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The Shape of Self-Motion Perception. II. Framework and Principles for Simple and Complex Motions

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THE SHAPE OF SELF-MOTION PERCEPTION—II. FRAMEWORK AND PRINCIPLES FOR SIMPLE AND COMPLEX MOTION

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Abstract—There have been numerous experimental studies on human perception and misperception of self-motion and orientation relative to the earth, each focusing on one or a few types of motion. We present a formal framework encompassing many types of motion and including all angular and linear components of velocity and acceleration. Using a mathematically rigorous presentation, the framework defines the space of all possible motions, the map from motion to sensor status, the space containing each possible status of the sensors, and the map from sensor status to perceived motion. The shape of the full perceptual map from actual motion to perceived motion is investigated with the framework, using formal theory and a number of published experimental results. Two principles of simple motion perception and four principles of complex motion perception are presented. The framework also distinguishes the roles of physics and the nervous system in the process of self-motion perception for both simple and complex motions.

The present rigorous development of the self-motion perception framework allows the scientist to compare and contrast results from many studies with differing types of motion. The six principles formalized here comprise a foundation with which to explain and predict perceptual phenomena, both those observed in the past and those to be encountered in the future. The framework is especially aimed to expand our capacity to investigate complex motions such as those encountered in everyday life or in unusual motion environments.

Key words: vestibular system, spatial orientation, mathematics, gravitation, space flight, models.

In the modern world of travel by plane, car, bicycle, train and even spacecraft, everyday motion of an individual consists of many types and combinations of motion: angular, linear, small, large, simple and complex. Not only are there many types and combinations of motion, but there are various factors governing the perception of self-motion and orientation, the two major players being physics and the nervous system. How do we as scientists handle the multitude of components and factors involved in self-motion perception?

Historically, investigators have handled this multitude of factors by studying just one or a few factors at a time in any given experimental set-up. For example, many experiments have been performed on angular motion alone, with a fixed vertical axis, or with a fixed horizontal or diagonal axis. Other studies have investigated linear motion along a fixed line of motion. In addition, large magnitude fixed-direction linear accelerations have been studied in the laboratory by the use of large centrifuges. These centrifuges and other experimental apparatus also make certain combinations of linear and angular motion possible

in the laboratory; many more combinations have yet to be tried (see Guedry,^{18,19} and Dichgans and Brandt¹³ for reviews of the literature).

Theory has been a major approach toward understanding the integration of the many factors involved in self-motion perception. The primary contribution in this area has been the development of computer models; one recent model focusing on human self-motion perception is that of Borah *et al.*⁷ Computer models typically take as input the stimuli to the sensors in the forms of velocities and/or accelerations, and give output in the form of perceived velocities and/or accelerations. In effect, the models perform a map from sensed velocities and/or accelerations to perceived velocities and/or accelerations.

In the present paper we apply a different kind of theory, through the development of a rigorous mathematical framework, principles and notation with which to describe motion of a subject. One goal is to give a means by which to compare and contrast results of many different motion studies, facilitating the identification of patterns in self-motion perception. Another goal is to distinguish the roles of physics and the nervous system in the process of self-motion perception or misperception. Still another

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goal is the rigorous formalization of principles of self-motion perception that describe the shapes of the maps involved.

The following four sections contain, in order: the development of the basic framework for simple motion and its perception, the resulting properties and principles derived and formalized from the application of this framework to experimental results, the development of the framework for complex motion and its perception, and the resulting properties and principles derived and formalized from the application of this framework to experimental results.

THE BASIC FRAMEWORK

The laws of physics and the nervous system are linked in the process of self-motion perception: a motion of the subject affects the subject's motion sensors according to the laws of physics and the biomechanics of the sensors, while the nervous system detects the perturbation of the sensors and produces a perception of motion. In this section, we develop a framework that clarifies and distinguishes the roles of physics and the nervous system in self-motion perception. This framework serves two main purposes. First, it allows us to examine any given experimental result on self-motion perception and determine how much, if any, of the perception can be explained directly by the laws of physics, and how much of the results are due to non-trivial processes in the nervous system. Second, the framework gives a means by which to compare and contrast many types of experimental results; by placing different types of results in the same framework, we can identify patterns in perception—patterns that may reflect patterns within the nervous system.

The framework consists of two main parts: the representation of motion affecting the sensors, and the representation of sensor status affecting the ensuing perception. To elaborate upon the first part of the framework, we note that motion of a subject affects the human sensors of motion according to the laws of physics and biomechanics; for example, angular acceleration causes the cupulae and hairs of the semicircular canals to deflect. The sensors are the vestibular hairs in this case. A particular motion of the subject results in a particular deflection of the vestibular hairs; therefore, we use the mathematical terminology of mapping, and say that there is a map from each motion to the appropriate hair deflection.

The nervous system then interprets the signals from the sensors to mean that the subject is undergoing a certain motion. The internal process that governs a subject's perception of motion can include many systems, such as the vestibular system and the visual system; the neurophysiology of these systems is a major topic of research.^{5,13,17,32} Despite several proposed locations of sensory processing for self-motion perception, such as the vestibular nuclei, the accessory optic system and cortical vestibular areas, the

proposed pathways and structures are still under consideration.⁹ This process of the nervous system is also a (complicated) map—a map from sensor status to (perceived) motion. The nervous system detects a certain status of the sensors and produces a perception of, or maps to, the motion that is perceived to take place.

In summary, there are two maps: a map from motion to sensor status, and a map from sensor status to (perceived) motion. The first map is governed by the laws of physics and biomechanics, while the second map is governed by the processes of the nervous system. (Of course, the nervous system, like everything, is also governed by the laws of physics on molecular and other levels, but that is another topic.)

To relate this language of maps to other research on self-motion perception, we must point out that most research concentrates on one or the other of these two maps. Many investigations concentrate on a single special portion of one of the maps, making the mention of maps unnecessary. For example, an investigation of self-motion perception may study on-axis rotation of a seated subject. On-axis rotation is a very special type of motion within the space of all possible motions, and the physical map from motion to sensor status for this special case is relatively simple (once the dynamics of the sensors are understood—a major area of research in itself), so the map from motion to sensor status is not usually mentioned as such. The bulk of the research in such a study usually lies in the analysis of the relationship between the stimulus and the perception. In other words, the “on-axis rotation” portion of the nervous system's perceptual map is under investigation. If the researchers propose a function to describe the relationship between the stimulus and the perception (as is often done in modeling studies), they are proposing an approximation to the shape of a piece of the nervous system's map. At the same time, research on biomechanics studies not the second, but the first of the two maps discussed above. Once again, usually a special type of motion is studied, meaning that a piece of the map from motion to sensor status is under investigation.

The present research requires a global viewpoint that allows discussion of both parts of the self-motion perception process, as well as the full maps. The full, global viewpoint allows a level of analysis unavailable in a piecemeal approach. Furthermore, for a solid foundation which can be used for future research, it is necessary to state the existence of these two maps explicitly. The optimal approach includes both global and partial treatments of the maps. For example, one goal is to clarify in any given situation which of the two maps is contributing to an observed perceptual phenomenon, because of the difference between the two maps' relationships to physiology. The first map can be discussed in terms of physical analyses such as in the companion paper²⁵ and in terms of the known dynamics of the sensors. The second map, admittedly

Fig. 1. Standard coordinate axes for specification of head motion. (A) Coordinate axes for linear motion, and standard unit vectors. (B) Coordinate axes for angular motion, and standard unit vectors.

more complicated, can be discussed in terms of established experimental results on self-motion perception. Experimental results are sometimes used to propose specific functions to describe pieces of the map, but we focus instead on global properties of the map. By expanding the results presented here, the complete shape of the full nervous system map, as well as of the physical/biomechanical map, could be identified, including both global properties and details.

In order to work with the two maps, they must be made more precise. In the following subsections, these self-motion perception maps and the associated “Motion Space” and “Sensor Space” are formalized.

Motions

A formal definition of motion is necessary in order to analyse the self-motion perception maps. Motion of a subject is often phrased in terms of accelerations and/or velocities, and we follow the definition given

Fig. 2. Perfect perception versus imperfect perception. (A) The map Physics from Motion Space to Sensor Space and the map Nervous System from Sensor Space to Motion Space combine to give perception of motions M_1 , M_2 and M_3 correctly from actual motions M_1 , M_2 and M_3 , respectively. (B) The maps combine to give the incorrect perception of motion M_4 from actual motion M_1 , as well as the incorrect perception of motion M_2 from actual motion M_2 and from the actual motion M_3 .

in Holly²⁴ and Holly and McCollum²⁵ using the standard coordinate system of Hixson *et al.*,²³ as displayed in Fig. 1. This standard was originally developed for accelerations of a subject; however, by including velocities, the coordinate

system becomes a subject-coincident coordinate system²⁴ in which special rules hold. (For example, acceleration is not in general the derivative of velocity; see Holly²⁴ for more details.)

Fig. 3. Notation for specifying linear motion and sensor status of otolith organs. (A) The upper circle represents a piece of the sagittal plane, with the standard x - and z -axes. Circles show ranges of equal magnitude. The lower circle represents a piece of the approximate plane of the utricular macula. (B) Example of specification of linear motion. Linear velocity v is represented by a point on the circles indicated by a " v ", linear acceleration a is given by an " a " and attitude a_g is given by a " g ". Amplitudes represented by the circles in this example are specified with the upper circle. (C) Example of specification of otolith organ status. The same two planes are used as in the notation for specifying motion, but the circles are shaded differently in order to distinguish the two notations. Displayed here is a representation of the sensory hairs responding to 1 g-unit resultant acceleration ($a + a_g$) in the z direction, such as is encountered when upright in the earth's gravitational field. This is the acceleration encountered by the subject in B.

