

Aspects of body self-calibration

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The representation of body orientation and configuration is dependent on multiple sources of afferent and efferent information about ongoing and intended patterns of movement and posture. Under normal terrestrial conditions, we feel virtually weightless and we do not perceive the actual forces associated with movement and support of our body. It is during exposure to unusual forces and patterns of sensory feedback during locomotion that computations and mechanisms underlying the ongoing calibration of our body dimensions and movements are revealed. This review discusses the normal mechanisms of our position sense and calibration of our kinaesthetic, visual and auditory sensory systems, and then explores the adaptations that take place to transient Coriolis forces generated during passive body rotation. The latter are very rapid adaptations that allow body movements to become accurate again, even in the absence of visual feedback. Muscle spindle activity interpreted in relation to motor commands and internally modeled reafference is an important component in permitting this adaptation. During voluntary rotary movements of the body, the central nervous system automatically compensates for the Coriolis forces generated by limb movements. This allows accurate control to be maintained without our perceiving the forces generated.

The body surface is represented in somatosensory cortex where there are multiple topographic maps of the body parts, with the magnification of the mapping dependent on the tactile acuity of the mapped area. These maps can change over time, even in the adult animal, depending on the relative use of the mapped area¹. Comparable neural spatial, sensory and pre-motor maps that represent the ongoing configuration and movement of the body and its mobile parts are just being discovered²⁻⁴. Unmyelinated Ruffini fibers in the joints of the body, often referred to as joint receptors, were once thought to provide potentiometer-like specifications of the angles of the body's joints⁵. It is now recognized that joint-receptor signals cannot code joint angles unambiguously, but that both muscle spindle and motor command signals are also involved in the position sense representation of the body, and (in the case of the hand) cutaneous mechanoreceptor signals as well^{6,7}. The otolith organs of the inner ear are responsive to linear acceleration, including the direction of gravity, and participate in a variety of reflexes that are related to ongoing body posture⁸. A cortical map that directly represents body orientation in relation to gravity has not been found, although vestibular projections to parietal cortex have been identified⁹.

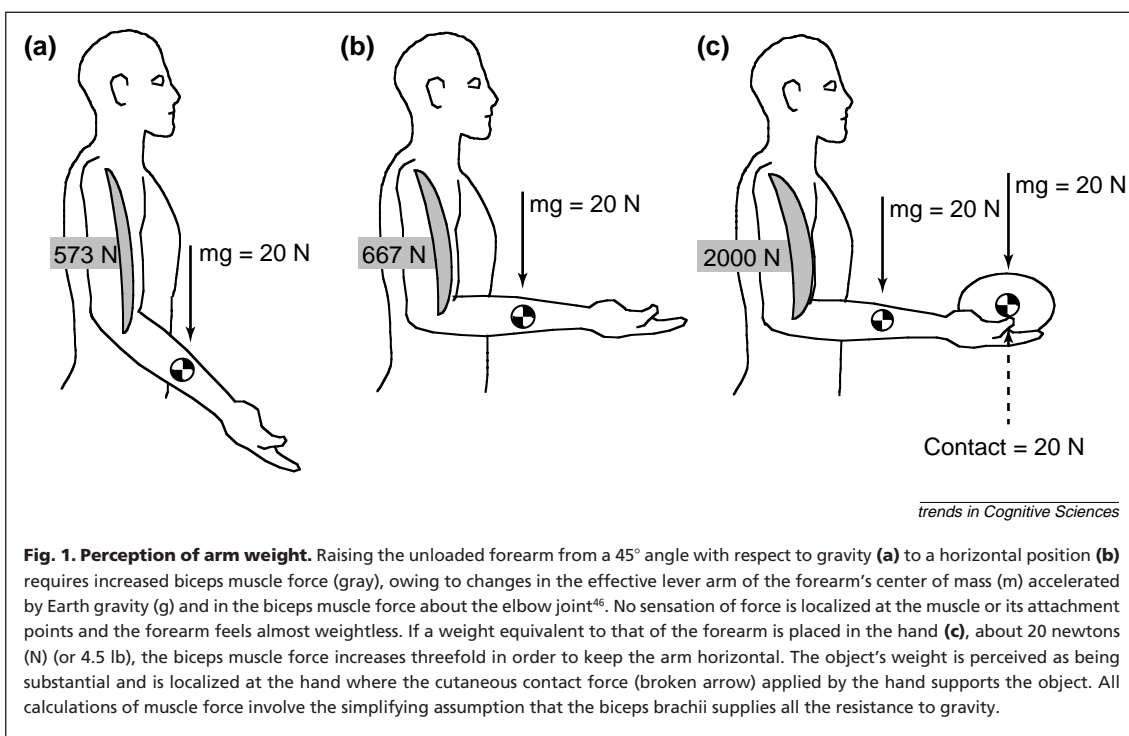
The situation with regard to representations of ongoing body configuration and of the vertical is akin to that of auditory localization. There are tonotopic maps of frequency,

