parker et al., 1985). We have argued that weightlessness is not characterized by altered specificity. This is because there is a genuine difference in constraints on the control of posture in weightless and terrestrial environments. Accordingly, the success of preadaptation programs will depend on the extent to which the dynamics of weightlessness can be mimicked on the ground. Appropriate preadaptation programs might include situations in which people execute head movements in pitch while lying on their side with the head supported (D. E. Parker & K. L. Parker, 1990). In this situation, pitch movements of the head are not constrained by the dynamics of balance. Because of this, control strategies for such movements may closely resemble those that would be appropriate in weightlessness, provided that the headrest does not resist the pitch movements (e.g., if it rests on ball bearings). This could be extended to situations that would place the entire body in neutral equilibrium. This is desirable because, in weightlessness, movement of any body segment will tend to perturb the entire body, thus requiring the animal to develop entirely new patterns of coordination. Neutral equilibrium could be achieved, in at least one axis, using magnetic levitation. During magnetic levitation, a supine person would be neutrally stable in the body's roll axis. The constraints on movement in this axis would be essentially identical to those of weightlessness, and so control strategies developed in this situation should show good transfer to the orbital environment. Neutral equilibrium can also be achieved underwater, but this is not a viable option for the present application. This is because the viscosity of water leads to constraints on movement that differ dramatically from those that obtain in weightlessness; different control strategies will be required in the two environments. The presence of motion sickness in weightlessness and its absence underwater underscore the different behavioral constraints that obtain in these two environments.

The susceptibility of an individual will be a function of his or her ability to maintain or reestablish postural stability in a given situation. Our analysis implies that people who are more susceptible will be less stable in provocative situations. Interest in individual differences stems from a desire to predict susceptibility in situations to which a given person has not previously been exposed. This will depend on the choice of a test situation whose environmental, organismic, and task constraints are similar to the situation in question. Analyses should evaluate the type and degree of postural control exhibited in the test situation. Only then will we have a basis for making predictions about

the extent to which the person can maintain postural stability in the new situation.

POSTURAL INSTABILITY AND DYNAMICAL DISEASES

We have proposed that motion sickness is caused by prolonged instabilities in the control of posture. We have suggested that, in the context of the perception and control of action, animals should be considered as adaptive nonlinear systems. Our analysis bears important similarities to recent work in which physiological processes are mathematically modeled as nonlinear systems (Glass & Mackey, 1988). In particular, our account of motion sickness, although developed independently, is compatible with the notion of dynamical diseases in adaptive nonlinear control systems (Mackey & Milton, 1987). Two common premises are that stability and instability are qualitatively different patterns of activity in dynamical systems, and that they have functional consequences at more global levels of analysis. Another similarity is that instabilities are not always self-limiting, but can be sustained pathologies in a system's behavior. Mathematical models of dynamical diseases are also important for our approach because they imply that analyses of instability (e.g., our speculative list of sources of information for postural instability) need not necessarily be ad hoc. In principle, the details of behavior in provocative situations are predictable.

In this article, we have argued that the details of action are of fundamental importance to an understanding of motion sickness. Not all approaches to the details of action will reveal the ways in which action is constrained by the dynamics of the animal-environment system. We have noted some similarities between our approach to motion sickness and the linear-control-theoretic approach adopted by Oman (1982). However, it can be argued that the assumptions of linear control theory are too restrictive. For example, we have emphasized the difficulties in differentiating "signal" from "noise" on the basis of amplitude and frequency (Stoffregen & Riccio, 1991). Mackey and Milton (1987) raised similar issues in the context of physiological systems:

a wealth of dynamical behavior ranging from periodic to irregular, noise-like oscillations can readily be observed in physiological control systems both experimentally and clinically. . . . Although many of these situations are familiar to the physiologist, the universal and fundamental aspects of their rich dynamical fabric does not yet appear to be fully appreciated. The importance of these qualities becomes more evident when it is realized that relatively simple nonlinear mathematical models have these same properties, thus implying that dynamic complexity may be the norm rather than the exception in nonlinear systems.

