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Constructive Perception of Self-Motion

Jan E. Holly* and
Department of Mathematics Colby College 5845 Mayflower Hill Waterville, Maine 04901
jeholly@colby.edu

Gin McCollum
Neuro-Otology Department Legacy Research Center 1225 NE 2nd Avenue Portland, Oregon 97232 mccollum@ohsu.edu

Abstract

This review focusses attention on a ragged edge of our knowledge of self-motion perception, where understanding ends but there are experimental results to indicate that present approaches to analysis are inadequate. Although self-motion perception displays processes of "top-down" construction, it is typically analyzed as if it is nothing more than a deformation of the stimulus, using a "bottom-up" and input/output approach beginning with the transduction of the stimulus. Analysis often focusses on the extent to which passive transduction of the movement stimulus is accurate. Some perceptual processes that deform or transform the stimulus arise from the way known properties of sensory receptors contribute to perceptual accuracy or inaccuracy. However, further constructive processes in self-motion perception that involve discrete transformations are not well understood.

We introduce constructive perception with a linguistic example which displays familiar discrete properties, then look closely at self-motion perception. Examples of self-motion perception begin with cases in which constructive processes transform particular properties of the stimulus. These transformations allow the nervous system to compose whole percepts of movement; that is, self-motion perception acts at a whole-movement level of analysis, rather than passively transducing individual cues. These whole-movement percepts may be paradoxical. In addition, a single stimulus may give rise to multiple perceptions. After reviewing self-motion perception studies, we discuss research methods for delineating principles of the constructed perception of self-motion. The habit of viewing self-motion illusions only as continuous deformations of the stimulus may be blinding the field to other perceptual phenomena, including those best characterized using the mathematics of discrete transformations or mathematical relationships relating sensory modalities in novel, sometimes discrete ways.

Analysis of experiments such as these is required to mathematically formalize elements of self-motion perception, the transformations they may undergo, consistency principles, and logical structure underlying multiplicity of perceptions. Such analysis will lead to perceptual rules analogous to those recognized in visual perception.

1. Introduction

Perception is often constructed from a recognized pattern of self-motion, as a whole, rather than moment by moment. For example, well-practiced walkers often cease to directly perceive the details of the motion, only noticing deviations from a well-known pattern. Similarly, subjects fail to perceive the details of forces necessary to produce well-practiced

Please address correspondence to GM. 090413.
*Author order alphabetical, by convention of equal contribution in the tradition of pure mathematics and theoretical physics.

arm movements, even when Coriolis forces are present, as long as torso movements are natural and voluntary (Cohn et al 2000). In contrast, when similar Coriolis forces are produced by experimental manipulations, subjects perceive them clearly as interference with the reaching movement. In both cases, the perception is of a whole reaching movement, in the one case well habituated to forces that are actively ignored.

The role of active, constructive processes in perception does not, however, depend on habituation alone. One example arose in an experiment in which subjects heard the list of familiar words "at, it, ate, aid" played repeatedly, with equal stress on each syllable (Lackner & Tuller 1976). Although subjects heard the list accurately at first, their perception changed to "Ah, it's fated. " Later, it reverted to the more accurate original.

This linguistic example displays several perceptual transformations that will be exemplified in self-motion data presented below. Most generally, phonemes are added, ignored, or replaced. For example, the "s" in "it's" is added, and the "t" in "at" is ignored. In addition, the "a" in "at" is replaced with the more open one in "Ah", a shift between two distinct pronunciations of "a". Although the vocal system is capable of producing a continuum of vowels, phonemes are discretized linguistically, according to the language. Similarly, self-motion perception displays discrete perceptual elements that are subject to transformation (§2).

Transformations help the perception, as a whole, to make sense. In the linguistic example, transformation of the component phonemes turns the list of words into a sentence with meaning. Like the phonemes and words, the sentence is a unit, but at a higher level, since it is composed of words. Similarly, the line drawing of the Necker cube is composed of lines (Fig. 1). The Necker cube springs into three dimensionality despite the fact that each individual line lies in the plane of the paper (Kaufman 1974). In self-motion perception, as in language and visual perception, constructive processes transform perceptions of whole movements (§3). For motions, "transformation" is best understood in the mathematical sense of a mapping of relevant variables, and will be so used throughout this paper.

The goal of "making sense" does not rigidify constructive perception. Instead, there are multiple distinct possibilities. The Necker cube, rather than resting in one orientation, typically reverses direction, with one square in front, then the other. For the Necker cube, "making sense" is being consistent with both the drawing and a three-dimensional percept. In the linguistic case, "making sense" motivates exchanging the actual list of words for the sentence "Ah, it's fated" (Lackner & Tuller 1976). In contrast to "making sense" linguistically, "making sense" in self-motion perception can be characterized as consistency properties. Such self-motion consistency properties may include physical properties such as velocity matching change in position, as well as the matching of sensory modalities and motion segments such as locomotor phases. Such consistency principles and other "top-down" constructive properties have long been a part of visual perception and linguistic research, while the "bottom-up" importance of the physical stimulus and its sensory registration have been well recognized. In contrast, a narrower, only "bottom-up" and input/output approach has standardly been taken to self-motion perception: studies of the sensory transduction of visual, vestibular, and somatosensory stimuli and their continuous deformation by sensory and neural properties (§5.2).

The purpose of this review is to raise awareness of constructive processes of self-motion perception and to initiate a categorization of them. Constructive perception takes place on at least two levels of analysis: transformations of motion properties (§2) and creating consistency of whole movements (§3). A change in either can affect the other. In addition, there is a multiplicity of possible perceptions of whole movements, given the same stimulus

(§4). The following sections review examples. In the Discussion (§5), we present more fully an approach to mathematical theory appropriate to these examples. Throughout this review, the word "mathematics" refers to rigorous logical systems (which are discussed in §5.3). The world of self-motion experience this review portrays is shaped by a discrete scaffolding and smoothed over by consistency relationships, where both the discrete† and the continuous are bound by principles that can be expressed mathematically. In referring to phenomena as "transformations" we intend to foreshadow a characterization in terms of discrete transformations, in keeping with the linguistic examples that conform to discrete linguistic rules (§5.3).

† The term "discrete" refers here to the mathematics of discrete transformations, such as exchanges, permutations, and reflections.

2. Transformations of Elements of Motion

A typical transformation in self-motion perception involves the addition or omission of individual elements of motion, for example, the addition of angular motion or its omission or replacement by linear motion. Illusions involving such simple transformations serve as a guide to the units of self-motion perception. These units are not arbitrary, but are the basis for an elaborate and typically accurate system for integrating sensorimotor behavior in physical space. Mathematical characterization of illusions can express not only the mathematical transformation but also the discrete set of elements of self-motion indicated by experiments such as the ones we review. Further investigation will be needed to illuminate the extent and reasons for discretizing elements of motion; here our intent is to provide examples and tentative framework.

2.1 Transformations Involving Yaw

A dramatic example of stimulus transformation occurs when subjects experience off-vertical axis rotation (OVAR) (Fig. 2A) (Guedry 1974, Denise et al 1988). Initially, many subjects' perceptions are veridical: they perceive rotation about an axis tilted from vertical. As the semicircular canal response returns to a resting level during a constant angular velocity motion, subjects perceive a motion along a conical or circular trajectory (Fig. 2B,C). However, these perceptions cannot be explained completely by the decay of the semicircular canal response: A conical motion as illustrated in Fig. 2B would involve an angular acceleration with continuously changing axis, but such an angular acceleration is not present. Therefore, a more complicated perceptual process must be involved. In this process, subjects transform actual rotation into perceived motion along a curved trajectory.

In OVAR (Fig. 2), both linear acceleration along a trajectory and tilt in gravitation are physically linear accelerations, and thus registered identically by the otoliths and other inertial sensors in the body (Mittelstaedt 1997). The combination of tilt and translation perceived in OVAR varies with the individual, trial, and especially the frequency (Guedry 1974; Glasauer 1995; Wood 2002). For lower frequencies, subjects tend to perceive more tilt, a physically arbitrary perception apparently habitual because slow linear accelerations are often associated with tilt (Mayne 1974). More tilt leads to a conical trajectory (Fig. 2B), as opposed to a more cylindrical trajectory at higher frequencies (Fig. 2C).

An extreme of OVAR with the subject tilted 90 degrees from vertical is called barbecue spit rotation (Fig. 3A). After an interval, subjects in barbecue spit rotation perceive a cylindrical motion (Fig. 3B) (Lackner & Graybiel 1978; Lackner & DiZio 2004). However, this motion perception fades when foot or head pressure is applied against the apparatus. In its place, another vivid perception is gradually established: in the case of foot pressure, a cone with the feet fixed (Fig. 3C); with head pressure, a cone with the head fixed (Fig. 3D) (Lackner &

Graybiel 1978; Lackner & DiZio 2004). In each case, pressure establishes a fixed point about which the body moves.

In a variation on the interchange of yaw rotation with curved movement in OVAR, subjects in visual experiments added motion along a path to rotation in place. Participants viewed a variety of translation and yaw motions in the form of optic flow patterns and demonstrated their perception by moving a small "vehicle" on a tablet (Bertin et al 2000). To a presented rotation in place (Fig. 4A), some participants added perceived motion along a curved trajectory (Fig. 4B). Many participants identified motion facing outward along a circular trajectory (Fig. 4B) as a rotation in place (Fig. 4A). Effects on yaw rotation were also explored by combining actual angular and linear motion (Ivanenko et al 1997) and by combining inertial with visual stimulation (Bertin & Berthoz 2004). It is also notable that one subject in a purely linear experiment added yaw motion to the self-motion perception (Wertheim et al 2001).

These interchanges of yaw motion cannot be explained by the decay of the semicircular canal responses alone; rather, they exemplify a constructive choice of perception. That yaw rotation and curved movement are freely interchanged is an explanation consistent with the point that the canal responses return to a resting level during sustained rotation. That is, because the canals can return to resting level, the perceptual system consisting of multiple neural centers may not distinguish rotation about the body axis very well from motion around a curve; this conflation may occur even when vestibular stimulation is not involved, as in the case of purely visual stimulation (Bertin et al 2000; Bertin & Israël 2005).

2.2 Transformations Involving Pitch

It is not only in yaw that rotation is transformed into motion along a curved trajectory. Stone and Letko (1964) submerged subjects in a rotating tank of water, as in a horizontal-axis washing machine, and rotated them in the forward pitch direction with the water (Fig. 5A). Instead of a tumbling motion in pitch, subjects perceived an upright motion along a curved trajectory, like that of riding a ferris wheel (Fig. 5B). Here, the interchanged rotation and curved movement are in the vertical plane.