We make the following definition:

Definition. A motion, referring to head motion at a given point in time, is specified by five vectors in the subject-coincident coordinate system of Fig. 1, those for:

1. Linear velocity, denoted by $\mathbf{v}$.
2. Linear acceleration, denoted by $\mathbf{a}$.
3. Angular velocity, denoted by $\boldsymbol{\omega}$.
4. Angular acceleration, denoted by $\boldsymbol{\alpha}$.
5. Attitude, denoted by $\mathbf{a}_g$.

The attitude vector represents the “pseudo-acceleration” upward due to gravity and its opposition by the support surface; the attitude vector has magnitude equal to 1 g-unit on the earth’s surface. Since each of the five vectors of motion has three components, a motion is technically a 15-dimensional vector. The set of all possible motions forms a 15-dimensional vector space which we denote by the term Motion Space.

As an example of a formally specified motion, a $60^\circ/\text{s}$ clockwise spin of an upright subject would be specified by the vectors $\mathbf{v} = \mathbf{0}$, $\mathbf{a} = \mathbf{0}$, $\boldsymbol{\omega} = -60 \mathbf{k}^\circ/\text{s}$, $\boldsymbol{\alpha} = \mathbf{0}$, $\mathbf{a}_g = 1 \mathbf{k}$ g-unit.

Motion Space plays a key role in the self-motion perception framework. It represents the various motions of a subject, and is used in two ways: first, its members can represent the actual motion of the subject; second, its members can represent the perceived motion of the subject (which may or may not match the actual motion of the subject).

Sensor status

As stated earlier, the laws of physics and biomechanics govern the map from motion to sensor status. We have formally defined the concept of a motion, and must do the same for sensor status. This definition is made in an open-ended fashion that allows individual experiments or research projects to dictate which sensors are relevant. In general, all sensors may be relevant, but in comparing, for example, the sensations of a pilot performing two different maneuvers, we may wish to ignore the taste of the pilot’s chewing gum in comparing the perceptions of self-motion.

The vestibular system is one system with relevant sensors, the sensory hairs. Therefore, in specifying sensor status, one set of information given will be the deflections of the sensory hairs of the semicircular canals and otolith organs. In later sections, we present notation for specifying these hair deflections.

Another relevant sense is vision. For the purpose of self-motion perception, the stimulus to the visual system consists of a stationary or moving retinal image, possibly in combination with information about eye movements relative to the head, to indicate movement of the visual surround relative to the head. Technically, a description of the sensor status must include the states of the various photoreceptors as functions of time. Which other sensors must be

included, such as those indicating contraction of the extraocular muscles, are a topic of debate.³⁸ It is known that velocity of the visual surround alone can induce “vection”, a perception of self-motion,¹³ and optokinetic stimulus evokes responses in cells of the vestibular nuclei that also respond to head motion.^{1,17,22,37} Only one motion studied in the present paper has vision available, with the visual surround rotating about a vertical axis through the subject. For this motion, we give a description of the visual sensor status by simply specifying the velocity of rotation of the visual surround. In studies that concentrate on the visual aspect of self-motion perception, it would be important to separate the particular components of the visual sensor status, unlike our simplification which causes part of the neural processing to be included in the stated “sensor status” for the one motion.

The proprioceptive and somatosensory systems both detect forces which are directly related to accelerations ($F = ma$), and because the vestibular system already detects acceleration there is redundancy in the information obtained by these three systems. Since the experiments discussed in the present paper do not separate the issues of somatosensory and vestibular detection of acceleration, we currently specify only the vestibular sensor status and, when relevant, the visual sensor status. In many cases, however, the somatosensory and proprioceptive information is included implicitly in our specifications because in specifying vestibular status, we indicate accelerations which are detected by the somatosensory system.

The term sensor status refers to the status of all sensors of interest at a particular time. For example, a subject may have hairs deflected in the horizontal semicircular canals in response to $30^\circ/\text{s}^2$ clockwise acceleration, while having saccule hairs deflected downward in response to gravity and visual stimulus due to the visual surround moving $60^\circ/\text{s}$ counter-clockwise relative to the head. The sensor status consists of the hair deflections in conjunction with the corresponding visual sensor status. Because there are three components of angular acceleration, three components of linear acceleration, three of angular velocity and three of linear velocity, the sensor status has at least 12 components.

The set containing each possible sensor status is called Sensor Space here, in analogy with Motion Space.

The maps

Physics takes us from Motion Space to Sensor Space, and the nervous system takes us from Sensor Space to Motion Space. The laws of physics and biomechanics perform the first half of the perceptual operation. For example, when a subjects sits stationary (a simple kind of motion), the laws of physics (in particular, Einstein’s Principle of Equivalence) determine that the subject’s saccule hairs are deflected

downward in response to the pull of gravity, or the "pseudo-acceleration" upward. To each motion, there is a corresponding status of the sensors. We denote this map from Motion Space to Sensor Space by the term *Physics*.

An implicit assumption in defining the maps is consistency of the maps. We use the term "map" as a synonym for "function" in the mathematical sense, so that each member of the domain is associated by the map to a single member of the co-domain (the space being mapped to). *Physics* is easily assumed to be a function for our purposes. However, the nervous system is more complicated.

Everyday perception of self-motion differs from individual to individual, and even a single person may have different cognitive influences or different internal "states" at different times. These factors, as well as motor control influences, may affect the nervous system's interpretation of sensory signals for motion. In the broadest sense, a single map cannot be ascribed to "the nervous system". Our first assumption in attacking this problem is that, in the ideal case, the nervous system of a single individual is under investigation. Unfortunately, the presentation of experimental research often averages data across subjects, and studies are not usually published about perceptions during different motions of a single subject, so the research presented here discusses perceptions of self-motion common to several subjects.

There are at least two ways to deal with the problem of cognitive influences and internal states. One is to include specifications of the cognitive influences and internal states in the description of sensor status, making "sensor status" a more general kind of neural and organismic status. Research could then compare, for instance, perceptions during various motions when the subject is told that the motion will be upward versus perceptions when the subject is told that the motion will be downward. By the same token, perceptions may vary from the first experience of a motion to the second experience of that motion. However, "internal states" are not so easily grasped. Therefore, we apply another solution to the problem.

We assume in the ideal case that all motions under study are of the same subject in the same state of mind and with the same cognitive influences. In addition, all motions under study must include the same relative movements of the head, limbs and body so that motor control influences are not compared inappropriately between motions. Technically, it does not matter which internal and motor states and which cognitive influences are present, as long as they are the same for all motions. Of course, only an approximation can be made to the above requirements during experimental work. Fortunately, many experimental results hold across a number of subjects and hold despite possible differences in past experience of

the subjects. We use experimental results of this type in the present work.

The processes of the nervous system are then represented by a map *Nervous System* within the framework. *Nervous System* maps from Sensor Space to Motion Space (of perceived motions). The perceived motion can be specified in the standard way (Fig. 1 and the Definition above) with velocities and accelerations. Therefore, the set of all possible perceived motions is the same Motion Space described earlier.

One relevant point about self-motion perception: sometimes a subject reports a perceived motion that is physically impossible, and sometimes a subject reports, "I simply feel disoriented." The latter situation is addressed further in the Discussion, but the former situation illustrates a strength of the self-motion perception framework. Because each motion is specified in terms of velocities and accelerations, a physically impossible motion can be specified just as easily as a common motion. For example, the motion of rightward roll while remaining upright—as is perceived during rollvection¹³—is specified by an angular velocity vector in the x direction (for rightward roll) and an attitude vector in the z direction (for "upright"). This physically impossible motion belongs to Motion Space because Motion Space allows for any combination of velocities and accelerations. In this way, Motion Space permits the representation of any motion that the nervous system perceives, even those that are confusing or impossible.

The framework

In summary, *Physics* maps from Motion Space to Sensor Space, and *Nervous System* maps from Sensor Space to Motion Space (of perceived motions). The full map through *Physics* and *Nervous System*, taking actual motion to perceived motion, will be called *Motion-to-Perception*.

What happens if perception is perfect—if the subject always perceives exactly the motion that is occurring? In this case, each time a motion occurred, the sensors would be affected, and the nervous system would perceive by the status of the sensors exactly which motion was occurring. The framework would then display an uninteresting pattern: each motion would be mapped by *Physics* to a status of the sensors, and that status of the sensors would be mapped by *Nervous System* exactly to the original motion (Fig. 2A). *Motion-to-Perception* would simply be the identity map.

By displaying self-motion perception with the maps, we can investigate questions of how, when, why and how much perception deviates from "perfect" (Fig. 2B).