Our observations stress the importance of careful experimental documentation of the time-dependent behavior of physiological control systems in health and

disease, particularly in response to changes in control parameters. Such observations not only provide important insights into the nature of the underlying control systems, but also place constraints on the features that proposed models must contain. Unfortunately, it is uncommon to find published time series for physiological phenomena . . . It is quite possible that both interesting and relevant dynamical changes are often observed but not published because their significance is not fully appreciated or the dynamical changes are wrongly ascribed to environmental noise and/or experimental error. (pp. 29–30).

The approach described by Glass and Mackey (1988) may be applicable to the study of perception and action (cf. Kugler et al., 1980; Kugler & Turvey, 1987). This approach (see also, Milton, Longtin, Beuter, Mackey, & Glass, 1989) starts with mathematics and attempts to develop models which exhibit behavior characteristic of dynamical diseases. Ultimately, however, we must consider the representativeness and meaningfulness of the parameters of such models (Coombs, Dawes, & Tversky, 1973). The entities and operations in the equations should correspond to properties of the modeled system that are meaningful primitives in an explicitly described epistemology. The most meaningful level of analysis for control systems addresses the observability and controllability of system states. We have built upon an ecological epistemology (J. J. Gibson, 1979/1986) to reveal primitives that are relevant to observability and controllability in animal–environment systems (Riccio & Stoffregen, 1988; Stoffregen & Riccio, 1988). The ultimate goal should be to develop mathematical models similar to those of Milton et al. (1989). Thus, we believe that there is complementarity, and ultimately convergence, between work in nonlinear dynamics and ecological psychology (Kugler & Turvey, 1987). Both need to recognize their mutual importance so that there can be convergence on a valid and rigorous approach to perception and action.

CONCLUSION

Any satisfying theory of motion sickness must make assumptions about perception, about action, and about relations between the two. These assumptions should be general enough to be compatible with broader theories of perception and action. In this article, we have argued that prolonged postural instability is the cause of motion sickness. This hypothesis has important implications for theoretical approaches to motion sickness. If we are right, any adequate theory of motion sickness must be compatible with theories of action that motivate the formulation of testable hypotheses about instability in adaptive nonlinear systems. Such a theory must also be compatible with theories of perception that can account for the possibility of intermodal specificity, and for the pickup of information that is available in patterns of intermodal stimulation. We have

argued that the sensory conflict theory of motion sickness is deficient in all these areas (Stoffregen & Riccio, 1991). The concept of sensory conflict derives from the assumption that patterns of stimulation are not specific to properties of the animal-environment interaction. If patterns of stimulation are specific to such properties, it follows that sensory conflict does not exist. Sensory conflict theory does not motivate hypotheses about instability. This is because generated sensory conflict is neutral with respect to the animal's state of stability or instability. We have identified nonprovocative situations in which conflict should be present in the absence of postural instability (Stoffregen & Riccio, 1991).

In analyzing motion sickness, we have assumed that there is a fundamental link between perception and action. Behavior is goal directed; animals seek out information about properties of the animal-environment system that have consequences for behavior, that is, they seek to perceive and exploit the affordances of interactions with the environment (J. J. Gibson, 1979/1986). We have considered factors that constrain (have consequences for) the control of posture. These are the dynamic properties of the animal, of the environment, and of tasks in which the animal is engaged. Variations in these dynamics will influence the relative effectiveness of different strategies for the control of behavior. We have concentrated on posture because postural control is fundamental to all behavior—to any perception-action interaction between the animal and the environment. We have argued that the symptoms of motion sickness are causally related to a specific property of animal-environment interactions, namely, prolonged postural instability. The existence of postural instability depends on the ability of the animal to control its own body; an animal that is fully restrained cannot become posturally unstable. Instability also depends on the extent to which the body is passively stable in the absence of restraint; the dynamics of water do not prevent motion, but they do promote passive stability and so greatly reduce demands on the animal's own control skills.