but cortical spatial maps of the location of sounds relative to the body have not been identified. Instead, spatial direction is computed by a neural network that relates interaural time-difference signals, pinnae-dependent refraction cues (head-related transfer functions), secondary reflections, visual information and other factors¹⁰. Similarly, multiple factors contribute to the computation of body orientation and configuration but specific sites where they are spatially and metrically represented have not been discovered.

Despite the conscious recognition of having to maintain balance and to avoid dropping objects, we are not directly aware of the consequences of gravity for the control of our body orientation and movements. Movement and support of our body in relation to gravity seem virtually effortless unless we are fatigued, and we do not perceive directly the actual magnitude of forces exerted nor where they are applied. For example, when we are standing, the force on the sole of each foot is equivalent to one half our body weight but we do not perceive the actual magnitude of these forces, they seem tiny. In shifting stance from two feet to one, we do not perceive a great increase in force on the sole of the stance foot although it has doubled¹¹. If, while standing, we raise our forearm up from our side, the muscular force required to support it against gravity increases until the forearm is horizontal and then decreases as it is raised further. We do not accurately detect the muscular force necessary to overcome

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the changing gravity torque on the arm, equal angular displacements seem to require equal effort (see Fig. 1 for an illustration of the actual forces involved). The weight of the arm feels distributed across the entire arm and is not localized at the muscles or muscle attachment points where the forces are actually generated to support the mass of the arm against gravity. By contrast, the perceived weight of an object in the outstretched hand is systematically scaled to its actual weight and is localized at the hand. The psychophysics of judging the weight and mass of external objects has been extensively studied¹², but comparable studies of the apparent weight of the body itself have not yet been undertaken.

Muscle spindles and position sense

Muscle spindle receptors feature prominently in the control and appreciation of body orientation, body configuration and movement execution. Spindle or intrafusal muscle fibers lie in parallel with the extrafusal fibers of striated skeletal muscle; the latter are innervated by the alpha motoneurons of the spinal cord and do the actual work of muscle contraction. The intrafusal muscle fibers have a middle equatorial region that contains sensory receptor endings, referred to as primary and secondary, with the primary endings giving rise to large myelinated Ia afferents and the secondary to myelinated group II afferents. These receptor types differ in their sensitivity to stretching, and potentially provide responses that are proportional to both muscle length and velocity (primaries) or to length alone (secondaries)⁶. The intrafusal fibers have contractile elements at either end that are innervated by gamma motoneurons of the spinal cord, which allows gain control of the spindle sensory endings in a manner that is partially independent of the length of the extrafusal muscle fibers.