The questions

The nervous system does not accomplish perfect self-motion perception. There are many classic

examples of motions that routinely result in misperception of self-motion.^{13,18} Some examples include circular vection, sensation of stationarity when rotat-

ing or moving linearly, the vestibular Coriolis effect and the optokinetic pseudo-Coriolis effect. Not all misperceptions of motion are created by contrived

Fig. 4. Systematic deviation in Motion-to-Perception. Results of Correia *et al.*¹¹ are diagrammed in the self-motion perception framework, with actual motion in the left column, sensor status in the middle column and perceived motion in the right column. The notation of Fig. 3 is used with a modification: since the subjects were asked to report angle but not magnitude of resultant linear acceleration, only the angle of the resultant horizon and its associated perpendicular resultant acceleration vector (represented by "A") are shown, as dashed lines on the circles in the first and last columns. (A) Subjects upright in a 1 g-unit environment. (B) Subjects under 1.5 g-units z -directed resultant acceleration. (C) Subjects under 2.0 g-units z -directed resultant acceleration. From A to B to C, the perceived tilt shown in the right column increases systematically with increasing resultant acceleration.

experiments, and we ask questions that apply not only to unusual motion situations, but also to everyday motion perception.

Question 1: Which vestibular “illusions” can be explained by the laws of physics, and which are due to non-trivial processes of the nervous system? With the framework distinguishing these two key players in self-motion perception, we have a way to separate the two roles. Experiments in the past have often used quite simple motion stimuli, so distinguishing the two roles has not always been a problem, but as research moves toward more and more complex motion, especially natural motion, the distinction becomes more complicated.

Question 2: Do distinct motions of the subject produce distinct perceived motions? We know that perception is not perfect, but we can still ask whether it can at least distinguish one motion from another.

Question 3: Are the motion components—velocity, acceleration, angular movement, linear movement—independent in self-motion perception? If the components are independent, then a subject’s perception of linear motion, for example, is determined solely by the subject’s linear motion and not by the angular motion.

Question 4: In what way is the independence or dependence of components, or the distinguishability of motions, affected by physics versus the nervous system? In other words, given a subject’s report, should it be attributed to the laws of physics or the nervous system?

These are a few of the many possible questions that can be asked within the framework of self-motion perception. By finding patterns arising from certain types of motion and sensor stimuli, we can begin to deduce patterns in the processes of the nervous system, showing the overall shape of perception.

PRINCIPLES OF SIMPLE MOTION PERCEPTION

The simplest type of motion is sustained motion; accelerations of the subject remain constant relative to the subject’s head, and velocities change only in magnitude, not direction (under the given definition^{24,25}). In these situations, a subject usually has a clear idea of what the perceived motion is. However, this does not mean that the subject’s perception matches the actual motion. Such a combination of a clear, simple motion and a clear (although perhaps incorrect) perception forms a solid base for the investigation of the shape of perception.

In this section, we present two global properties of self-motion perception during sustained motion, followed by a mathematically rigorous statement of the resulting principles.

Collapse in Motion-to-Perception

The first global property of self-motion perception during sustained motion is that the Motion-to-Perception map includes a collapse, causing many

motions to be indistinguishable. This statement actually consists of several statements, since the assumptions about available sensors (is vision available?) are left unstated. In fact, we shall demonstrate that the property holds when vision is available, as well as when vision is not available.

There are two ways to demonstrate the property of collapse: through experimental evidence and through formal proof. For experimental evidence, it is possible to quickly note some well-known examples. One example is the sense of stationarity that a subject feels when sitting in the dark on a chair rotating at, say, 60°/s. After an initial start-up period, the subject will have a perception of stationarity even though the chair continues to turn (see Guedry¹⁸ for a review of the literature). The motion of rotating and the motion of sitting stationary are mapped by Motion-to-Perception to the same motion—sitting stationary. Another example is that of circularvection: subjects surrounded by a visible, rotating vertical drum will often feel as though they themselves are turning, instead of the drum (see Dichgans and Brandt¹³ for a review of the literature). The motion of sitting stationary surrounded by a rotating drum and the motion of subject rotation are mapped by Motion-to-Perception to the same motion—subject rotation. There are many other examples^{13,18} in which the subject cannot distinguish two different motions.

An even stronger property can be demonstrated through formal proof:

Claim. The Physics map already includes a collapse.

In other words, by the laws of physics, many motions cause the same status of the sensors. If this claim holds, then Motion-to-Perception certainly includes a collapse because the Nervous System map has no means to recover information lost in the Physics map to sensor status. The nervous system can use only the sensor status in its production of motion perception—it cannot “see” the actual motion—so two motions that cause the same sensor status are indistinguishable.

To give a formal proof of the claim above, we simply apply the results of the companion paper:²⁵ there are large classes of motions that cannot be distinguished in the dark due to the fact that they cause the same status of the sensors. Even with vision available, there are pairs of motions that cause the same stimulus to the sensors. Therefore, Physics includes a collapse.

The formal proof that Physics includes a collapse not only gives a strengthened result from that according to experiment alone, but also demonstrates a much broader domain upon which there is a collapse in Motion-to-Perception. This domain includes motions that may have never been used in experiment.

This discussion brings up an interesting additional question: Does the Nervous System map itself include a collapse? In other words, do the processes of the

Fig. 5. Notation for the angular part of simple motion. (A) The axes for the three components. There are three separate axes for plotting rotation about the three rotation axes: the approximate axis of the horizontal semicircular canals, the approximate axis of the right anterior (and left posterior) semicircular canal and the approximate axis of the right posterior (and left anterior) semicircular canal. The axes are labeled according to their corresponding right semicircular canals: horizontal, anterior and posterior. The axes are drawn so as to show the approximate direction of chin movement during movement about the axis in question. (B) Example of a diagrammed angular motion. The symbol " ω " and " α " are used to plot the angular velocity and angular acceleration, respectively; the motion here is $8^\circ/\text{s}^2$ acceleration in rightward yaw with $40^\circ/\text{s}$ rightward yaw velocity. The " ω " symbol on the horizontal canal axis is to the right of center because the chin moves to the right during rightward yaw. The values are zero on the other axes. (C) Examples of diagrammed angular velocity. The chin moves in essentially the direction indicated by the combined effects from the three axes.

nervous system cause two motions that are distinguished by the sensors to be indistinguishable when it comes to the perception? If so, then Motion-to-Perception collapses even more, having inherited collapse from both Physics and Nervous System. We come back to this question in the Discussion.

Systematic deviation in Motion-to-Perception

The second global property is that Motion-to-Perception deviates systematically from the identity map which represents perfect perception. The claim is that the deviation from perfect perception is not random, but is systematic.

We demonstrate the claim with well-established results on perception in different force fields. The particular experimental example we use for this purpose is that a subject's perceived tilt is systematically related to the magnitude of the resultant linear acceleration.

First, we introduce notation, to be used both here and later, for specifying linear acceleration and velocities. Since motion takes place in a three-dimensional space, it is necessary to represent three dimen-

sions in a diagram. For this purpose, we draw two sets of axes: one represents the xz (sagittal) plane and one represents a plane close to the xy (horizontal) plane. In particular, the second plane is taken to be the approximate plane of the utricular macula, tilted 25° backward (in pitch) from the stereotaxic xy plane (Fig. 3). Linear velocity, linear acceleration and attitude are specified by points on the diagram marked by the symbols " v ", " a " and " g ", respectively.

Notation for sensor status (Fig. 3C) is similar to the notation given for motion above. The same two planes are used: xz plane and the plane tilted 25° backward from the stereotaxic xy plane. These planes are chosen only as a rough approximation of the planes of the otolith organs. Resultant linear acceleration ($\mathbf{a} + \mathbf{a}_g$) detected by the vestibular hairs is indicated on the diagram by points marked by the symbol "H".

Perception during different magnitudes of resultant acceleration demonstrates systematic deviation of Motion-to-Perception. The basic thesis here is that a subject experiencing greater than 1 g-unit resultant acceleration in the z direction will have a sensation

of being in a pitch-back position. Various experiments^{11,33} have been done on this phenomenon, and we use the reports of Correia *et al.*¹¹ for our diagrams. Subjects were placed in several different resultant linear acceleration environments by means of rotation in a large centrifuge. For the sake of brevity, we concentrate only on the cases with 1 g-unit, $1\frac{1}{2}$ g-units and 2 g-units resultant acceleration, and in which the subjects were upright relative to the resultant acceleration vector. In each case, the subjects reported the perceived pitch angle (more details can be found in Correia *et al.*¹¹).

Placing this experiment into the framework, Fig. 4 displays the Physics map from actual motion to sensor status and the Nervous System map from sensor status to perceived motion, in each of the situations. Here, the sensor status is obtained from the resultant acceleration; this is exactly what the laws of physics accomplish. The perceived motion, following the Nervous System map in each case, is displayed as reported by the subjects in the experiment.

As seen in Fig. 4, there is a systematic deviation of the perceived motion (resultant acceleration here) from the actual motion. The deviation is displayed in the disparity between the actual angle and the perceived angle of the resultant acceleration vector. Correia *et al.*¹¹ report that this systematic deviation is related to a tangent function; for a motion in upright position relative to the resultant, the angle of pitch in the perceived motion is approximately equal to $\arctan(A \tan(30^\circ)) - 30^\circ$, where A is the magnitude of resultant acceleration in g-units. (Ideal perception would simply give the angle as 0° .) Regardless of the exact function used to model this phenomenon, we know that perceived pitch-back angle is a monotone increasing function of resultant acceleration magni-

tude. In other words, the deviation from identity is systematic.

The most common explanation for the phenomenon of pitch misperception is that, because the utricular macula is tilted backward, a greater acceleration upward on the body results in a greater backward deflection of the utricular hairs, and a backward deflection of the utricular hairs is usually interpreted to mean backward pitch position of the body.^{11,18,33} As stated, this explanation might seem to imply that both the laws of physics and the processes of the nervous system are at fault in the inaccurate perception of pitch; the laws of physics make the hairs deflect backward, and the nervous system interprets this deflection as backward pitch.