The wide variation in dynamics across situations (principally across environments and tasks) means that brief postural instabilities should be common in daily life. In most cases these instabilities will be under the animal's control. This is primarily because the animal can vary the demands on postural control, and hence the consequences of any given instability, at will. The animal does this by varying the goals of behavior, which determine the demands on postural control at any given moment. In our view this ability is central to understanding postural instability in any given situation, and hence to understanding the incidence of motion sickness.

It will also be important for understanding susceptibility and/or adaptation across situations: We have argued that adaptation may be specific to the dynamic constraints of particular tasks within a given environment. Adaptation depends on the ability of the animal to detect the consequences of instability for

postural control. That is, the animal must detect the manner in which changes in the dynamics of the animal–environment system mandate adaptation in the control of posture. Instability will persist until such changes, and their consequences (affordances) for postural control, are detected and acted on. In order for such changes to be detected they must be specified in stimulation within or across perceptual systems. We have argued that states of postural instability are specified in patterns of sensory stimulation, and we have suggested possible sources of this information. We have also maintained that information for the dynamics of the animal–environment interaction is available in patterns of stimulation across perceptual systems. These patterns of stimulation provide veridical information in provocative as well as nonprovocative situations.

Methodological Implications of Adaptive Control

Our analysis of adaptation has important implications for the study of motion sickness (Stoffregen & Riccio, 1987). We have argued that instability (and hence susceptibility) will be influenced by the demands on postural control. These demands are in turn influenced by the suprapostural goals of the animal. The extent to which these demands are met will depend on the animal's state of adaptation, that is, on the extent to which it has learned control strategies that promote postural stability in a given environment. It follows that there is no simple relationship between the provocative environment and the incidence of motion sickness. The nauseogenic properties of any given environment will depend on the animal's attempted behavior within it.

It is therefore imperative that experimenters measure both postural control and suprapostural performance. Measures of performance alone are not sufficient. This is because a given level of suprapostural performance can result from a variety of combinations of task-related effort and postural instability. Consider the case in which a participant exhibits a low level of performance on some suprapostural task, such as compensatory tracking. On the one hand, attempted performance could be degraded by postural instability. On the other hand, the participant could opt to reduce performance in the interest of minimizing postural instability. Measures of postural instability should be sufficient to predict motion-sickness symptoms ("Is this participant going to be sick?"). However, data on postural instability alone will be insufficient for evaluating the extent to which participants have adapted to the provocative environment (and hence the extent to which they are still susceptible to symptoms: "Can this participant become sick at all in this environment?"). Consider again postural stability in the context of a compensatory tracking task. A given level of stability could result from adaptation to the nauseogenic situation, in which case tracking performance should be high. However, the same level of stability could be found in an unadapted participant who had simply reduced or abandoned performance on the task, thereby reducing demands on postural control.

We pointed out elsewhere (Stoffregen & Riccio, 1991) that measurements of body movements are rare in studies of motion sickness. Recently, some investigators have placed accelerometers on the head in provocative situations and have reported average amount of movement (Anderson, Willems, & Guignard, 1984; Oman et al., 1986). In these studies the activities of the participants were not constrained by the experimenters. Thus, we do not know the participant's postural and suprapostural task demands. For this reason, the motion data cannot be interpreted with respect to motion sickness.

Research Issues

Many research issues are implicit in the discussions that make up this article. We conclude by briefly outlining some promising areas of research that are motivated by our approach.

1. It follows from our approach that susceptibility to motion sickness should be a function of the degree of passive restraint. By contrast, sensory conflict theory would have to predict that degree of restraint would not affect susceptibility, for example, if participants in a whole-body motion device produced low-frequency oscillation (< 1.0 Hz) of the device through manual control.

2. Susceptibility should also be related to the degree of restraint of the head and torso in flight simulators: Greater restraint should lead to reduced susceptibility.