A typical explanation is that the ferris-wheel motion has a rotating linear vector, just as detected by the tumbling subject, and correctly reflects a lack of perceived angular velocity as the subject's perception of rotation decays to zero. However, this explanation only partially explains the perception. A ferris-wheel motion actually has a rocking, not a rotating, linear vector, unless the circular motion is so fast that the subject experiences greater than 2 g at the bottom of the circle; in that case, the ferris wheel's linear vector rotates in a very oblong fashion, not in a circular manner like the tumbling motion's linear vector.

The ferris-wheel perception, therefore, does not fit a simple explanation of perception by passive transduction. In the actual pitch rotation, the gravity vector, which in this case is the whole gravito-inertial acceleration (GIA), rotates with respect to the subject. Similarly, the perceived ferris-wheel motion involves a rotating linear acceleration vector; however, the perceived vector is the result of linear movement that changes direction along a curved trajectory. Another difference is that a ferris-wheel motion would have a considerably asymmetric rotating GIA, or even just a rocking GIA with fluctuating magnitude. In other words, the actual and perceived motions differ in that the perceived ferris-wheel motion also has a superimposed constant linear acceleration vector due to gravity, causing the rotating vector to be offset by a constant amount in the vertical direction. The subject nevertheless transforms the pure rotating vector into an offset rotating vector, just as subjects in the visual experiments presented above ignore translation in misperceiving a rotation in place as a movement along a trajectory (Bertin et al 2000; Bertin & Israël 2005). The ferris-wheel transformation can alternatively be viewed as an insertion: the offset itself, i.e. the constant gravity, is inserted into the perception.

In the pitch-rotation experiment, at high frequencies, around 55–60 rpm, a distinct perception arises, that of straight up-down motion (Fig. 5C) (Stone & Letko 1964). (Curiously, actual vertical linear oscillation can be misperceived as well, Wright 2002; Lackner & DiZio 2004; Wright et al 2005, §4.1.) In contrast to the ferris-wheel motion, up-down motion does not include a rotating vector. However, it still has in common with the actual rotation a periodic fluctuation in vertical acceleration. In this case, the subject transforms a rotating vector into a straight vertical fluctuation, with an offset as described above. In other words, more is involved than in the ferris-wheel example: the transformation involves both a neglect of the naso-occipital component of acceleration and an insertion of the vertical offset. From another point of view, this up-down perception strips all positional detail, leaving only frequency, which is segmented into two simple phases.

2.3 Additional Examples

The transformation of rotation into motion along a curved trajectory, along with that of tilt into linear acceleration along a trajectory, may be common components of illusions because of their practical significance, as when associating tilt with a rotating curved trajectory while riding a bicycle. A number of additional examples of transformations exist such as in the hilltop illusion, in which a linear movement is perceived to include tilt in the direction of motion, so that it feels like motion back and forth over a hilltop (Glasauer 1995). Further examples, involving vision and posture as well, are presented in Sections 3 and 4. For example, the perception of a rotating visual surround is transformed into a perception of bodily rotation (Brandt et al 1972; Bles & Kapteyn 1977; Marme-Karelse & Bles 1977; Kapteyn & Bles 1977; Melcher & Henn 1981; Probst et al 1985; DiZio & Lackner 1986; Ohmi et al 1987). This involves a change in perception of posture which can be quite elaborate (DiZio & Lackner 1986, §4.2). Not only posture, but the motion trajectory may be transformed (Wright 2002; Lackner & DiZio 2004; Wright et al 2005; §4.1), and even the sense of one's own body shape (Lackner & DiZio 1988, §3.3; Lackner 1988). The submerged acceleration experiment (Stone & Letko 1964) provides a transformation of the stimulus into a different perception entirely.

3. Whole Self-Motion Perceptions that Make Sense: Gestalt Self-Motion Perception

Four corners are enough for perception to construct a square (Fig. 6A) (Wertheimer 1955; Goldstein 2002). Similarly, the perception of a bicycle can be actively constructed with enough corroborating cues and without a complete view (Fig. 6B). However, two opposite corners are not enough to construct a square (Fig. 6C). Similarly, in sensorimotor control, perceptions are constructed according to the corroborating cues that are available. In some cases, the physiology of corroborating cues is suggested by the experimental observations. For example, the perception of depth in visual movement depends not only on the movement itself but also on the movement of the subject (Ujike & Ono 2001; Nawrot 2003). In general, perceptual transformation of stimuli can be mathematically characterized to understand the principles involved. Of course, theoretical research, rather than a review of experimental research, will be required to specify these principles with precision. This section presents examples of whole movement perceptions that involve transformations of the stimulus to form a self-motion Gestalt. Unlike the linguistic example, self-motion Gestalt examples invite mathematical relationships expressing sensorimotor or even neural relationships that nervous systems and behavior require be satisfied.

3.1 Gestalt of Visual Self-Motion Perception

Optic-flow experiments give examples in which whole-movement Gestalten can be seen as combinations of transformations of elements of movement perception. The previous section's examples illustrate the transformation of one movement property into another, such as when a rotation in place is transformed into movement along a curved trajectory and vice versa (Fig. 4). In the more general construction of whole-movement perceptions, there can be several transformations and deletions. In one example, outright replacement occurred in multiple ways when participants were presented with a yaw rotation plus a linear motion (Fig. 7A). In a typical response, the linear motion was replaced with a curved one (Fig. 7B). At the end of the actual motion, the subject is moving backward. This clear backward motion is replaced with a lateral motion.

3.2 Gravity and Deep Knee Bends

People doing deep knee bends have a sense of effort, the feeling of pressure on the soles of their feet, and the assumption that the floor is fixed, all of which join to form a coherent perception of down-up movement with respect to a fixed floor. However, when the deep knee bends are performed in modified g-levels in an airplane in parabolic flight, the usual cues no longer fit together coherently (Lackner & DiZio 1993b). In order for the new combination of cues to make sense together, the perception of time changes and the floor seems to rise or sink (Fig. 8). The resulting perception makes sense as a whole, following physical consistency principles, with the individual cues fitting together. Time of rising and falling is an early lesson for humans standing and walking in a gravitational field, because we must be adept at the exchange of kinetic and potential energy required by conservation of energy (McCollum et al 1995). Evidently, in this case the relationship between time and distance is a stronger cue than the assumption of the fixity of the floor.

3.3 Locomotion Matched to the Speed of a Rotating Drum

A similar constructed Gestalt occurs when walking in a circle, where cues include motion of the visual surround, vestibular cues, sense of locomotor effort, and tactile cues. When the circle is within a closed drum and on a rotating support surface, these cues can be modulated independently (Fig. 9A) (Lackner & DiZio 1988), with subjects reporting perceptions of motion that may or may not match the actual motion. The perceptions are based upon making sense of the stimulus in such a way that the cues corroborate one another. For example, an illusion of constant-velocity motion is produced by support surface and visual drum rotation with neither vestibular cues nor actual circular motion of the subject; this illusion is consistent with the fact that the perceptual system is accustomed to semicircular canals returning to a resting level during rotation.

Another illusion arises in conjunction with the obvious requirement that the foot reaches the floor, when it touches it. In particular, when the optokinetic drum moves faster than the subject walks on the turntable, the subject has a problem reconciling the visual with the somatosensory and proprioceptive cues. Some subjects perceive their shanks to stretch as they push off, so that the apparent stride length matches the speed of the drum (Fig 9B). This perception is a solution to the apparent inconsistency between cues. The perceived motion, as a whole, makes sense of the combination of cues. Such an experiment is illuminating because one might expect the nervous system to make sense of the situation by noting that the drum is moving faster than the subject is walking. However, few subjects take that route. Some instead perceive leg stretch -- and others a variety of illusions -- as part of a whole motion that makes sense of the combination of cues.

The cues involved in this rotating drum experiment display an inside/outside dichotomy, with somatosensation (touch and musculoskeletal senses) being inside, while vision relates primarily to the external world. Self-motion perception must resolve this inside/outside dichotomy. In contrast, the hierarchy in visual perception is primarily "top-to-bottom"; Hochstein & Ahissar (2002) make the important point that consciousness and learning operate from "top" or more constructed levels. In self-motion perception, a hierarchy will not be enough; a partially ordered set of constraints will be required. Mathematical constraints formalizing results such as observed in the rotating drum experiments will likely relate inside to outside perceptions.

3.4 Concordance of Position, Velocity, and Acceleration

In a physical motion, non-zero velocity corroborates a change of position. In a veridical perception of a physical motion, velocity and a change of position would imply each other, confirming that the motion is physically possible. Similarly, a change in velocity would corroborate the occurrence of an acceleration, and constant velocity would assure the absence of acceleration. However, self-motion perception of an organism with separate senses, one registering velocity and the other acceleration, is slightly different (Holly 1996). For example, a subject facing forward in a centrifuge sees constant forward motion and feels, nevertheless, a non-zero lateral acceleration. In self-motion perception, experimental protocols and methods of analysis must be open to unusual combinations of time derivatives, such as position, velocity, and acceleration, even if they are registered by the same sensory receptor.

An example of the non-physical perception of position and velocity occurs in a decelerating centrifuge. Guedry et al (1992) used a centrifuge with carriage that continuously adjusted the tilt of the subject to keep the sum of the centripetal acceleration and gravitational vectors lined up in the subject's mid-sagittal plane, while the subject was seated facing in the direction of motion. During centrifuge deceleration, subjects reported strong non-veridical perceptions, of pitching or tumbling forward, and of ascending from the earth. Because the actual motion itself is complex, an analysis of the motion-perception relationship requires additional tools. The tools must take into account the fact that subjects do not perceive rotation during the constant-velocity portion of the centrifuge run, and therefore begin the deceleration with a perception of stationarity, if they are without vision. With this in mind, mathematical development and computer simulation (Holly 2000) of the accelerations has displayed the three-dimensional motion that would be reported by a perfect processor of acceleration information that begins with a perception of being stationary. Such a three-dimensional motion is what a subject would report if the detected accelerations were accurately transduced into a perception. The resulting motion is of ascending from the earth while tumbling continuously forward, and then eventually descending during the tumble. There is also a slight wobble in the motion. Experimentally notable is that subjects generally reported the pitch motion but not the wobble.

Many subjects report forward pitch motion only to a different attitude, sometimes to a face-down or head-down position, rather than full tumbling (Guedry et al 1992). In essence, the subjects focussed on the beginning of the centrifuge deceleration and formed a perception out of that portion (somewhat like the visual example shown in Fig. 7). In fact, a typical perception was of continuing tumble even while remaining in a constant nose-down pitch position. This perception is basically a continuous repeat of the initial portion, in which the subject is oriented pitch forward while rotating forward in pitch. A similar illusion happens in music, in which a descending scale can be played on a keyboard with more than one octave, the lowest note periodically dropping off to be replaced by a high note, with the result that listeners hear a forever-descending scale that never goes off the keyboard. Just as this paradoxical musical Gestalt can be perceived, so can paradoxical self-motion Gestalts be constructed. A related example is "the leans", in which a pilot feels a continuing sense of sideways tilt, even after flying straight and level for minutes or even hours (Young 1984; Benson 1978).