In 1972, Matthews and his colleagues demonstrated conclusively that muscle spindles contributed to the conscious appreciation of limb position¹³. Before their work it

was thought that limb position sense was provided by the Ruffini type receptors in the joints of the body. They had blindfolded subjects seated with their elbows resting on a table match the apparent position of their forearms while the biceps or triceps muscle of one arm was mechanically vibrated. Such vibration, 100 Hz, activated the spindle receptors within the vibrated muscle, which caused it to shorten reflexively and to displace the forearm. Subjects who matched the apparent position of the forearm of the vibrated arm with their other forearm showed positional errors that were consistent with the vibrated muscle being longer than it actually was, for example, vibration of the biceps led to the forearm being perceived as more extended than its true position, and more flexed for triceps vibration. Later it was shown that if the Achilles tendons of a restrained blindfolded subject were vibrated the subject perceived forward body tilt, some subjects even experienced continuous 360° pitch rotation of their body¹⁴. Those who experienced continuous tilt exhibited 'reflexive' compensatory movements of their eyes, a nystagmus like the one that would be elicited by actual body rotation in pitch. These experiments indicate conclusively that muscle spindle activity contributes both to limb position sense as well as to perceived body orientation relative to the upright. Later experimental developments are summarized in several sources^{15,16}.

Haptic calibration of visual and auditory localization

The representation of limb position and of body position influences visual and auditory localization, and provides a mechanism for calibrating these sensory systems. Several simple examples illustrate this influence. If a small target light is attached to a subject's index finger (in an otherwise dark chamber) and the biceps brachii of that arm is vibrated while the forearm is mechanically immobilized, the subject will experience extension of the forearm and see the target move and displace spatially, in keeping with the apparent

rather than true position of the index finger^{17–19}. Similarly, if an auditory target is attached to the hand, it will be heard to move and change its spatial position as the forearm is perceived to move²⁰. This means that proprioceptive information about hand position influences visual and auditory localization relative to the head.

Figure 2 shows a subject in the dark viewing small target lights attached to each of his or her index fingers. If the apparent positions of the forearms are altered using biceps or triceps brachii muscle vibration, to create illusions of forearm extension or flexion, the subject will see the separation of the two target lights change. When the fingers feel farther apart, the target lights will be seen farther apart, and closer together when the fingers feel closer together²¹. This visual change occurs for monocular and binocular viewing; it is not accompanied by eye movements nor by changes in the apparent depth of the targets. Similarly, subjects who experience illusory body motion induced by vibration of postural muscles will perceive a stationary target light they are fixating as changing in spatial position in keeping with their own apparent motion¹⁴.

These findings address the fundamental issue of how auditory and visual spatial localization are calibrated and updated over time so that accurate localization can be maintained. There is extensive knowledge of how the signals from the retinae are channeled and analyzed in the multiple cortical maps devoted to vision; specialized regions are present for binocular disparity, motion perception, and so on²². However, other factors also influence vision, including convergence and divergence of the eyes, accommodation, and intraocular separation, which changes in the course of development. Similarly, the separation of the ears, the interaural distance, changes during development. Periodically, perhaps continuously, calibration needs to be updated so that visual and auditory cues related to direction and distance can be validated using information about actual target location. It is well known that vision influences auditory localization. For example, if the visual world is displaced by prism spectacles in front of the eyes, sounds will be heard to originate from the seen rather than the true location of their sources²³. Experiments in which barn owls are reared with displacing prism spectacles have shown shifts of the auditory receptive fields in the tectum that correspond to the magnitude of the visual displacement²⁴. These types of experiments show that vision can influence auditory localization through physiological reorganizations. However, they leave unanswered the question of how visual localization and motor control are calibrated to allow the achievement of accurate behavioral performance.

Such calibration can be achieved through interactions with the hand, for example, the sight of the hand in relation to the body, of the hand contacting an object, and so on. The hand and arm can be used to gain accurate information about the distance and direction of external objects from the body and their sizes. This means that the hand and arm can be used mutually to calibrate themselves, as well as to calibrate visual space perception, including velocity perception, through interaction with external objects²⁵. The hand and arm provide a spatial metric for calibrating sensory–motor space. In the absence of arms (e.g. in animals), the legs and feet could provide a similar function; in the absence of both, vestibular