However, the nervous system is solely responsible for the inaccurate pitch perception of the resultant acceleration vector; the framework makes this clear. As displayed in Fig. 4, the nervous system has chosen a map from sensor status to perceived motion that is relatively accurate for 1 g-unit resultant acceleration but relatively inaccurate for greater than 1 g-unit. Nevertheless, there is a map that would be accurate for both 1 g-unit and greater than 1 g-unit resultant acceleration, by taking into account both the utricular and saccular hair deflections. The hair deflections indicated in Fig. 4 contain all the necessary information for the nervous system to deduce the actual pitch of the resultant acceleration—the Physics map governed by physics is accurate—but the nervous system has chosen a map whose range of accuracy is confined to 1 g-unit.

Thus, the processes of the nervous system deviate in a systematic way from ideal production of self-motion perception. This means that not only does Motion-to-Perception deviate systematically from the identity map, but Nervous System itself deviates systematically from the identity map.

Fig. 6. Notation for the angular part of complex motion. Each of the three components of rotation is displayed as a sequence moving out from the center of the diagram. The example here shows backward pitch acceleration with increasing backward pitch velocity. The " ω " values are increasingly above the time axes as the sequence progresses because the "chin-upward" velocity increases. ("Upward" means "toward the head's z-axis", which is not necessarily the same as upward relative to the earth.)

Principles of self-motion perception for sustained motion

The properties above result in the following formal principles:

Principle S1. The Motion-to-Perception map is many-to-one (i.e. maps more than one motion to the same perception).

Principle S2. The Motion-to-Perception map deviates systematically from the identity map.

When analysed, neither of these principles comes as a surprise to the researcher well-versed in self-motion perception. Our intention is to state these principles explicitly and formally.

By stating the principles explicitly, at least three goals are accomplished. First, the principles can be proved because they belong to a formal framework. Second, a researcher who encounters an instance of self-motion misperception may be able to ascribe the instance to one of the two principles, as opposed to "just another case of misperception." If one of the

principles does not apply, the researcher may be able to form a hypothesis about a possible third principle. Third, the principles form a foundation upon which to build further principles, upon which to elaborate the existing principles, or by which to judge possible models. Because individuals and states differ, humans use a class of Motion-to-Perception maps, not a single map. The most precise specification of Motion-to-Perception is by a class or a complete set of principles.

THE FRAMEWORK FOR COMPLEX MOTION

A complex motion can be viewed as a sequence of simple motions. For example, the motion of a stationary upright subject who experiences forward linear acceleration followed by deceleration to a stop could be specified as a sequence of four simple motions: stationary, accelerating, decelerating, then stationary. The specification of the simple motions in sequence allows clear analysis of the velocities and accelerations as they change over time. Even if the motion involves a continuously changing acceleration, for example, the motion can be displayed as a sequence with time steps chosen to display the relevant properties of the acceleration change.

The framework

For purposes of formal mathematical analysis, a complex motion is defined to be a sequence of simple motions, where a "simple motion" is a motion given by the five vectors, as defined earlier. Formally, a complex motion is a member of the Motion Sequence Space containing sequences of simple motions. A complex motion can be displayed by using the same notation and conventions as were used for simple motions by displaying the appropriate simple motions in sequence. We require that the first motion in any complex motion sequence be a sustained motion, while the later members of the sequence can be any kind of simple motion. This requirement ensures that a subject's complex motion is analysed from its beginning; we are not jumping into the middle of a full complex motion. In addition, the sensor status is known for sustained motions since it can be assumed that the sensors have reached a steady state; the Nervous System map is also well-studied experimentally for many sustained motions.

Associated with each complex motion is the status of the sensors. Since a complex motion is a sequence, the associated sensor status is also a sequence. Formally, the sensor status sequence is a member of the Sensor Sequence Space. If a particular complex motion is a sequence of length $n > 0$ (i.e. is a sequence of n simple motions), then the corresponding sensor status is a sequence of length n .

The perceived motion is also a sequence, a sequence of simple motions; however, during most complex motion experiments, the actual sequence and timing of perceptions have not been given in reports

by subjects. The main exceptions are experiments to determine the time course of perception, where a subject reports sensation during or after angular acceleration or similar stimulus (see Guedry¹⁸ and Dichgans and Brandt¹³ for reviews of the literature). Because data on timing of sensations are not yet available for many types of complex motion, and perception data are usually given as shorter sequences often only describing the final sensation, we give the perception of motion as a short sequence of simple motions, often of length one or two.

In summary, the laws of physics and biomechanics map from Motion Sequence Space to Sensor Sequence Space, and the nervous system maps from Sensor Sequence Space to Motion Sequence Space (of perceived motions). The former map will be called Physics-C and the latter map will be called Nervous System-C to distinguish from the maps for simple motion. The full map for complex motion perception is denoted Motion-to-Perception-C. Once again, the nervous system is quite complicated and we must take into account influences such as cognition. To do so, the same assumptions used for the analysis of sustained motion and described with the basic framework are used here.

As an example, the upright individual who accelerates forward, decelerates, then stops can be placed in the framework as follows: the complex motion is specified by a sequence

(stationary, accelerating,
decelerating, stationary)

in Motion Sequence Space. In practice, details such as the magnitudes of vectors would be specified in the sequence. Next, Physics-C map to Sensor Sequence Space. Looking simply at the otolith organs, hair deflections closely reflect the resultant acceleration if the time frame is of the order of hundreds of milliseconds or longer (the relevant time constants being insignificant, of the order of tens of milliseconds^{16,36}). Therefore, the sensor status shows the resultant acceleration at each of the four steps of the motion. Considering that gravity gives an upward "pseudo-acceleration", the sensor status sequence is then

(upward resultant acceleration, diagonal
forward-and-up resultant acceleration,
diagonal back-and-up resultant
acceleration, upward resultant acceleration)

in Sensor Sequence Space. Finally, Nervous System-C maps to the motion that is perceived. Depending on the subject's report, the perceived motion may be a single simple motion, or may be a sequence. In the ideal case where the subject has perfect perception, the result is

(stationary, accelerating,
decelerating, stationary)

in Motion Sequence Space. As we have seen earlier, perfect perception may be the exception rather than the rule. In any given situation, we use subjects' reports of self-motion in order to write down the result of the Nervous System-C map.

A fundamental difference exists in our approaches towards Physics-C and Nervous System-C. Since the relevant laws of physics are known and to the extent that the dynamics of the sensors (e.g. vestibular hairs) are well-studied, we can derive sensor status from the actual motions by appropriate calculations. In this way, the calculations for Physics-C are not necessarily trivial, but the process is well understood. On the other hand, derivation of the Nervous System-C result is simple: human subjects give us reports of perception, completing the map from sensor status to perceived motion. However, despite the ease of obtaining the Nervous System-C map, the process (of the nervous system) is not well understood. The dynamics behind the neural processing are not known in the way that the dynamics of the sensors are; rather, research is aimed toward the understanding of the nervous system, and uses the known properties of sensor dynamics as one component.

Notation

The notation for complex motion is derived from that for simple motion. Since each complex motion is a sequence of simple motions, the linear part of a complex motion can be diagrammed using a sequence of pairs of circles, just as a simple motion is diagrammed (Fig. 3) using a pair of circles. Similarly, the sensor status sequence can be diagrammed using a sequence of pairs of circles, just as simple sensor status is diagrammed (Fig. 3C) using a pair of circles.

Besides linear motion, angular motion must be diagrammed; the basic notation is shown in Fig. 5. Three axes are included, one for rotation in each of the three approximate planes of the semicircular canals. The horizontal semicircular canal lies approximately in a plane tilted 25° backward (in pitch) from the stereotaxic horizontal plane,⁶ so we use this as the rotation plane for the "horizontal" axis. The other two axes are used to denote rotation in the two vertical planes at 45° angles from the sagittal plane. These two planes serve as approximations to the planes of the anterior and posterior semicircular canals.⁶

For complex motion, sequences of angular motion are diagrammed in the notation of Fig. 6, an expansion of the simple angular motion notation of Fig. 5. The first simple (sustained) motion is diagrammed as before, at the center of the diagram. The angular velocities and accelerations plotted outward from the center specify the ensuing sequence of simple motions; rotation about each of the three axes is plotted as a sequence in its own third of the diagram.

Sensor status for the semicircular canals is displayed in the same notation as given above for the complex motion, except an "H" is used to indicate

physical hair response to angular acceleration instead of the " ω " and " α " that are used in the notation for motion.

In summary, we have notation for simple linear motion (pair of circles), complex linear motion (sequence of pairs of circles), simple angular motion (three axes) and complex angular motion (three axes with extension away from center). A simple motion that includes both linear and angular components can be specified by displaying a pair of circles along with the three-axis angular notation. A complex motion that has both linear and angular components can be specified by displaying both the linear and angular complex motion notations together. Sensor status is treated similarly.

The questions

Once again, we ask questions about the shape of self-motion perception. As in the simple motion case:

Question 1: Which vestibular "illusions" can be explained by the laws of physics, and which are due to non-trivial processes of the nervous system? In the complex motion framework, the two key players in self-motion perception—physics and the nervous system—are clearly distinguished.

Question 2: Do distinct complex motions of the subject produce distinct perceived motions?