4. Multiple Distinct Possibilities

A given stimulus may produce more than one distinct perception, between subjects and/or within subjects. In the linguistic case (§1) or in perception of a Necker cube (Fig. 1), a satisfactory percept is replaced after some time, out of seeming perceptual restlessness. Despite changes over time, each percept is clear and specific, even if non-veridical. In the case of the Necker cube, the universe of possibilities contains only two options, the two three-dimensional orientations of the cube, and perception alternates between the two (Fig. 1). In other cases, there may be many distinct possible perceptions.

Like the previous section, this section includes experiments that balance the right amount of concordance and discordance between sensory cues to allow the subject the freedom to display perceptual processes (as discussed in DiZio & Lackner 1986). This kind of experimental design contrasts with experiments that are focussed specifically on sensor properties. By mathematically formalizing the consistency principles that unify these multiple distinct perceptions, one states clearly the nature of the perceptual space within which they are constructed. Patterns of perceptual transition occur within that space and must be specified there. Response spaces may be expressed in neuronal populations that include neurons sensitive to whole movements (Rizzolatti et al 1987; Graziano & Cooke 2006).

This section illustrates two examples in the perception of self-motion. In the first, impoverishment of the stimulus satisfies this balance of concordance and discordance by inviting the nervous system to construct more of the self-motion perception. Unlike vision, where simply less can be seen, self-motion requires a perceived position and motion for the whole body all the time. Acceleration alone, for example, without position or velocity, leaves the nervous system to choose among an equivalence class of motions (Holly 1996; Holly & McCollum 1996).

4.1 Vertical Linear Oscillation

For vertical linear oscillation, the space of perceptual options is large, including all three translational degrees of freedom and various curvatures of both signs (Fig. 10) (Wright 2002; Lackner & DiZio 2004; Wright et al 2005). One might imagine that simple vertical linear oscillation, in which motion is aligned with gravity, would be clearly perceived; however, this motion allows an unusually wide diffusion of percepts.

Participants oscillating slowly (0.2 Hz) up and down in a chair without visual or auditory information perceive the motion veridically for approximately three minutes, after which they (mis)perceive a change in motion (Wright 2002; Lackner & DiZio 2004; Wright et al 2005). The perception changes to a vivid illusion from among a wild array of oscillatory trajectories: forward-backward and sideways climbs, swings, hilltops, S's, J's, ovals, and forward-backward and sideways straight trajectories (Fig. 10). Now and then, subjects (mis)perceive a new change in motion. As in the rotating drum experiment (Lackner & DiZio 1988, §3.3), perceptions may be paradoxical. As in OVAR (Guedry 1974; Denise et al 1988; Wood 2002) and submerged pitch (Stone & Letko 1964) participants make no errors in frequency. There may be phase errors, but the question of phase is still open to specific investigation.

Such diverse perceptions are not limited to the vertical direction. Wertheim et al (2001) found a similar variety of motion perceptions in subjects who were kept completely naïve about the nature of the motion they were about to experience, which was horizontal and linear. Notably, subjects who had seen the linear sled also eventually shifted to a perception that added curvature.

4.2 Rotating Disk

A wide array of distinct perceptions can also be produced by visual motion alone. In one experiment, participants lying still and viewing a rotating disk perceived body rotation and readjusted body position perception in a variety of ways (Fig. 11) (DiZio & Lackner 1986). In this experiment, all participants correctly perceived condition A (not illustrated), which was lying straight and horizontal, viewing a disk rotating in the horizontal plane. In conditions B and C, in which the disk was tilted, participants nevertheless perceived body rotation in the horizontal plane. This is an example of a centering perception, in the sense that participants remanded a perception to the straight, horizontal, or in some way normal perception. The segmental components of these preferred perceived orientations can be thought of as more in register with each other or more "centered". In conditions B-D, almost all participants had misperception of body position, transformed from the veridical in a way that centers one or more aspect of body position to straight and horizontal (Fig. 11).

This experiment demonstrates a large response space of perceptions, and subsequent work has related the results to perceptual transformations. The perceptions can be explained mathematically by sequences of physiological perception transformations, which form a semigroup that mathematically characterizes the perceptual dynamics (Hanes 2006). Each transformation takes an orientation to another orientation that is more centered, in the sense explained in the previous paragraph. The final orientation is the one perceived by the individual subject. Perceptions differ because pairs of segments can be centered separately. The analysis shows that different subjects take different paths through the transformations. In addition, mathematical completion of the semigroup, by taking all the compositions of the transformations, provides predictions of illusions that might be encountered in a larger subject population or as yet unexplored experimental conditions. Such studies indicate the possibility of understanding illusions that are caused by neither physics (Holly & McCollum 1996; Holly 1997, 2000, 2003) nor sensor properties, but by the normal actions of the nervous system itself.

5. Discussion

This paper reviews experimental evidence of constructive processes in self-motion perception, in order to display phenomena open to mathematical characterization and explanation. The review is organized in three sections, based on suggested mathematical approaches: (1) addition, deletion, and exchange of translation and rotation, which suggest a mathematics of discrete transformations, (2) Gestalt self-motion perceptions, which suggest transformations (as in point 1) to make components compatible for the whole motion, along with the mathematical characterization of consistency principles, (3) multiplicity of distinct perceptions in the absence of full information, which suggests not only mathematically-specifiable consistency principles but also a dynamics of shifting perceptions on a response space. While the sensorimotor system seems to have a protean ability to associate sensory stimuli and movements (e.g., Ernst 2007), physical space and gravitation put stringent requirements on posture and movement for functionality. However, all sensorimotor behavior, including posture, movement, and self-motion perception, is based on physiological principles that lead to inaccurate perceptions in certain cases, allowing us to determine these physiological principles.

To accurately reflect the actual dynamics of self-motion perception, theorists ultimately need to mathematically characterize these discrete transformations, consistency relationships, and properties of the response space. Section 2 presents examples of the discrete transformation of features of the stimulus in constructing a perception. In OVAR, visually presented yaw rotation, and actual pitch rotation, perception can add a component, delete a component, or interchange aspects of the motion. The observed perceptual dynamics could potentially be mathematically characterized in a straightforward way by using the mathematics of discrete transformations. Section 3 illustrates the way whole movement perceptions are actively constructed to form a coherent whole out of the stimulus combination, rather than passively transducing the individual pieces of the stimulus toward an incoherent result. In active body movements and in a centrifuge, subjects have perceptions that are non-veridical but that make sense of the unusual combination of stimuli. In an additional example of optic-flow motion, subjects report a more familiar and less complex whole motion than the contrived motion presented (§3, Fig. 7). These perceptions are at the same time the transformation of features of the stimulus and Gestalt constructions of a whole self-motion perception. What is the nature of sensorimotor consistency? Theoretical studies are needed to mathematically characterize the observed consistency relationships, which are observed to act as constraints on perception. Section 4 presents cases in which the same stimulus gives rise to a multiplicity of responses. This multiplicity is apparent during both actual vertical linear oscillation, where the same individual may change perception of the same stimulus over time, and visually-presented rotation, where different individuals may have distinct perceptions. This constructive process suggests the use not only of discrete transformations and consistency relationships, but also of a perceptual space with its own dynamics. To accurately characterize observed self-motion perception will require the use of mathematics that reflects these dynamics properties in a straightforward way.

Before describing in more detail the mathematical development we envision characterizing most helpfully the experiments we have reviewed (§5.3), we briefly discuss constructive perception in a visual context (§5.1) and the computational models typically used to describe self-motion perception as a continuous deformation of transduced stimuli (§5.2). In §5.3, after discussing self-motion perception in general, the ability of the nervous system to reflect the properties of physical space, and principle-based mathematics, we discuss discrete transformations, consistency principles, and response spaces in turn.

5.1 Comparison to Constructive Visual Perception

The concept of constructive self-motion perception is related to the phenomena of constructive auditory (§1) and visual perception. In vision research, passive transduction is sometimes referred to as "direct" perception, and constructive perception as either "indirect" or "directed" perception. For example, consider a row of four lights. Let the first three blink on and off, then the last three blink on and off. If these blinks are alternated at a high enough frequency, an observer sees three points of light moving back and forth (Ternus 1926). In this case, there is no motion in the stimulus, only blinking. The response space is clearly a constructed entity, distinct from the set of stimuli, because it contains motion.

A further principle is drawn from this experiment: observers have a tendency to perceive the three lights as a single configuration, rather than as single lights blinking on and off (Ternus 1926). That is, as discussed in §3, the perception is organized in terms of the movement of a whole entity, just as is demonstrated in the present paper to occur in self-motion perception. In these visual experiments, researchers have distinguished the response space from the stimulus and designed test stimuli, thus allowing the delineation of further properties of the constructive visual perception process (Rock 1997). One important discovery, relating to perceptual organization in terms of whole entities, was that absolute change in position is often less important in shaping the perception than is relative position of objects. An object that dominates, for example by size or by surrounding another object, tends to be used as a stationary reference for the movement of other objects. Similar discovery of principles for constructed perception of self-motion can be expected from analysis and design of self-motion experiments. One likely finding is that, in analogy to the principle of visual perception that a dominant object serves as a stationary reference for the movement of other objects, the sensation of being stationary may provide a reference from which additional movement is sensed. This occurs even if the stationarity is illusory and predictable from known properties such as the decay of rotation sensation (§3.4).

Vision research has a long history of recognizing "top down", i.e. constructive, processes in perception. To mention a few traditions, the Gestalt approach emphasizes the role of recognition of whole objects, the Gibsonian (ecological) approach emphasizes the extraction of information from typical environmental configurations, and the empiricist approach is based upon the idea that perception is more than the registration of sensations (reviewed in Gordon 2004). These processes describe neural dynamics, and mathematical characterization of them provides a rigorous way to determine the consequences of constructive perceptual principles.

5.2 Comparison to Existing Self-Motion Perception Models

In the study of self-motion perception, on the other hand, the predominant approach has been to recognize "bottom-up" processes in an input/output format, viewing perceived motion as a function of the stimulus. This approach stems from classic experiments in which habituation or adaptation can explain illusions, or in which illusions arise because tilt and translation cannot be distinguished by the sensors (reviewed in Guedry 1974). These illusions are not among those reviewed in the present paper because they fall in the category of those explained by the "bottom-up" approach; they include the diminishing perception of rotation while continuing to rotate, the increasing perception of tilt while on the arm of a rotating centrifuge, and other illusions that fit standard continuous models.

