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Internal Directional Reference Frames for  
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Several decades ago, Graham Brown (11) found that the spontaneous walking of a high-decerebrate cat can be continuously transformed from rectilinear locomotion into either circling or uphill/downhill progression by appropriate changes of head position. The cat's performance thus carries with it an attribute of "spatial directionality" which can be independently regulated by the CNS; and the method of regulation relies, in this instance, upon postural biases created by tonic neck and labyrinthine reflexes.

Recently, experiments using decerebrate cats similar to Graham Brown's have indicated that activity within the olivocerebellar system of the brainstem is associated with postural alterations resembling those elicited from neck and labyrinths (4,5). These, too, bias the locomotor musculature so as to influence the overall directionality of walking in a wide variety of ways. However, there is one area in which the directional control exerted by the olivocerebellar system differs considerably from that seen by Graham Brown: It has "memory", in that a posture adopted by an animal as a function of olivocerebellar activity is retained for many tens of seconds after that activity ceases. By contrast, the postures of Graham Brown's animals reflect only the current position of the head, without any apparent recollection of previous positions. The directional skews associated with head movement can thus be changed in "real time" from step to step, while olivocerebellar skews establish an enduring postural context within which many steps (or other activities) may occur. It thus is tempting to hypothesize that the olivocerebellar system exists in the CNS to regulate, via postural mechanisms, an internal directional reference frame within which motor actions are elaborated and, perhaps, evaluated. But then, why should such a faculty exist?

The idea of an internal directional reference for movement was first derived theoretically from consideration of CNS mechanisms to simplify the controllable degrees of freedom in the skeletomotor system (2,8; P.H. Greene, this volume). The technique for doing this is to create functional dependencies (e.g., fixed ratios) amongst movement parameters affecting different joints, as is frequently encountered experimentally (10,9). One particular form of functional dependence employs so-called "muscle linkages" (3) of synergists at different joints, the activities of which covary in some prescribed manner (cf., ref. 12 for experimental examples). Actions carried out with such a linkage are characterized by a distinct directional skew that becomes quite apparent as the covarying parameters of the linkage are altered. Graphic illustrations of such a process may be seen in, for instance, Graham Brown-like changes in the coactivation of human leg musculature (elicited with galvanic labyrinthine stimulation) as a continuous function of neck position (13). Consequently, one might well see olivocerebellar directional biasing as just another way to parameterize muscle linkages and simplify the motor control process. But this would provide no facile explanation for the extended time-course of such

biasing, nor would it define the conditions that presumably spur the olivocerebellar system into establishing a particular directional reference frame.

A speculative approach to the last question is suggested by neurophysiological studies of the olivocerebellar system and its role in regulating eye movement (ref. 1 for review). In brief, activation of the appropriate (anatomically) part of the system institutes a seconds-long nystagmus of the eyes seemingly equivalent to the olivocerebellar postural biasing of the skeletal muscles described above. This nystagmus also resembles the phenomenon of optokinetic after-nystagmus (OKAN) that occurs in humans and animals following exposure to whole-field motion of the visual world. It may come as no surprise, therefore, that the olivocerebellar system has proved to receive retinal image-motion cues which are nearly optimal for optokinetic eye movements. What is more interesting is that, in stationary human subjects, the development of OKAN is associated with illusory sensations of self-motion or "vection", which, in darkness following exposure to the moving visual stimulus, persist for prolonged periods of time (7). The rationale for this persistence, or "memory", would appear to involve an appreciation for momentum: The subject feels accelerated to some velocity by the moving visual world, and has no reason to feel decelerated when that world is no longer visible. While appropriate studies seem not to have been done, it seems reasonable to suppose that humans and animals experiencing vection will alter their motor behavior as a function of this sensation, just as they would were they experiencing actual self-motion. Because of the long time-course associated with vection, such motor adjustments will likely take the form of "static" postural biasing altering the directionality of movement. Might this be the sort of directional skewing produced by the olivocerebellar system? Might the perception of self-motion along particular trajectories be associated with the creation of olivocerebellar directional reference frames for movement?

The arguments above have been helped somewhat by the demonstration that vection sensations (and accompanying "OKAN") can be released by proprioceptive cues from the limbs (6)-- which, besides providing a role for the massive somatosensory input to the olivocerebellar apparatus, indicates that self-motion cues derive from multisensory processing. Those cues probably also owe themselves to knowledge of efferent command signals, since the quality of self-motion illusions depend upon a subject's assumptions about movement he or she is producing voluntarily. Fortunately, it appears possible to go back to Graham Brown's cat and its olivocerebellar system to see whether the directional skewing it participates in can be triggered by those conditions leading to vection in humans. Work is now underway toward that end.

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