Question 3: Are the motion components—velocity, acceleration, angular movement, linear movement—independent in complex self-motion perception?

Question 4: In what way is the independence or dependence of components, or the distinguishability of motions, affected by physics versus the nervous system? Where should we concentrate our efforts when making predictions about perceptions in new motion environments such as spaceflight?

Question 5 (an additional question for complex motion): Are the steps of the complex motion sequence independent in self-motion perception? If the steps are independent, then each part of the perceived motion sequence depends only on its corresponding step in the actual motion sequence, and the analysis of complex motion perception reduces conveniently to the analysis of simple motion perception, in sequence.

Once again, many additional questions can be asked, including the general question, "What are the shapes of the Physics-C, Nervous System-C and Motion-to-Perception-C maps?" By seeking patterns in complex motion perception, we pursue the understanding of natural, active motion as well as of complex motion during travel in vehicles and within unusual motion environments.

PRINCIPLES OF COMPLEX MOTION PERCEPTION

As in the case of simple motion, we present global properties and principles of self-motion perception during complex motion. Four properties are

Fig. 7. Diagram of self-motion perception for the centrifuge acceleration experiment of Guedry *et al.*²¹ (see text for details), with time step of 3.82 s. The first step represents the situation before the acceleration begins, the second step represents the start of the acceleration and the succeeding steps represent the situation at intervals of 3.82 s. The top third of the diagram shows the actual motion, with the linear part of the motion displayed in a sequence of circle pairs (as in Fig. 3), and with the angular part of the motion displayed in the notation of Figs 5 and 6. The middle third of the diagram shows the sensor status sequence, with linear and angular parts displayed in an analogous fashion to the motion display. In this figure and all others, the angular sensor status is plotted on a relative scale; the H's indicate relative hair deflection, and units of measure are arbitrary. The bottom third of the diagram shows the motion that is perceived. The main aspect of perceived motion that is described^{19,21} is that of pitch position during or following the acceleration, so we display the perceived attitude of 15° pitch-back by a dashed line marked with "g". Very little pitch plane angular velocity was reported,¹⁹ and this is displayed here by ω s close to zero on the right anterior and posterior canal axes. The beginning of the angular part of the sensor status sequence is highlighted with bold face Hs for comparison with Fig. 8. Here, the Hs stay relatively close to the time axis, representing only small deflection of the semicircular canal hairs in the beginning.

demonstrated through experimental example and formal proof.

Collapse in Motion-to-Perception-C

The first global property of complex motion perception is that the Motion-to-Perception-C map includes a collapse causing many motions to be indistinguishable. We restrict the discussion here to motions in which vision is not available; similar results can be obtained when vision is available, but are outside the scope of the present paper. Like the simple-motion version of this principle, there are two means of demonstration: through experimental evidence and through formal proof.

One experimental observation of this property is the fact that a subject on a rotating chair in the dark who then undergoes a deceleration will feel the same as a subject who is stationary in the same chair but then accelerates toward a rotation in the opposite direction.¹⁸ More specifically, a complex motion consisting of a sequence of two simple motions, “rotating counterclockwise at $60^\circ/\text{s}$, then decelerating at $10^\circ/\text{s}^2$ ”, is mapped by Motion-to-Perception-C to the same (perceived) complex motion as is the complex motion “sitting stationary, then accelerating clockwise at $10^\circ/\text{s}^2$ ”. As stated earlier, the first motion of the sequence is continued long enough to be considered sustained. Even though this experimental result about complex motion ambiguity is quite simple, it serves to illustrate the property of collapse.

A formal proof that Motion-to-Perception-C includes a collapse is more complicated than the corresponding proof for simple motion, and contains quite detailed mathematical results. Therefore, the proof is not presented here, but we sketch the idea behind it: each complex motion is composed of simple motions, beginning with a sustained motion. Since each sustained motion is indistinguishable from many other sustained motions in the dark,²⁵ each complex motion is indistinguishable from the many other complex motions correspondingly composed of indistinguishable simple motions.

The formal theory holds for motions of any complexity. Given any complex motion, no matter how complicated, there are many other complex motions that are perceptually indistinguishable from the given complex motion.

Which part of the motion map is responsible here—physics or the nervous system? It turns out that physics is the responsible party this time. This does not preclude a possible contribution of the nervous system to the collapse within the full Motion-to-Perception-C map. This issue is discussed later in the section, and in the Discussion. In any case, the present arguments indicate that physics plays a major role in the collapse.

Temporal dependence

The second global property of complex motion perception is that the steps in the sequence of complex

motion perception cannot be analysed independently; the perception at any given stage during a motion depends on other stages of the motion. For example, the motion perceived by a subject during a particular angular acceleration may depend on how early or late the angular acceleration lies in the motion sequence.

Unlike some of the other properties of self-motion perception, the temporal dependence has both physics and the nervous system playing major roles. We clarify the two roles using both physiological and psychological evidence. In addition, we propose that the beginning of a complex motion plays a greater role in production of perception than do the later stages of the motion, when other factors are equal.

The cupulae of the semicircular canals, in detecting angular motion, have an especially prominent time-dependent property. In particular, the displacement of the cupula lags the angular acceleration, and is most commonly modeled as a heavily-damped torsion pendulum.^{17,39} One common way to describe the movement of the cupula is to say that it is approximately a velocity-transducer at high frequencies (e.g. 0.5 Hz) and an acceleration-transducer at low frequencies (e.g. 0.01 Hz).

These properties of cupula dynamics demonstrate the role of physics and biomechanics in the “non-independence” of the different steps of a motion. If the different steps of a motion were independent, then we (and the laws of physics) could deduce the sensor status at any given time by simply looking at the subject’s motion at that instant. However, this is impossible. The sensor status, and in particular, the cupula displacement, depends not only on the present motion, but on the previous motions; if the present motion is “sitting stationary”, for example, the cupula could presently be displaced in either direction depending on whether the previous motion was an angular acceleration, and depending on the direction and magnitude of that angular acceleration.

Psychophysical evidence also supports the nervous system’s role in temporal dependence. One well-established set of results pertains to subjective judgement of angular velocity during constant angular acceleration. The complex motion in these experiments consists of sitting stationary followed by constant angular acceleration over a period of time (see Guedry¹⁸ for a review of the literature). During the angular acceleration, a subject first reports angular velocity of increasing magnitude over time. However, after approximately 25 s, the subject reports angular velocity of decreasing magnitude. This phenomenon is not explained by physics or biomechanics; the cupula is still displaced during the later portion of the acceleration, and its displacement does not decrease during constant acceleration. Therefore, processes in the nervous system, whether they be primary afferent responses or processes in the CNS, are responsible for the different perceptions during the different stages of the motion.

Fig. 9. Example of a continuous graph of angular acceleration, such as used by Guedry *et al.*²¹ (Guedry *et al.* also nicely supplement such graphs with displays of rotation arrows.) The information in this graph corresponds to the α s in the top right display of Fig. 7.

Another interesting observation is made by Guedry *et al.*²¹ in a set of complex motion perception experiments. We briefly describe one of the experiments. Subjects were placed 20 feet from the center of a large centrifuge, and the centrifuge accelerated slowly counterclockwise for approximately 20 s, then after a significant period of constant angular velocity the centrifuge decelerated at the same rate (for about 20 s) to a stop. The subjects were positioned in the forward-facing tangential direction, and while the centrifuge was turning, the carriage holding the subject swung so that the resultant linear acceleration in the yz plane remained along the subject's z -axis. The maximum z -directed resultant linear acceleration was of magnitude 3 g-units.

The motions in this experiment can be described as consisting of two complex motions: the acceleration and the deceleration. The acceleration begins with the sustained motion of "stationary" and proceeds through an angular acceleration to end with a non-zero angular velocity. The deceleration is exactly the reverse; it begins with a sustained non-zero angular velocity and proceeds through an angular acceleration of the opposite direction to end with the simple motion "stationary". The total angular pitch motion (while the carriage is tilted) is the same in the two complex motions, so one might guess that subjects would perceive the same magnitude of pitch motion

during the deceleration as during the acceleration, but with reversed direction.

The surprising result of this experiment is that subjects report quite different magnitudes of pitch perception during the deceleration compared with the acceleration. In particular, pitch-down positions of about 90° were reported during deceleration as opposed to pitch-up perceptions of about 15° during acceleration.¹⁹ Why is this? There is a thorough and interesting discussion in Guedry *et al.*²¹ on many possible factors. We concentrate on those relevant to temporal dependence.

The self-motion perception framework can be used to display the results of this experiment, as shown in Figs 7 and 8. The complex motion is divided into equal time steps that display the shape of the motion. It is worth commenting on the two methods of displaying a complex motion: the sequence method as used here, and the continuous graph method, as used in Guedry *et al.*²¹ A continuous graph of angular acceleration versus time is a traditional method of diagramming motion, as shown in Fig. 9. These graphs are especially useful when analysing a particular component of the motion independently of the other components. We have opted for the notation of Fig. 7 because it displays all components of the motion at once, as well as the sensor status and perceived motion. By doing so, we have sacrificed

Fig. 10. Comparison of right anterior semicircular canal hair deflection with three different assumed values of τ_1 , during centrifuge acceleration of Fig. 7. (A) With $\tau_1 = 6$ s. (B) With $\tau_1 = 10$ s. (C) With $\tau_1 = 15$ s. The overall pattern of cupula displacement is the same in all three cases.