To date, models of self-motion perception are dominated by the "bottom-up" and input/output -- not constructive -- approach. Existing three-dimensional models thus are consistent with many classic experimental findings, and have used a variety of "bottom-up" and input/output approaches. To combine vestibular and visual input, optimal control approaches (Ormsby & Young 1977) have been used including Kalman filters and somatosensory input (Borah et al 1988) as well as optimization under coherence constraints (Droulez & Darlot 1989) and with cost functions (Reymond et al 2002). Internal models have also been introduced in models with both acceleration and velocity input (Merfeld 1995), to process combinations of linear and angular acceleration (Glasauer & Merfeld 1997; Bos & Bles 2002), and in focusing on sensory weighting (Zupan et al 2002). Laws-of-physics generated baselines have been introduced to compare with perceptions (Holly 1997), and the continuous deformation given by time constants have been added to represent perceptual tendencies (Holly 2004). Bayesian modeling has included stochastic input to the vestibular signal (Laurens & Droulez 2007) and priors for determining spatial orientation from visual and vestibular input (MacNeilage et al 2007) and can explain inter-subject variability within the realm of "bottom-up" and input/output approaches.

"Top-down" and constructive analyses have been sparse. However, to understand the interaction of the various levels of analysis involved in shaping self-motion perception, it will be essential to mathematically formalize principles of self-motion perception, whether at the transduction level, at the organism level, or in between. The present paper encompasses a broader view of experimental results that fail to fit the standard "bottom-up" and input/output approaches, in order to categorize types of experimental results and to indicate the type of mathematical characterizations that will be helpful. The following section reviews principle-based mathematical approaches and discusses the way experiments such as those reviewed may lead to a fuller understanding of self-motion perception.

5.3 Mathematically Characterizing Dynamics of the Self-Motion Response Space

We envision a mathematical theory that displays self-motion perception, as observed, following logically from biological, perceptual principles, as linguistics is based on biological, linguistic rules. Although self-motion perception and language are both biological -- in the sense that they follow principles shaped by organisms -- there are major differences in function and in relationship to the environment. What is self-motion perception for? Broadly, it is for monitoring the physical movements of the body, just as vision is for monitoring the environment at a distance. More specifically, self-motion perception in everyday life helps us to integrate body motions in activities such as typing, cooking, gardening, skiing, and riding a bicycle. A visual analogue is the integration of details into a scene either spatially or temporally. Spatial examples include the many instances of judging the size or color of an object by its visual context, for example, olive green may be seen as grey when surrounded by more saturated greens (Land et al 1983; Wehrhahn 1987; Werner et al 1988; Moutoussis & Zeki 2000; Brainard et al 2006; Werner 2007). A temporal example is the Ternus experiment with blinking lights described above (§5.2) Similar to the self-motion principles exemplified in §3, the visual principle drawn from such experiments is that perception is organized in terms of the movement of a whole entity rather than an unconnected assemblage of details.

Symmetry group mathematics is an example of principle-based mathematics that addresses the logical structure of a phenomenon. Vestibular projections have been found to have spatially-related symmetry groups (McCollum & Boyle 2004; Foster et al 2007; McCollum 2007). A biological example of the difference between numerical form and logical structure is the right-left symmetry of the two hands. Considering the shape of the hands, there is approximate right-left symmetry, which fails to be exact because of differences in details such as the lengths of corresponding fingers. Consider instead the connectivity of the bones of the hands, which could be considered the basic principle of hand construction. The metacarpal bones radiate from the wrist and are continued by a series of phalanges. In this bony connectivity, the right-left symmetry is exact. Approximate numerical, morphological right-left symmetry typically follows. Bony connectivity, along with that of muscle and connective tissue, provides a discrete scaffolding for hand function and may link function to principles of morphological development. Discrete scaffolding in language includes syntax, vocabulary, and the language-specific discretization of phonemes, each with principles that provide logical structure to language. Symmetry groups of vestibular projections provide discrete scaffolding for spatial functions. Symmetry groups provide not only spatial geometry but also a menu of movements (Golubitsky & Stewart 2002). Thus they subserve dynamical multistability appropriate to a geometry. The canal vestibulo-olivo-nodular projection has the symmetry group of the square, not only establishing right-left canal planes, as opposed to homologous pairing, but also providing for rotational symmetry in the horizontal plane (Foster et al 2007; McCollum 2007). More intricate and perhaps more surprising, the disynaptic excitatory/inhibitory connectivity from canal nerves to neck motor neurons carries the symmetry group of the cube, including all rotational symmetries (McCollum & Boyle 2004; McCollum 2007). By carrying logical structure related to physical space, vestibular projections provide a foundation for sensorimotor functions.

The examples given in this review demonstrate that there exist also logical-structure principles of self-motion perception that await formalizing. Principle-based mathematics deduces consequences from principles, typically stated as axioms; numerical consequences follow, as they do in theoretical physics, rather than driving a simulation, as in computational curve-fitting. In one of the cases we reviewed, the logical structure underlying the experimental data has already been formalized in principle-based mathematics: the rotating-disk experiment (§4.2; DiZio & Lackner 1986) follows the logical structure of a semigroup (Hanes 2006, 2007). The major perceptual principle found in this analysis is that somatosensory perceptions are aligned to be consistent with certain preferred perceptions, especially that the rotating disk is horizontal and that body segments are in preferred, centered positions. There are several options for aligning body segments and several degrees of alignment, as specified by the semigroup, including several illusions that were not reported but might be with a larger sample size (Hanes 2006, 2007). The semigroup characterizes perceptual dynamics in which subjects approach preferred percepts.

The principles and logical structure underlying other observations remain to be analyzed. In §2, we began with the simplest case: examples in which elements of a perception are added, deleted, or interchanged. The experimental paradigms included OVAR, visually presented yaw rotation, and actual pitch rotation. On a deeper level, these examples suggest that the self-motion system can analyze continuous motions into a discrete set of elements, subject to simple transformations such as addition, deletion, and interchange. An important result of mathematical characterization will be to specify the particular set of elements the perceptual system uses in each case.

In self-motion perception, discreteness is not perceived, in many cases. For example, people in parabolic flight now and then perceptually invert, so that they find either themselves or everyone else upside-down. With normal vision, these inversion experiences do not involve a rotation from right-side-up to upside-down; rather, right-side-up fades out, then upside-down fades in (Lackner & DiZio 1993a). A non-perceptual example involves subjects on a posture platform, where the support surface, visual surround, or both may abruptly and without the subject's knowledge shift from being earth stationary to moving with the subject. Subjects with full sensory capabilities typically do not perceive such shifts; evidently they transition to a different coordination mode constraining their orientation senses, without their own knowledge (Nashner et al 1982; Black & Nashner 1984; Black et al 1988; McCollum et al 1996). These examples are in keeping with the proposal by Damasio (1989) that perception is based on the coordinated activations of separate neural centers. Presumably such coordinated activations occur and then fade or are disbanded in favor of another, as are the sensory states of subjects on the platform or the perceptions of right side up and upside down, and can be characterized as the application and then relaxing of consistency constraints. This ability to apply then relax consistency constraints is essential for shifting self-motion perception to supply the requirements of each new activity in everyday life, such as writing or walking.

Section 3 presents examples that suggest principles of consistency, self-motion principles analogous to the linguistic-perception principle that led subjects to exchange a list of random words for the sentence "Ah, it's fated, " which makes sense, that is, has meaning as a sentence. The kind of consistency in the Damasio scheme may similarly involve a meaningful juxtaposition. Self-motion constraints can occur by various processes. An example of a constraint that is likely applied at the behavioral level is the task used by Wright and Glasauer (2003, 2006) and Wright et al (2009): holding a glass upright during passive motion. At the transduction level, constraints would include limits on the sensitivity of sensory organs. Most of the constraints involved in the experiments we review are intermediate to the behavioral and the transduction levels, so that "top-down" is perhaps less accurate than something like "intermediate-level" perceptual constraints.

Ivanenko et al (1997) suggest a conditional constraint, in which otolith activity only contributes to the perception of unidirectional motion, which would imply that a conjunction or sequence of angular and linear motion provides the condition for linear perception.

Similarly, Bertin & Berthoz (2004) found that inertial motion strongly affected the perception of visual stimuli, perhaps providing a condition allowing vividness.

Theoretical analysis of the results of each experiment is required to mathematically characterize the nature of the consistency constraint the nervous system uses in that situation. Clearly the perception of a bouncing floor is inconsistent with the veridical situation, and the perception of a stretching shank is inconsistent with previous experience and knowledge. Rather, the results of the rotating-drum experiment (Lackner & DiZio 1988) described in §3.3 may match a different constraint on sensory modalities or components of movement. A mathematical characterization of the consistency constraint at play in the rotating-drum experiment would then provide a parsing of sensory and motor components, along with predictions of illusions that could occur in situations in which the same constraints obtained.

A famous constraint is that objects travel more slowly than the speed of light. The "light cone" is the region of four-dimensional spacetime enclosed by possible paths of light. For example, light radiating from one point in spacetime is a growing sphere. Any object heavier than light that leaves that same point (at the same time) must stay inside that sphere. In developing the theory of relativity, Einstein derived the consequences of motion approaching the speed of light: it is time and space that change, rather than light-speed, which is fundamental to physical processes. The adjustment of time and space were originally seen as paradoxical, like the stretching shank. The rotating drum data clearly indicate that there is a constraint linking visual and somatosensory cues for speed, such that directions of motion and even lengths of bone are adjusted to maintain that constraint.

A visual example of a constraint is the three-dimensional size constancy illusion (Fig. 12). The figure shows two copies of a stick figure, of the same size, at two ends of a quadrilateral. Because the visual system tends to impute three-dimensionality, given the shape of the quadrilateral, it imposes a constraint on the perception of size within the drawing: that a figure of constant absolute size decreases in apparent (or drawn) size in the drawing, as it moves along the quadrilateral "wall". Thus, one stick figure is perceived as farther away and therefore of greater absolute size. This example demonstrates not only a constraint but also a response space that is three-dimensional whereas the stimulus is two-dimensional.

The examples in §4 present a variety of perceptions, indicating the extent of the response space, along with its dynamics. Many experiments yield a variety of perceptions. Often the variability is considered an inadequacy of the experiment, perhaps from insufficient controls of the stimulus, instructions, or preparation of subjects. Instead, the experiment may have been particularly well designed to demonstrate the natural biological variability of behavior, as discussed in DiZio & Lackner (1986), so that the results are particularly suitable to analyze for the response space and its dynamics. The experiments in §4 are of this type, as is the effort of Wertheim et al (2001) to ensure that the subjects are unaware of the linear sled motion. Both the vertical linear oscillator (Wright 2002; Lackner & DiZio 2004; Wright et al 2005; §4.1) and linear sled (Wertheim et al 2001) results indicate that the response space is distinct from the stimulus space: the response space includes both linear and angular motion. In addition, there is a clear dynamic in the vertical linear oscillator results, with subjects changing perception every few minutes.