3. It is commonly believed that sensory conflict will be generated whenever an animal does not have a stored expectation that matches current patterns of input. This should occur when terrestrial animals are immersed in water. We have predicted that animals at neutral equilibrium under water should be immune to motions that lead to sickness under other conditions. This prediction should be tested. One way to do this would be to have a neutrally buoyant person execute coriolis movements under water.

4. To test our central hypothesis—that prolonged postural instability is the cause of motion-sickness symptoms—it is necessary to measure postural control in provocative situations. We predict that the incidence of motion sickness will be correlated with postural instabilities across participants and trials. These instabilities should be manifest, and hence measurable, before the onset of symptoms.

5. We have suggested that there may be characteristics of instability that are general across a wide variety of dynamical systems. This could be evaluated by measuring postural control in different provocative situations, such as weightlessness, low-frequency vibration, and flight simulators. Similar postural instabilities should be evident among participants that get sick across these situations.

6. Our analysis of the nauseogenic properties of low-frequency vibration

suggests that people may adapt to such motions simply by shifting the frequency of their postural control so that it is further from the range of imposed motions. This could be manifested in control strategies that are more jerky or intermittent than normal.

7. Our hypothesis about the characteristics of natural postural control is expressed in terms of humans. It suggests that other species could be made sick by imposing frequencies of motion that characterize their postural control.

8. Severe motion-sickness symptoms are often observed following loss of vestibular function (through disease, injury, or surgery). This is sometimes attributed to the physiological insult that causes the loss. We have suggested that adapted LDs may adopt more stable control strategies than normals. Motion sickness following vestibular loss would then reflect a period of instability while the animal acquired new control strategies that did not depend on the availability of vestibular stimulation. This hypothesis suggests that the index of susceptibility following vestibular system loss should be inversely related to the amount of activity posttrauma. Therefore, patients who are passively restrained beyond the period of physiological recovery may nevertheless become sick when they are finally allowed to move.

9. We have argued that the reported immunity of LDs to motion sickness may be accounted for by changes in their postural control rather than by the absence of the vestibular system *per se*. One way to address this hypothesis is to compare the control behavior of LDs and intact animals in situations in which the intact animals experience motion sickness. Differences in control across the two groups would mandate caution in assigning a central role to the vestibular system in motion sickness.

10. In principle, perceptual systems other than the vestibular system could be sensitive to some or all of the sources of information for instability that have been discussed in this article. One way to demonstrate the pickup of such information by other systems would be to induce motion sickness in LDs by generating postural instability in them. This might be possible using vibratory myesthetic stimulation of postural muscles (cf. Lackner & Levine, 1979), or optical stimulation within the postural range of LDs (cf. Lestienne et al., 1977), in a situation in which they were required to maintain high task demands (e.g., reading).

11. We have suggested that sensitivity to the axes of the body rotation (the joints around which the body is rotating) is important for the coordination of movement, and for the detection of postural instability. It would be interesting to determine the relative sensitivity of the vestibular, visual, and somatosensory systems to such information. This could be done by subjecting LDs and intact animals to whole-body rotation, and to rotation of the visual surround, with the eyes open and closed. The main independent variable would be the distance between the head and the axis around which the body was rotated. The dependent variable would be sensitivity to that distance.

12. In our discussion of adaptation to provocative situations, we suggested that both instability and systematic exploration can serve important roles in generating information about the dynamics of the animal-environment interaction. These behaviors are generally nonlinear and cannot be easily accommodated within control theories that assume that all behavior is directed toward minimizing distance from some reference condition. The importance of these behaviors in adaptive nonlinear control systems suggests that they should be an important focus for both theoretical and empirical work (Kugler & Lintern, 1990; cf. Beek, 1989; Canudas de Wit, 1988; Chalam, 1987; van Emmerik, 1990; Newell et al., 1989).

The ecological approach to perception and action has given us a fresh perspective on motion sickness. This has led to new insights about body control in changing environments. The importance of these insights will be determined by their ability to motivate useful research.

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