Fig. 11. Diagram of the linear sensor status and motion perception during the beginnings of the centrifuge acceleration and deceleration experiments of Guedry *et al.*²¹ (see text for details), with time step of 1.91 s. The first step represents the situation before the movement begins, the second step represents the start of the movement and the succeeding steps represent the situation at intervals of 1.91 s. (A) Acceleration results. The leftmost pairs of circles display the sensor status sequence and the rightmost pair of circles displays the perceived attitude. The “...” indicates that the full diagram has additional components, as in Fig. 7. (B) Deceleration results. The leftmost pairs of circles display the sensor status sequence and the rightmost pair of circles displays the perceived attitude. In both A and B the *z*-directed sensor status (representing otolith hairs detecting resultant linear acceleration) is highlighted with bold face Hs.

some of the exactness that is contained in a continuous graph because the motion is displayed in a finite number of discrete steps; however, the choice of time step is made so that the shape of the motion is still displayed, so no relevant details are lost.

The components of the complex motions, displayed in Figs 7 and 8, are those used in the

experiment. Angular and linear velocities and accelerations are computed from the values in the experiment, using $6.4^\circ/\text{s}^2$ as the angular acceleration of the centrifuge. We have neglected minor linear motion due to the fact that the subjects' heads are probably not in line with the swing axis of the carriage. It turns out that angular cross-coupling (or “Coriolis”) effects

are significant in this experiment, in comparison with the angular acceleration of the centrifuge, so the values in Figs 7 and 8 reflect not only the centrifuge acceleration, but also the cross-coupled angular components.

The sensor status, as displayed in Figs 7 and 8, is obtained by showing the otolith hairs deflecting in response to the resultant linear acceleration, and the semicircular canal hairs deflecting as indicated by the standard model^{17,39} of cupula displacement:

$$\Theta \frac{d^2 \xi}{dt^2} + \Pi \frac{d\xi}{dt} + \Delta \xi = \Theta \alpha(t),$$

where $\xi(t)$ is angular displacement of the endolymph, and the time constants governing the movement are $\tau_1 = \Pi/\Delta$ and $\tau_2 = \Theta/\Pi$. The value of τ_2 in the squirrel monkey is approximately 0.003 s,¹⁵ and the value in the human is approximately 0.004 s.³⁰ The value of τ_1 is less clear. In the squirrel monkey, it is approximately 6 s,^{15,17} but the human semicircular canals are larger so that the value in the human may be closer to 10 s. Theoretical work^{14,29,30,35} has investigated the influence of canal morphology on the fluid mechanics and cupula time constants; taken in conjunction with anatomical measurements,²⁶ there are indications that the time constant τ_1 in human may be of the order of 1.7 times that in squirrel monkey.¹⁵ Therefore, we take τ_1 to be 10 s, as is also used in Borah *et al.*⁷ For the sake of completeness, however, we compare possible cupula displacements during a representative motion under three different assumptions about the value of τ_1 : $\tau_1 = 6, 10$ and 15 s, as shown in Fig. 10. The overall pattern of cupula displacement is the same in all three cases, so the exact value of τ_1 within these limits does not affect the results of the present research.

The complex motion at the conclusion of the Nervous System-C map is given by subjects' reports of perceived motion (and position). The acceleration experiment yielded about 15° pitch-up perception (Fig. 7), while the deceleration experiment yielded about 90° pitch-down perception (Fig. 8).

Why the difference in perceptions? After all, the acceleration (Fig. 7) results in a final vertical canal hair displacement of greater magnitude than the deceleration does (Fig. 8). Hair displacement in the otolith organs does not indicate position of pitch forward or pitch backward. Somehow, the nervous system gives a distorted interpretation of the information provided. A classical explanation of forward/backward perceptual differences involves the fact that the utricular macula is tilted backward. However, that explanation does not work here; other experiments in the same paper²¹ show that deceleration has a stronger effect than acceleration even when the subject is oriented in different positions with respect to the centrifuge motion.

The property of temporal dependence can be applied here in relation to the nervous system. The final hair displacements in the semicircular canals are

similar for the two experiments, but the nervous system apparently does not simply use current hair displacement to determine which motion is to be perceived; it gives significantly different perceptions in the two cases. Therefore, it is necessary to look at the entire sequence of sensor status (hair deflection, here) for clues. In particular, during the deceleration (Fig. 8), the vertical semicircular canal hairs are deflected almost immediately in a direction to reflect pitch-down motion, whereas the same hairs in the acceleration experiment (Fig. 7) are not significantly deflected until the fourth or fifth step of the complex motion. While there are quite likely also other relevant factors (discussed later), this observation about hair deflection indicates that the beginning of a complex motion may play a greater role in the nervous system's production of perception than do the later stages of the same motion.

Additional physiological evidence¹⁷ supports the hypothesis that the nervous system contributes to temporal dependence. The existence of regular and irregular primary afferents in the vestibular system, with tonic and burst properties, respectively, shows that the nervous system treats the beginning of a motion differently than the middle or end of a motion. More precisely, at the start of an acceleration both regular and irregular afferents have firing rates reflecting the hair displacement; however, as the acceleration continues, the irregular afferents adapt to the continuing acceleration, and their firing rates return toward the resting rate. In this way, the nervous system treats the beginning of a motion differently than the middle or end, and even does so at the primary afferent level. There may also be processes at secondary and other levels in the CNS that treat the different stages of a motion differently, in addition to the primary afferent contribution to temporal dependence.

Both physics and the nervous system are thus responsible for temporal dependence. In order to determine the perceptions associated with any given complex motion, the laws of physics and biomechanics, the nervous system, and we as scientists must view all steps of the complex motion as a whole rather than analysing each step independently.

Interdependence of linear and angular components

The third global property of complex motion perception is that perceived angular motion depends on both the angular and the linear motion, as does perceived linear motion.

We discuss this property by illustrating a hypothesis arising from discussions in Guedry *et al.*²¹ and Guedry.¹⁹

Hypothesis. Perceived angular acceleration is directly related to magnitude change of the resultant linear acceleration.

We display the relevant portions of a centrifuge run²¹ by means of the self-motion perception

framework. As discussed in the previous subsection and illustrated in Figs 7 and 8, the deceleration of a centrifuge resulted in greater pitch-change perception than the acceleration of the centrifuge. The beginning of the linear component of these examples is displayed in Fig. 11, with a shorter time-step than before. A distinct difference between the acceleration and the deceleration is

that the magnitude of the hair deflections for the otolith organs starts small and increases (slightly) during the acceleration (Fig. 11A), but starts large and decreases during the deceleration (Fig. 11B). This is one example in which a decreasing otolith hair deflection in the plane of a detected angular acceleration results in a strong perception of angular motion, while an increasing otolith hair

Fig. 12. Diagram of the vestibular Coriolis effect, with clockwise angular velocity and rightward head tilt. Since magnitudes of linear motion are smaller than in previous figures; only the innermost circles of the linear notation are used, magnified here. Angular velocity of $60^\circ/\text{s}$ and a head tilt of 45° with duration 1.5 s is displayed here, assuming a tilt velocity approximating a half cycle of a sine curve. (Other assumptions about tilt velocity profile such as trapezoidal or triangular give the same results for our purposes.) The usual notational conventions hold. The perception of backward tumble is displayed at the bottom, and the notably similar final angular sensor status is highlighted by bold face Hs.

Fig. 13. Diagram of the optokinetic pseudo-Coriolis effect, with counterclockwise angular velocity of the visual surround and rightward head tilt. Angular velocity of $60^\circ/\text{s}$ and a head tilt of 45° with duration 1.5 s is displayed here, assuming a tilt velocity approximating half a cycle of a sine curve. (Other assumptions about tilt velocity profile such as trapezoidal or triangular give the same results for our purposes.) The counterclockwise angular motion of the visual surround at start is displayed in a box at upper left, and the resulting direct optokinetic stimulus to the sensors is displayed in the same notation. This visual sensor status notation is used here as an abbreviation for the status of the photoreceptors in possible combination with eye movement information; motions concentrating on vision would require a more precise notation. The perception of backward tumble is displayed at the bottom, and the final angular sensor status is highlighted by bold face Hs representing the essentially undeflected semicircular canal hairs.

deflection in the plane of a detected angular acceleration results in a weak or non-existent perception of angular motion.

We propose that the Hypothesis above gives an explanation for differing pitch-change perceptions. This explanation also applies to an experiment by

Cohen *et al.*,¹⁰ in which subjects reported little or no angular motion perception¹⁹ despite angular motion and presumed deflection of the semicircular canal hairs. In that experiment, angular motion was accompanied by *x*-directed linear acceleration (and associated otolith hair deflection) that increased to approximately 4 g-units, then decreased. Upon consulting the Hypothesis above, we see that the beginning of the motion, with increasing resultant linear acceleration in the plane of the angular motion, should contribute more to the perception than the later part of the motion. Indeed, in all motions described here, the lack of angular motion perception can be attributed to an increasing linear vector.

The Hypothesis is illustrated by these examples, showing that the perception of angular motion depends strongly on the actual linear motion. Here, the resultant linear acceleration does not turn within the plane of angular motion, but it changes in magnitude. Increasing resultant linear acceleration in this plane causes smaller perceived angular motion than does decreasing resultant linear acceleration in this plane.

Initial perception effect

The fourth global property of complex motion perception is that the perception of motion at the start of a complex motion profoundly affects the ensuing motion perception.