One might expect that a simple stimulus, such as linear motion, would produce bored subjects with simple perceptions. On the contrary, the data show a large array of perceptions; it would seem that the very simplicity of the stimulus invited divergence of response. For one thing, a purely linear movement has symmetry within a linear/angular

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response space, and symmetry invites oscillations (Golubitsky & Stewart 2002). The particular, multistable experiences of subjects in such experiments gives us an opportunity to analyze the actual response space and its actual dynamics, giving biologically realistic mathematical theory. In addition, we may be able to relate these response spaces and their multistability to symmetry groups of vestibular projections.

The dynamics of perception may also relate to the naturally shifting constraints imposed on everyday movements. It may be an essential feature of everyday self-motion perception to dissolve perceptions at a certain natural frequency, to avoid excessive rigidity.

In everyday life, self-motion perceptions are typically suitable and unremarkable. We typically have more self-motion cues than we need to construct a self-motion perception that is consistent with our knowledge of the surroundings and our bodies. Also, those cues are not artificially manipulated. Experiments can be designed to take normal processes to their logical limits, exposing the logical structure and principles of self-motion perception we use on a daily basis, without being aware how remarkable and counter-intuitive they are.

A particularly dramatic visual example of a response space that is distinct from the stimulus space is color vision. The physical stimulus is light frequency, which varies in one dimension. From the differing responses of three cone types, the visual system constructs a three-dimensional color space.

In the rotating-disk experiment (DiZio & Lackner 1986, §4.2), the response space is not very different from the stimulus space: angular positions of joints. However, the dynamics on the space are distinct, because they approach a set of preferred positions, not specified by the stimulus (Hanes 2006).

The task of scientific theory is to mathematically characterize the observed dynamics, not to make the dynamics conform to a preconceived formalism, such as continuous deformations of the transduced stimulus. Theoretical research, in particular, is charged with finding the principles underlying empirical observations; it is the principles that lead eventually to numerical agreement with experiment. The reviewed illusions evidence essential logical structures underlying self-motion perception and not conforming exactly with physics. By mathematically formalizing more of the phenomena, we create more of the fertile "edge habitat" in theoretical neurobiology, in which experimentalists will see phenomena to explore and theorists will see connections between perceptual principles and neural function. Mathematically formalizing perceptual spaces characterizes the dynamical landscape within which perception occurs. Recall that we refer here to principle-based mathematics: a set of principles and their consequences. Mathematical characterization based on perceptual principles provides (1) the dynamical landscape of the perceptions themselves, for example, any deletions that are likely to occur, (2) a rigorous characterization of constraints imposed by neural phenomena at an intermediate level or organism level, which constrain both neuronal dynamics and behavior, and (3) the nature of the perceptual spaces themselves, especially their intrinsic dynamics.

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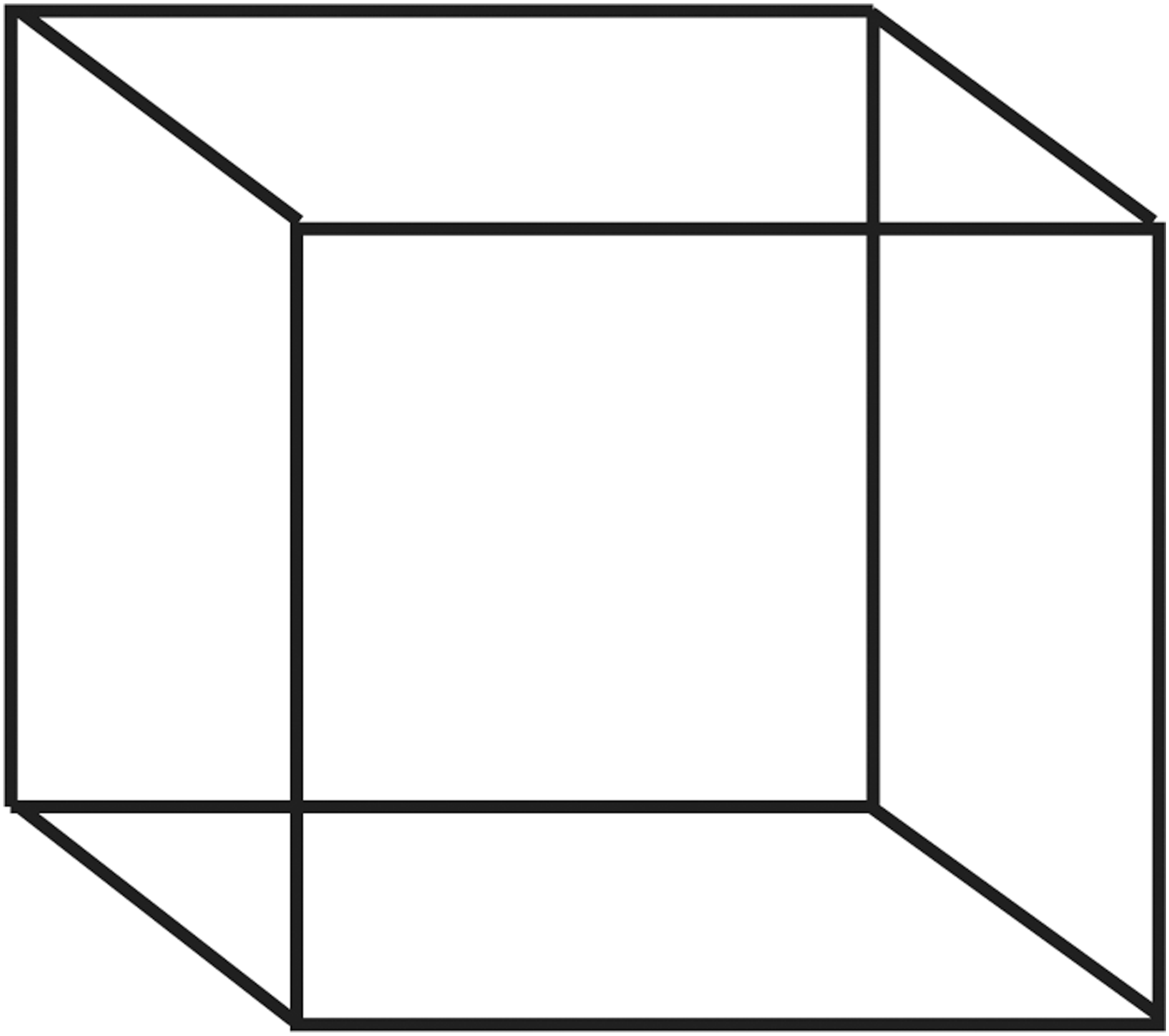

Fig. 1. Necker Cube

Constructive perceptual processes transform a planar line drawing into a three-dimensional cube. Furthermore, active perception selects which square face is in front.

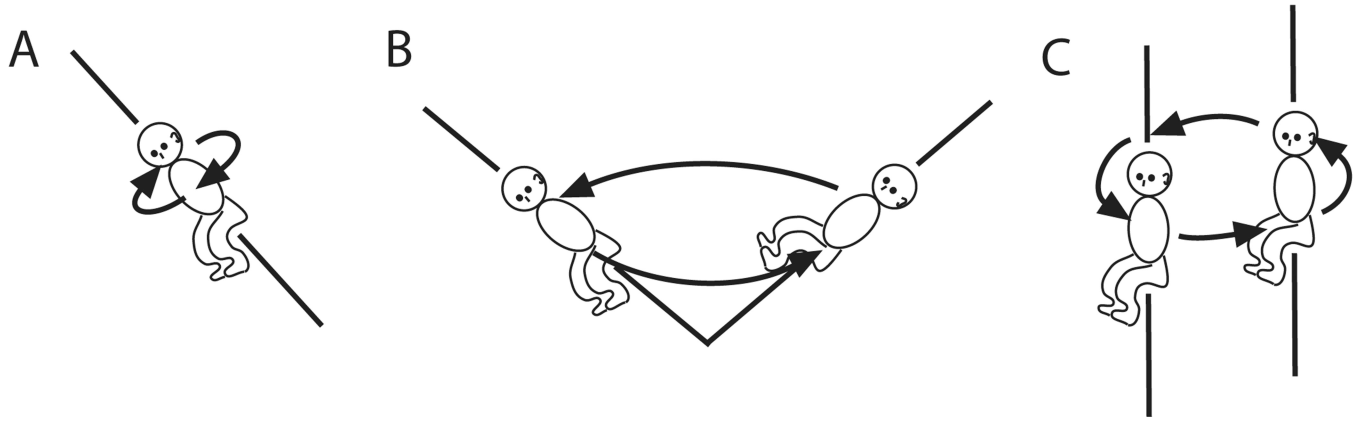

Fig. 2. Off-Vertical Axis Rotation (OVAR)

A. Actual motion: a rotation about the body axis, when the body axis is tilted from vertical. B. Perceived conical trajectory motion at low frequency. C. Perceived cylindrical motion at higher frequencies.

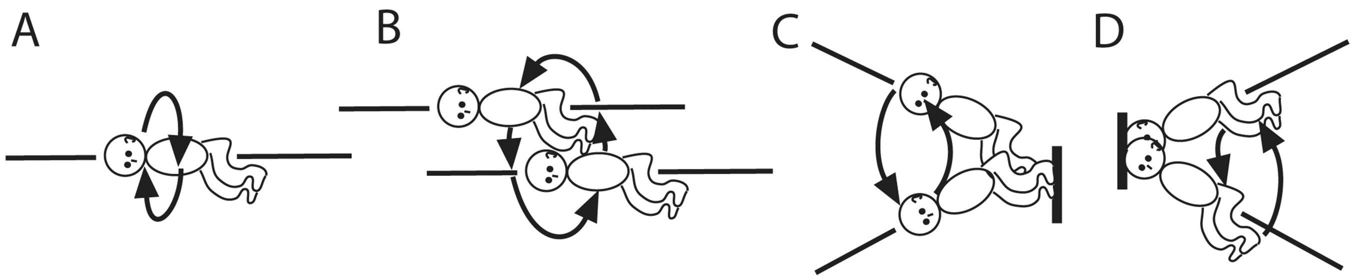

Fig. 3. Barbecue Spit with Foot and Head Pressure

Foot or head pressure results in a self-motion perception with the pressed part fixed. A. Actual motion: a rotation about the body axis, when the body axis is tilted 90 degrees from vertical. B. Perceived cylindrical motion in the absence of head or foot pressure. C. Perceived conical motion when the subject exerts pressure with the feet against the apparatus. D. Perceived conical motion with head pressure against the apparatus.

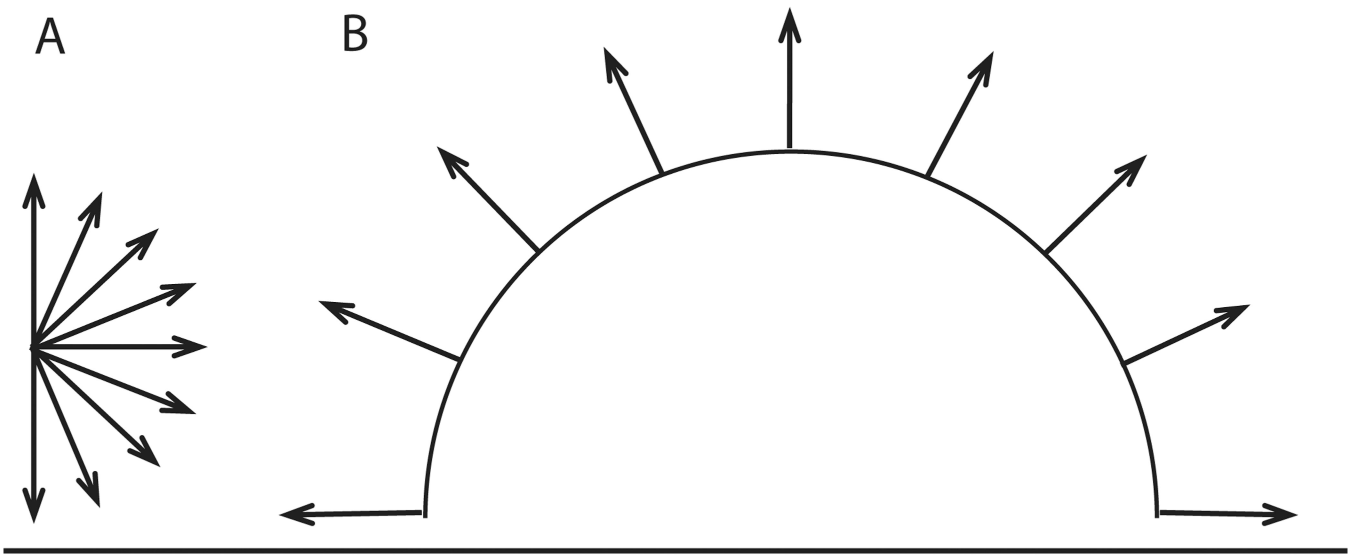

Fig. 4. Addition and Omission of Circular Trajectory, Given Orientation Yaw
Arrows indicate the orientation (noseward direction) of the subject, as viewed from above. The tail of the arrow follows the subject's trajectory. A. Rotation in place. B Semicircular trajectory with orientation outward. As in A, the orientation in B rotates by 180 degrees. However, sideways motion is added. (Bertin et al 2000. Redrawn with permission.)

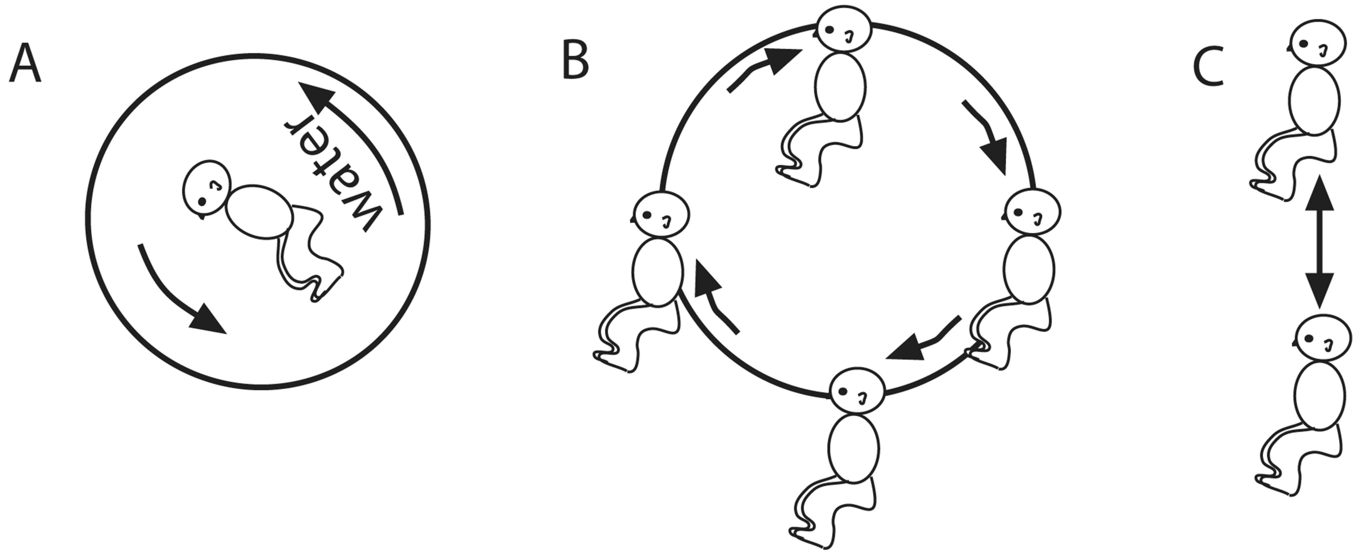

Fig. 5. Submerged Motion Stimulus

A. Actual tumbling motion. B. Perceived Ferris wheel motion. C. Up-down motion perceived at higher frequencies. (Modified from Meiry 1966)

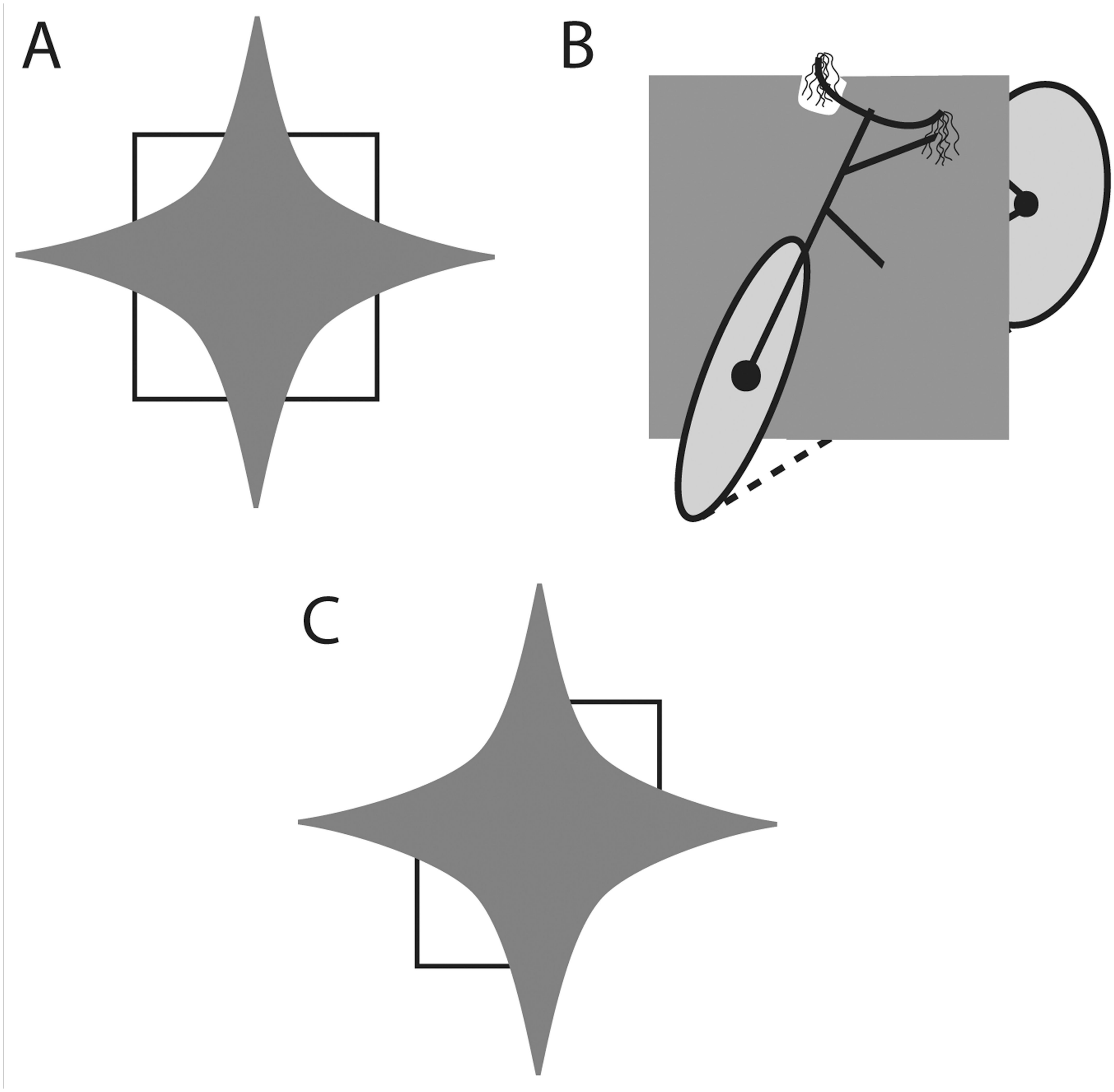

Fig. 6.

As the Gestalt psychologists pointed out forcefully in visual contexts, we see whole forms, even when some of the parts are obscured. Cues corroborate each other. A. The square is clearly visible behind the other form, even though four line segments are absent. The four corners corroborate each other, so that the nervous system constructs a square. In addition, the whole diagram is automatically segmented into two shapes, one on top of the other. B. The front of the bicycle and the back wheel are enough evidence to corroborate each other in constructing a clear perception of a bicycle, even though parts are missing. Again, the diagram is segmented into a bicycle and a square, even though neither is complete. C. Two corners are not enough corroboration to perceive a square; other percepts are possible, such as two smaller squares corner to corner.