The perception of motion at the start of a complex motion has associated with it an expectation of ensuing motion. We propose that expectation, which is directly related to initial perception, explains certain cases of self-motion perception, especially during active motion. Active motion is the type of motion most often experienced by humans in everyday life, and we proceed toward understanding not only passive motion perception, but also active motion perception.

Expectation in relation to sensory systems has been studied in a number of different contexts,^{4,8} which we do not attempt to review here. Expectation does not imply a conscious awareness, but rather a state of the nervous system indicating anticipation of certain sensory input. During perception of sustained motion with impending active motion, the nervous system most likely expects a certain impending complex motion. For example, if a subject sits stationary and is asked to bend forward, the nervous system prepares itself for the reafference, the sensation of bending forward. This anticipation of the sensation of bending forward may be conscious or unconscious, and probably affects motor pathways in the nervous system, in addition to sensory pathways.⁸ The entire combination of perception, expectation and sensory-motor interaction has a profound effect on the perception of self-motion during the actual motion.

For the current context, we illustrate the concept of expectation with the vestibular Coriolis effect and the optokinetic pseudo-Coriolis effect. The vestibular

Coriolis effect is a classic vestibular phenomenon,^{18,39} also sometimes referred to as the “cross-coupled effect”.^{18,20} The optokinetic pseudo-Coriolis effect was reported by Dichgans and Brandt¹² to evoke the same perception of self-motion as does the vestibular Coriolis effect. Before we begin, it is important to point out that perception for both these phenomena tend to be confusing to the subject, and sometimes contradictory reports of motion occur. According to some reports, the optokinetic pseudo-Coriolis effect could perhaps be better called the “pseudo-Purkinje effect”. We first diagram the classic perceptions of the two phenomena, and then briefly discuss the phenomena in terms of both the classic perceptions and other possible perceptions.

For the vestibular Coriolis effect, a subject sits upright in a rotating chair, and at some specified point in time, tilts the head. For our diagrams, we use the case of 60°/s clockwise rotation, with a 45° rightward roll tilt of the head taking 1.5 s, and assume the entire motion takes place in the dark. This motion classically results in a perception of tumbling backwards, i.e. backwards pitch motion, which can be

Fig. 14. Explanation of the optokinetic pseudo-Coriolis effect, by “expectation”. (A) The angular motions that are expected, occur, and are perceived in the optokinetic pseudo-Coriolis effect. The expected motion is perceived even though it does not occur. (B) Table showing perceived motion based upon expectation and motion that occurs. The circled YESs are from the vestibular Coriolis effect and the optokinetic pseudo-Coriolis effect; an unexpected motion that occurs is perceived, and a motion that is expected but does not occur is nevertheless perceived.

Fig. 15. Perceptual map with shape that fits the results of the present paper. Both the Physics and Nervous System maps are many-to-one (i.e. include a collapse), and there is a systematic deviation from the identity map.

explained by cross-coupled angular velocity vectors. We diagram this motion and its perception in Fig. 12.

For the optokinetic pseudo-Coriolis effect, a subject sits upright surrounded by a vertical visible drum that is rotating about a vertical axis, and at some specified point in time, tilts the head. For our diagrams, we use the case of $60^\circ/\text{s}$ counterclockwise drum rotation, with a 45° rightward roll tilt of the head taking 1.5 s, and assume the subject has eyes closed during the head tilt. This motion also classically results in a perception of tumbling backwards, i.e. backwards pitch motion,¹² which cannot be explained by cross-coupled angular velocity vectors. We diagram this motion and its perception in Fig. 13.

We elaborate on the perceptions associated with these two motions. First, the complex motion associated with the vestibular Coriolis effect begins with the sustained motion consisting of rotation in the dark. The perception associated with this sustained motion is a perception of sitting stationary.^{18,25} When the head tilts, a backward pitch impulse is detected by the semicircular canals so that the subject reports backward pitch perception. On the other hand, the complex motion associated with the optokinetic pseudo-Coriolis effect begins with the sustained motion consisting of sitting stationary while viewing a rotating drum. The perception associated with this sustained motion is a perception of rotation in the opposite direction^{12,13} (clockwise here). The subject has a perception of rotation of the kind that the subject in the vestibular Coriolis experiment is actually experiencing. When the head is tilted, the subject perceives a non-existent backwards pitch impulse.

In other words, the optokinetic pseudo-Coriolis subject perceives something that would have happened (a backwards pitch impulse) if the beginning motion had been the subject's beginning perceived motion. In some sense, the subject then perceives the expected motion instead of the actual motion (Fig. 14).

This phenomenon and its explanation contradict the usual explanation for expected sensations. Usually, it is reasoned that the nervous system effectively tunes itself to accept the expected input and respond in particular to the unexpected part of

the input, or to the difference between actual and expected.^{2,3,4,8} Along this line of thought, it could be argued that if a subject expects a stimulus but the stimulus does not occur, then the subject will have the opposite perception to some degree. For example, if an automobile passenger expects the car to slow for a nearing stop sign but the car does not slow down, then it is predicted that the person will have a perception of continuing at the same speed or even speeding up. One would not predict that the

- ① Pitch perception experiment of Correia, Hixson, and Niven¹¹
- ② Acceleration stage of centrifuge experiment of Guedry, Rupert, McGrath, and Oman²¹
- ③ Deceleration stage of centrifuge experiment of Guedry, Rupert, McGrath, and Oman²¹
- ④ Centrifuge experiment of Cohen, Crosbie, and Blackburn¹⁰
- ⑤ Optokinetic pseudo-Coriolis effect¹²
- ⑥ Vestibular Coriolis effect^{18,37}

Fig. 16. Examples of combinations of linear and angular motion in a complex motion. Several different motion profiles are listed—zero, non-zero constant, increasing, etc.—for linear and for angular acceleration. Also quite relevant to a motion are the relative linear and angular motion orientations, which are not reflected in this figure; the number of resulting combinations is quite large. Experiments discussed in connection with the self-motion perception framework are marked in the chart according to their linear and angular acceleration profiles.

passenger has a perception of slowing when it does not occur.

We claim that even the automobile passenger is perceiving a motion that is expected and does not occur. In analogy with the optokinetic pseudo-Coriolis experiment, we look at the subject's head motion. In the automobile, the passenger expects to prevent the head from falling forward during the impending deceleration of the automobile by contracting muscles in the back of the neck. Perhaps these muscles even contract. However, when there is no deceleration, the passenger has a perception of the car speeding up, perhaps because of a sensation of the head moving backward—exactly the motion to be expected if the muscles in the back of the neck contract.

One major difference between the person in the automobile and the person in the optokinetic pseudo-Coriolis experiments is that the latter is typically held by a head-holder to prevent the head from moving outside the tilt plane. At first glance, this fact seems to add confusion to the expectation explanation. On the contrary, this fact clears up one of the original sources of confusion: subjects sometimes give reports of self-motion in a direction opposite to the classical tumbling direction. Perhaps a subject who does not give the classic report of tumbling perception in the optokinetic pseudo-Coriolis experiments is interacting with the head-holder in a different way than a subject giving the classic tumbling report.

The vestibular Coriolis effect, like the optokinetic pseudo-Coriolis effect, can result in confusing and contradictory reports by subjects. We predict that perceptions are closely related to the exact circumstances of an experiment—for example, whether a head-holder is used during the motion. The general prediction would be that subjects making active unconstrained head movements would report a perception of tumbling in the direction opposite to that diagrammed in Fig. 12 (the classic perception). The active and unconstrained aspects of such motion cause motor influences to become prominent; Lackner and DiZio²⁷ provide an interesting discussion of the possible affects of muscle spindle gain on the linear component of Coriolis effects.

In summary, the vestibular Coriolis effect and especially the optokinetic pseudo-Coriolis effect illustrate the strong effect of initial perception on the ensuing perception during complex motion. In the optokinetic pseudo-Coriolis effect, the unusual perception of tumbling upon tilting the head to the right is due to a mismatch between initial perception and actual motion. If the initial perception had matched the actual motion, then the head tilt would almost certainly have resulted in the simple, accurate perception of head tilt.

An additional outcome of this analysis is an answer to a question raised in the discussion of collapse in the maps. The nervous system does contribute to the collapse within the full Motion-to-Perception-C map.

As indicated in Figs 12 and 13, the sensor status associated with the two motions is quite different, but the direction of motion perception is the same. Two different motions map to the same perceived motion, this time with the nervous system being responsible for the collapse instead of the laws of physics.

Principles of self-motion perception for complex motion

The properties above result in the following formal principles:

Principle C1. The Motion-to-Perception-C map is many-to-one.

Principle C2. The Motion-to-Perception-C map is not a sequence of independent maps on Motion Sequence Space.

Principle C3. The linear and angular components of Motion-to-Perception-C are interdependent.

Principle C4. The initial perceived motion profoundly affects the ensuing perception during complex motion.

Once again, we state principles explicitly and formally in order to accomplish several goals. First, the principles can be analysed and proved within a formal framework, as developed above. Second, particular instances of self-motion perception and misperception can be ascribed to the operative principle. Third, the principles form a foundation for the refinement of our understanding of self-motion perception; this refinement may include the recognition of additional principles, or further investigation of the above principles.