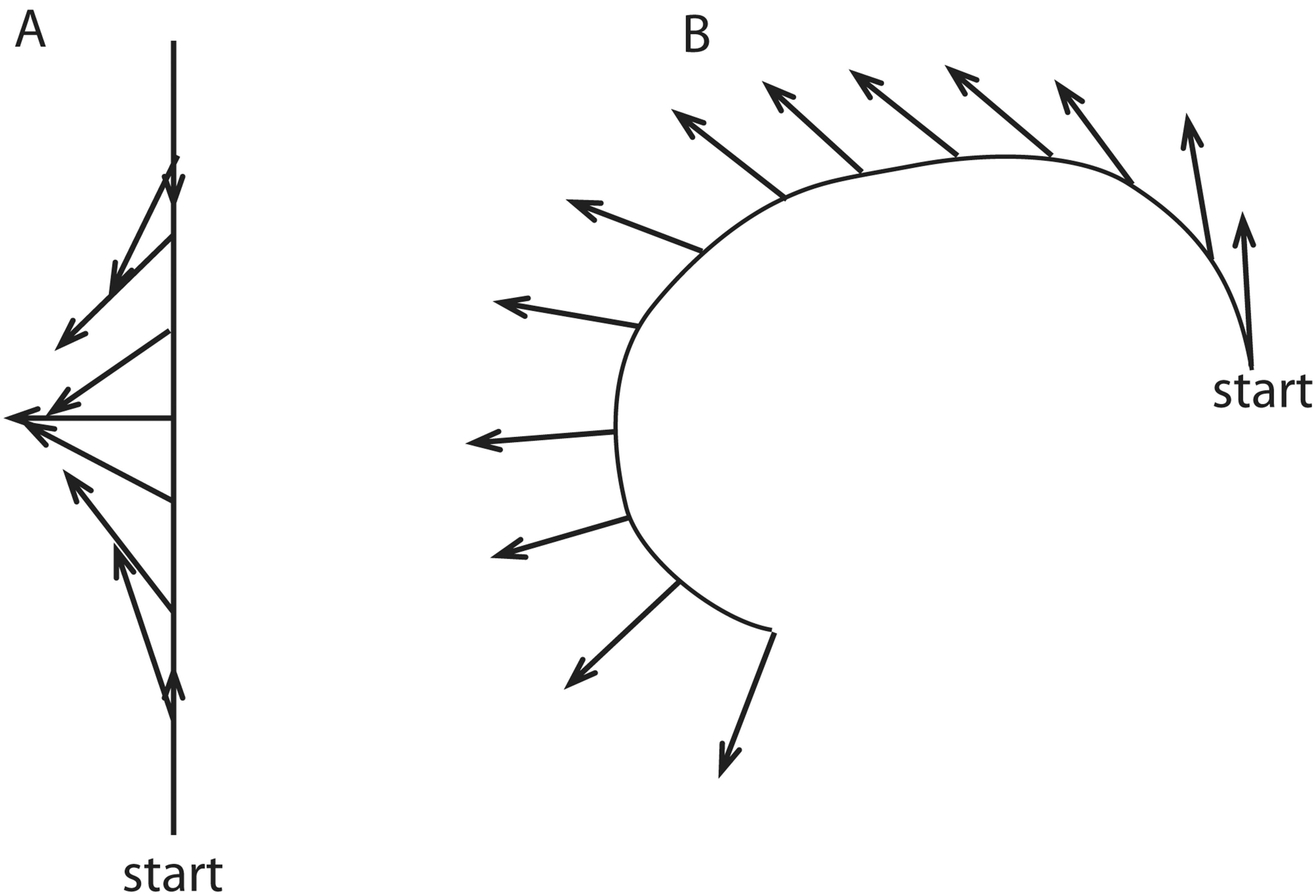

Fig. 7. Replacement of Motion Property in the Percept

From a top view, arrows indicate the orientation (noseward direction) of the subject. The tail of the arrow follows the subject's trajectory. A. Actual straight trajectory with orientation beginning forward and turning 180 degrees to face backward at the end of the movement. B. Fairly typical perceived trajectory in response to visual flow A, showing both exchange of orientation for trajectory yaw and segmentation into one response based on early characteristics of the visual flow (Fig. 2(i) in Bertin et al 2000). The fact that the movement is backwards at the end, which is quite salient in the stimulus, is ignored or replaced with a lateral motion. (Freely redrawn, with permission, from Bertin et al 2000 and Bertin & Israël 2005)

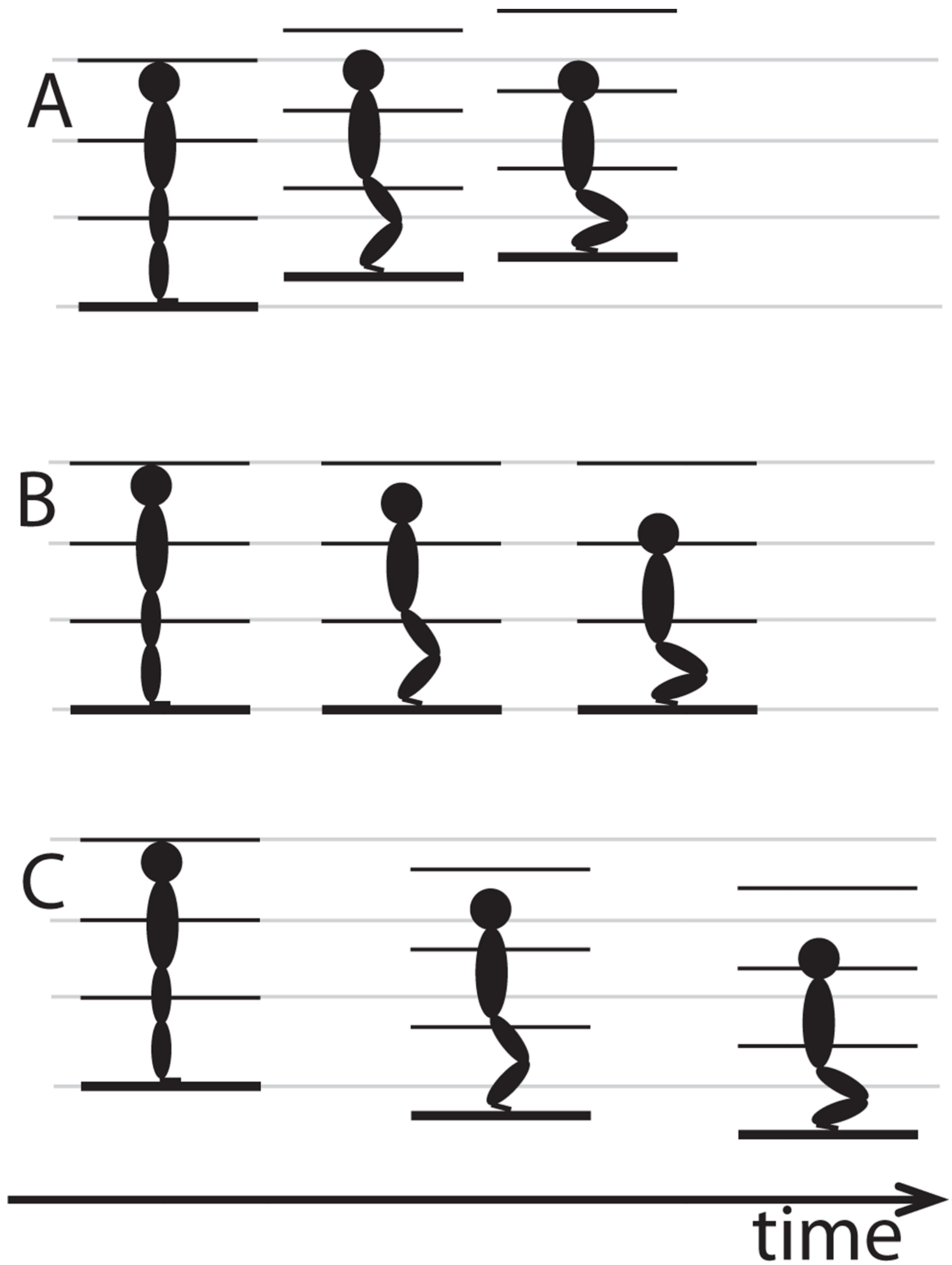

Fig. 8. Stretching Time and Moving Floor

A. Perception of normal deep knee bend in 1.8–2.0g, when the subject is adapted to 1g. As the floor is perceived to rise, the deep knee bend is perceived to happen faster than intended. B. Perception of deep knee bend in normal conditions. Also when the subject is adapted to 1.8–2.0g, the normal perception is regained. C. Perception of normal deep knee bend in 0.3–0.5g, when the subject is adapted to 1g. As the floor is perceived to sink, the deep knee bend is perceived to happen more slowly than intended. A similar perception occurs in 1g after adaptation to 1.8–2.0g. (Redrawn with permission from Lackner & DiZio 1993.)

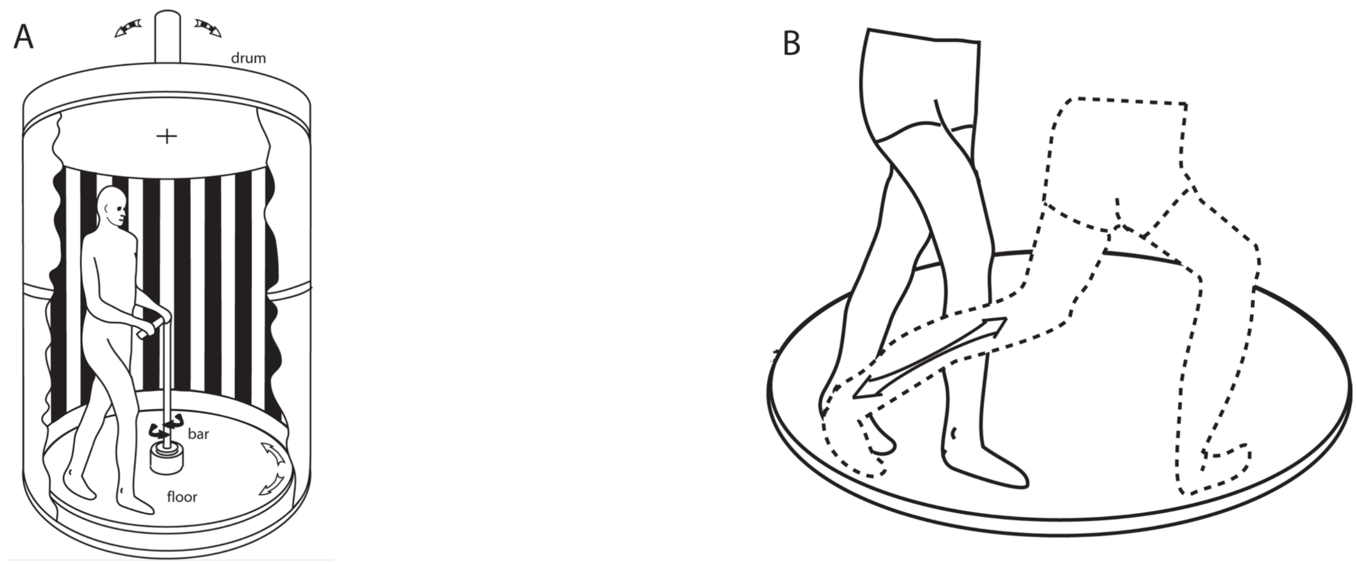

Fig. 9. Rotating Drum and Leg Stretch Illusion

A. Experimental apparatus, which allows independent motions of the drum, the turntable, and the bar. B. Illusion of leg being longer than it actually is. This illusion occurs during the push-off phase of locomotion, when the speed of the rotating drum indicates a walking speed faster than the actual walk. (Redrawn with permission from Lackner & DiZio 1988.)

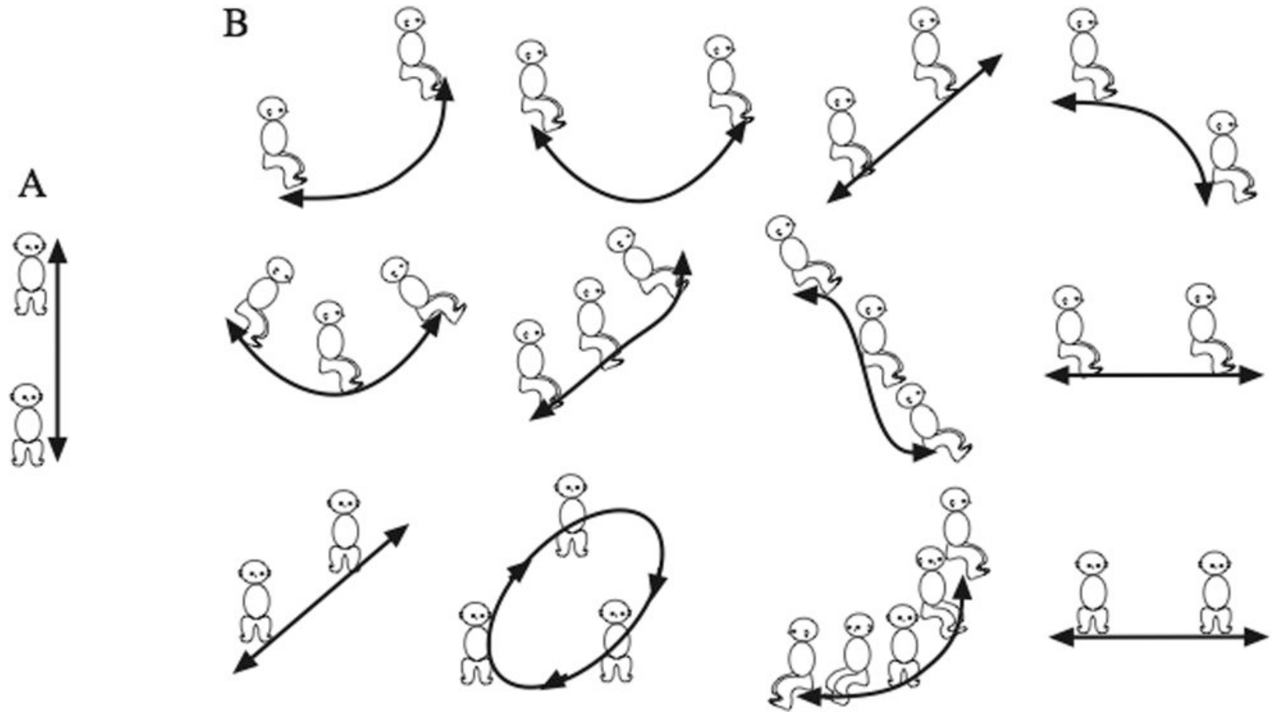

Fig. 10. Perceptual Options during Vertical Linear Oscillation

A. Vertical linear oscillation stimulus. B. Variety of perceived motions during vertical linear oscillation. (Redrawn with permission from Wright 2002)

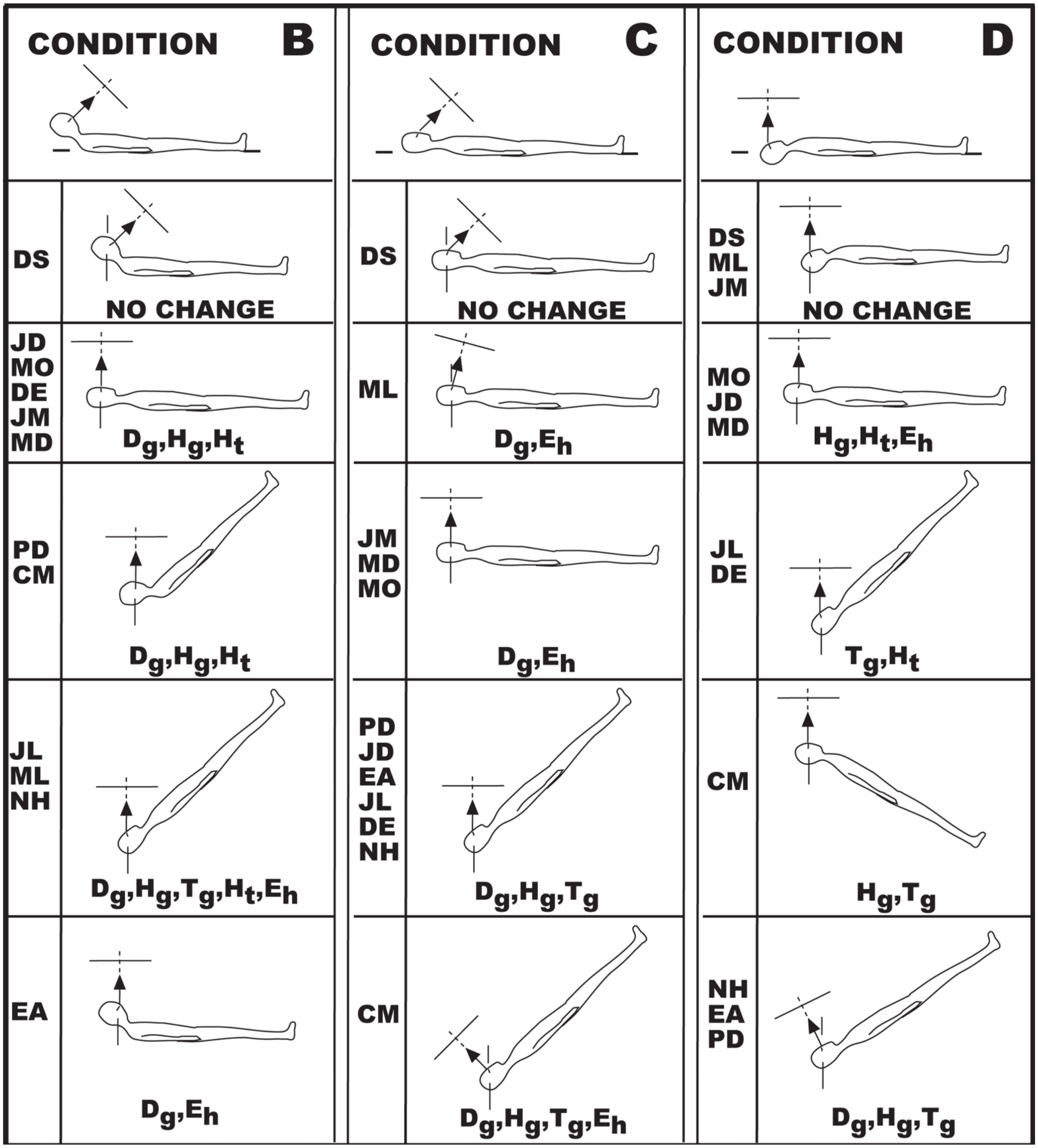

Fig. 11.

Somatosensory illusions induced by rotating disk during conditions B-D. (Redrawn with permission from DiZio & Lackner 1986)

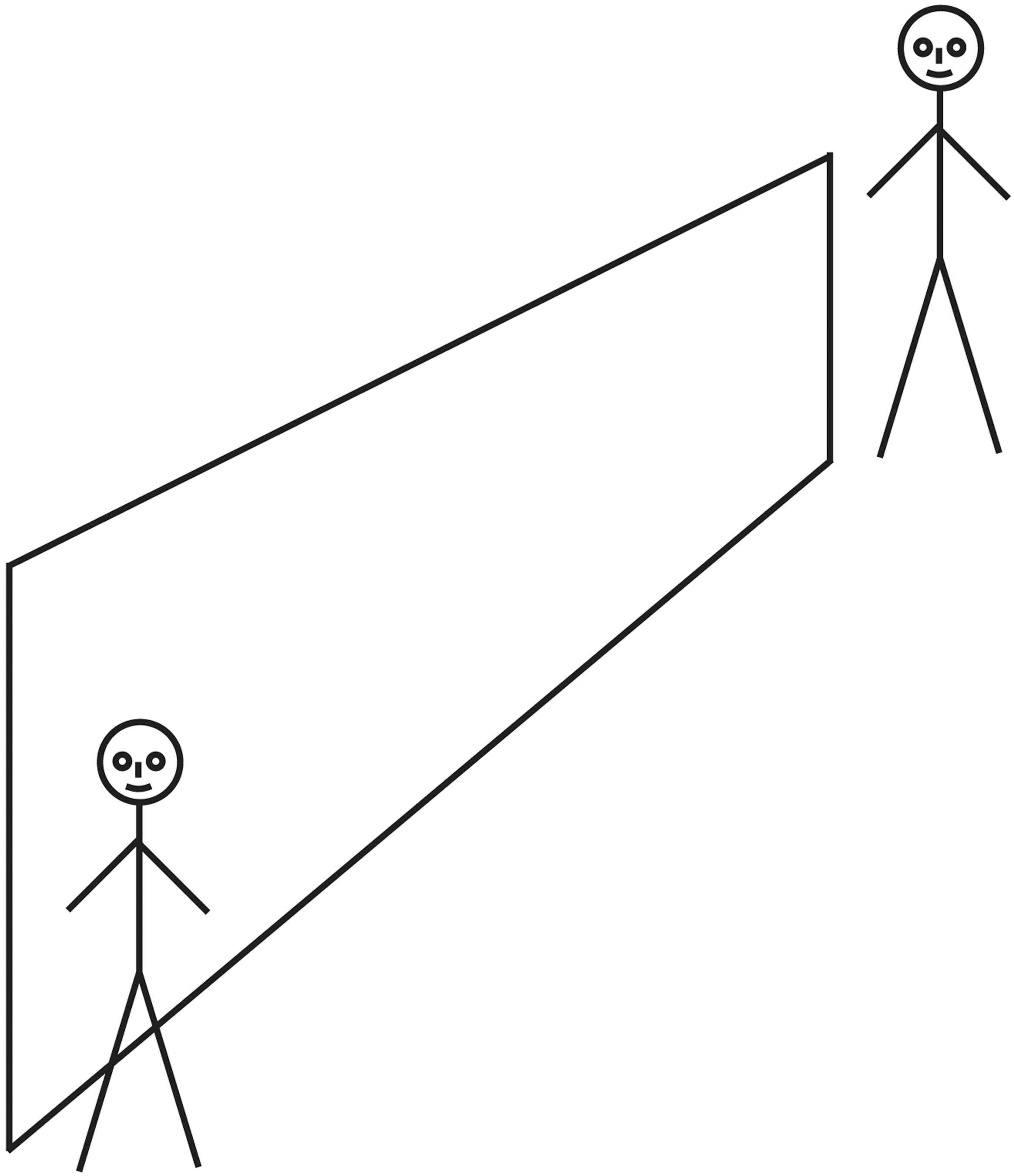

Fig. 12. Size Comparison Illusion

A same-size copy of the human stick figure is shown in the two-dimensional drawing, at each end of the quadrilateral. However, the visual system assumes three-dimensionality, given a shape like the quadrilateral shown, as it does in the case of the Necker cube (Fig. 1). This assumption of three-dimensionality constrains perception of the size of the stick figure, so that the more distant one is seen as larger.