DISCUSSION

This paper has analysed the full map from motion to perception, distinguishing physical from nervous system contributions and evaluating experimental results for principles determining the overall shape of the map. The goal of comparing and contrasting different motion studies has been accomplished through the investigation of experimental results.^{10-12,19-21} The roles of physics and the nervous system have been distinguished by the development of a formal framework that includes sensor status as an intermediate step between actual motion and perceived motion. In addition, the evaluation of experimental results has resulted in two principles of simple motion perception and four principles of complex motion perception, describing the shapes of the self-motion perception maps: the map from actual motion to sensor status, the map from sensor status to perceived motion, and the full map from motion to perception.

Physics and nervous system distinguished

The formal framework has provided the means by which to attribute certain properties of self-motion perception to physics or to the nervous system.

Physics is a major contributor toward the indistinguishability between many distinct motions, while the nervous system is solely responsible for the interdependence in the perception of linear and angular motion. Physics and biomechanics contribute to the dependence in perception of the steps of a complex motion, but the nervous system also plays a major role in causing the dependence. At the same time, the nervous system is solely responsible for the systematic misperception of tilt in different resultant acceleration environments. The framework also provides a means by which to distinguish the roles of physics and the nervous system in future experimental results.

According to these guidelines, a report of self-motion perception or misperception can be attributed either to the laws of physics or to the nervous system. For example, if a subject reports different perceptions of linear motion in different angular motion environments with identical linear components, then the misperception must be attributed entirely to the nervous system because the nervous system is solely responsible for the interdependence in the perception of linear and angular motion.

Shapes of the maps

Within the framework developed here, self-motion perception takes a certain shape, manifested by a combination of the shape of the Physics map from motion to sensor status and the shape of the Nervous System map from sensor status to (perceived) motion. The type of map shown in Fig. 2A has been ruled out. On the other hand, a map such as shown in Fig. 15 fits the principles developed.

One characteristic of the full map from motion to perception is that it is many-to-one. In other words, the map collapses many actual motions down to the same perceived motion. While this property has been attributed here mainly to physics, it is appropriate to ask to what degree the nervous system maps contribute to the collapse; the perceptual similarity between the classic vestibular Coriolis effect and the classic optokinetic pseudo-Coriolis effect is evidence of the nervous system's contribution to a collapse. Perhaps we have not encountered the nervous system's many-to-oneness in full form, simply because of an experimental bias toward motions of a certain simplicity. It would not be unreasonable to guess that during especially complex motions, subjects may report "confusion" or may report perceptions of motion lacking some of the complexity of the actual motion; such reports have already been observed in the centrifuge experiment in which subjects reported perception of linear motion only, despite the presence of both linear and angular motion.^{10,19} If the trend toward simplification within perception of a complex motion generalizes, then the nervous system may contribute as much or more to the collapse within the perceptual map than the laws of physics do.

Another characteristic of the shape of the full map from motion to perception is its systematic deviation

from the identity map, the example given in this paper being the consistent increase in pitch-back perception for increasingly large z -directed resultant linear acceleration. Taken alone, this example might lead us to believe that the perceptual map is continuous, monotone and perhaps even linear in some sense. In fact, much experimental research benefits from the fact that in many small regions of motion space, results are relatively continuous, monotone and sometimes linear, making for nice data analysis. At the same time, present and future research is interested not only in small regions of motion space, but in large regions of motion space, and in the way the nervous system handles the entire space of possible (and impossible) motions.

In the future, more sophisticated mathematical techniques will help form the big picture of self-motion perception. One role of the framework presented here is as a foundation upon which mathematical techniques and results can be applied. A likely candidate for application is the Intermediate Value Theorem,³⁴ with which results can be obtained about regions of a space that lie between other well-studied regions. Other types of mathematical results that may apply especially in the case of micro-gravity, where singularities can exist at zero gravity, are those of fixed points and singularities and their properties. A classic result of this type is that "You Can't Comb a Coconut," resulting from the fact that every continuous map of a sphere into itself either has a fixed point or sends some point to its antipode.³¹ Fixed points in a perceptual map would be points of perfect perception that are interspersed with regions of imperfect perception.

Principles

The two principles of simple motion perception and four principles of complex motion perception presented in this paper are stated formally in order to be demonstrated rigorously and used in conjunction with experimental results. The presentation of these six principles leaves open the possibility of additional principles, and forms a foundation upon which to elaborate the existing principles and develop new principles. The experimental results discussed in this paper have been confined to a few examples; it has not been our intention to do a review of the literature. Rather, we have selected a few intriguing perceptual phenomena with which to illustrate or elaborate upon the principles.

As an application of existing principles and their elaborations in the present paper, one may predict that a subject undergoing angular acceleration with decreasing magnitude fixed-direction resultant linear acceleration in the plane of the rotation in the beginning stage of the motion would have a perception of motion that includes a significant angular component. An elaboration of Principle C3 states that increasing resultant linear acceleration in the plane of rotation causes smaller perceived angular

motion than does decreasing resultant linear acceleration in that plane. This result allows us to predict the outcome of the following type of experiment. A subject sits facing the center of a centrifuge rotating at constant velocity, then the centrifuge decelerates while the subject is moved radially away from the center and is also rotated on-axis to keep the horizontal-plane component of the resultant linear acceleration directed along the subject's x -axis. If the centrifuge's angular deceleration profile and the subject's radial movement are such that the x -directed linear acceleration decreases, then the principles would predict that the subject's report of perceived motion will contain a significant angular component.

Extensions to further research

The present framework generally considers motion of the body as a whole, as is encountered during passive motion in a vehicle. Motions are compared and contrasted only when they have comparable relative head-trunk orientation. An obvious extension of the present work would be to incorporate additional parameters to describe the relative limb, head and trunk orientations. As it turns out, the relative positions of head and trunk affect self-motion perception even when the body moves as a whole. An example of recent research on this topic is that of Lackner and DiZio²⁸ on the differing perception of whole-body orientation depending on the pitch position of the head on the body.

Another possible extension of the present research would be to include corollary discharge associated with motor commands. This would be especially important when concentrating on active movement and comparing perception between motions with different active movements. Discussion of corollary discharge and/or reafference would also be important for studies on vision during self-motion perception, because contraction of the extraocular muscles affects the interpretation of the image detected by the retina.

The analysis of vision is a particularly complicated matter, because the visual field has many characteristics that are relevant to self-motion perception. Ultimately, the motion of the visual field must be described by more parameters than just linear and angular velocities. The direct stimuli to the sensors are not velocities; rather, velocities are an interpretation after neural processing of the image. For instance, velocity can only be derived from a retinal image if an estimation of distance to the visual surround is made. Factors like these show that the processing of visual images can be incredibly complicated. An entrance into the literature can be found in Wertheim³⁸ and the contained references.

A goal of the formal framework is to lead to the discovery of global patterns in perception and global patterns in the processes of the nervous system, tying together specific patterns found in studies of specific types of motion. It has been necessary to make certain assumptions about other influences in percep-

tion. As discussed earlier at length, the ideal case would have the same subject with the same cognitive influences performing all of the motions under study. In the long term, global patterns exhibited by the nervous system that are discovered in a formal study could be used in conjunction with results of neurophysiological research to determine how the neural pathways and processes work in order to reflect the patterns found.

Experimental studies

At the present time, existing experimental results on perception of complex motion are sparse within the space of possible complex motions (Fig. 16), but the existing results are quite intriguing; we have looked at only a few here. However, because of the present sparsity of known results in the motion space, it is difficult to apply the framework to a more sophisticated mathematical analysis of the maps involved in perception. The addition of new experimental results across the spectrum of possible combinations of angular and linear motions will contribute toward our ability to formally investigate and analyse the motion perception map as a whole.

The optokinetic pseudo-Coriolis effect and the vestibular Coriolis effect give an interesting arena for investigation because of the possible roles of motor control and interaction with the mechanical headholder. Technically, the framework must be expanded to include not only passive, but active head role in order to properly investigate the factors behind the scenes. Once active movement is included, the relevant parameters include: passive vs active, restrained vs unrestrained and expected vs unexpected. Considering past variability in the direction of perceived angular motion, we would predict that some combinations of the relevant parameters lead to certain perceptions while others lead to opposite perceptions. At the same time, certain combinations probably lead to more inconsistency than others. These motion perceptions may have a highly individualized character so that the patterns are not found through averaging the data from each type of motion, but through analysing the shape of each individual's perception across the various types of motion, and finding patterns across subjects in those shapes.

In general, while most experiments rely upon data averaged across a number of subjects, the framework gives a means by which to investigate patterns at a higher level. The shape of an individual's perceptual map (or part of it) can be determined by experiment with motions of several different types or magnitudes. Instead of averaging the data across subjects for a single motion, one may be able to "average" the shapes of the perceptual maps across subjects. We have not performed such an average of shapes in the examples here because most published experimental data are presented in the traditional form with an average across subjects, and it would be necessary to have the same subjects undergo several different

motions in order to perform such an average on the maps. Nevertheless, a higher-level data analysis is possible through the framework, and may be especially useful for the more puzzling perceptual phenomena.

CONCLUSION

Comparison of experimental results leads to principles, which in turn lead to results about the shape of the perceptual map. In reality, there is not just one perceptual map, but a whole class of perceptual maps across individuals and across subject states. Therefore, a precise analysis of motion perception involves principles rather than equations; the principles encompass the global shape of perception and rule out

the possibility of certain types of perceptual maps from among the set of all possible maps. As more data are gathered about the nervous system, the variation among individuals and trials will be treatable not as an annoyance, but as a property of families of curves. The maps under investigation can be described quantitatively and precisely through formalism, despite the fact that the nervous system never gives exactly the same response twice.

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