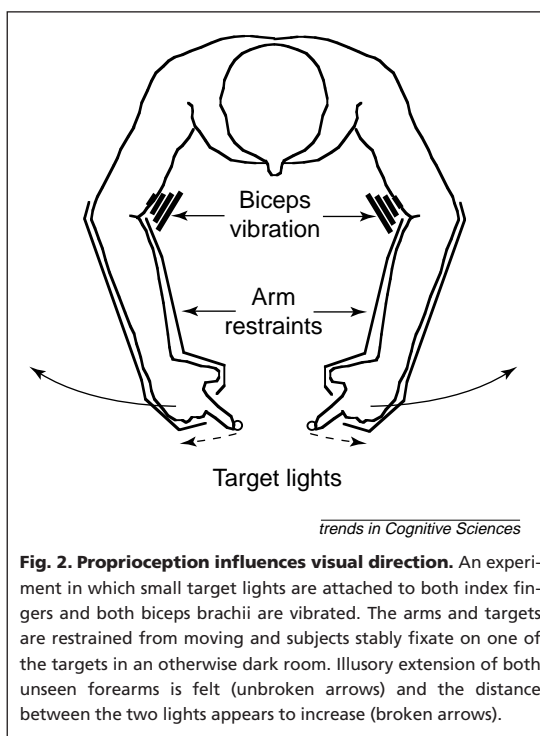


Fig. 2. Proprioception influences visual direction. An experiment in which small target lights are attached to both index fingers and both biceps brachii are vibrated. The arms and targets are restrained from moving and subjects stably fixate on one of the targets in an otherwise dark room. Illusory extension of both unseen forearms is felt (unbroken arrows) and the distance between the two lights appears to increase (broken arrows).

signals associated with passive body displacement coupled with mechanical contact information might be used.

The apparent position of the hand can be biased by visual misinformation about its location. When the hand is viewed through displacing prism spectacles, it will initially be felt where it is seen visually. The important point, however, is that as soon as the hand is actively moved and used to interact with the environment, recalibration will occur so that accurate coordination of the hand to external objects is regained²⁶. In preliminary experiments, it has been demonstrated that when a pointing movement is made to a target, the pattern of shear forces generated at the fingertip and the precise region of the fingertip stimulated are unique across the work space. These patterns actually provide a spatial map of hand position relative to the body and provide an immediate basis for updating spatial control of the arms²⁷.

Haptic calibration of the body schema

The hand and arm influence the body schema or spatial awareness that one has of the dimensions of one's body. The Pinocchio illusion provides a good example. If, while the nose is being grasped, illusory extension of the forearm is induced by vibrating the biceps muscle of the arm, then an illusion of nose elongation can occur²⁵. This illusion demonstrates how the perceptual representation of the body surface is influenced by haptic information about hand contact and about ongoing hand position: hand contact with the body, while arm position is remapped, leads to re-representations of body space and configuration. Hand contact, accordingly, provides a sensory–motor tool for updating the representation of the body schema; and, under normal circumstances it provides a natural, accurate spatial metric. Moreover, the hands can make physical contact with virtually any part of the body surface, including regions normally inaccessible to visual inspection, such as the back.

Haptic stabilization of posture

Haptic information from hand contact can have a profoundly stabilizing effect on body posture. Light touch of the index finger at mechanically non-supportive force levels is as effective as vision and vestibular function in attenuating body sway during quiet stance^{28,29}. Even subjects with grossly abnormal postural control benefit from this. For example, subjects without labyrinthine function can stand heel-to-toe for only a few seconds without falling to one side, even when allowed full sight of their surroundings. However, if they touch a stable surface lightly, with about 50 g of force (comparable to the force level applied by blind subjects reading Braille text), they can stand heel-to-toe virtually indefinitely without losing balance³⁰.

The hand in light contact with a stable surface serves as a sensory–motor probe for controlling body position. Stabilizing the finger probe at the contact surface, by minimizing force changes at the fingertip, automatically stabilizes the body and maintains sway at levels far below those adequate to stimulate the vestibular system or ankle proprioception. If in this circumstance, without the subject's knowledge, the finger contact surface is oscillated at low amplitude and frequency, the subject will become entrained to the oscillating touch surface and will sway at the same frequency^{31,32}. The subject will be unaware of the induced sway and will perceive the oscillating touch surface as being stationary. If the subject is told beforehand that the touch surface can be oscillated, then it is much less effective in influencing sway; and, in trials in which the surface is in fact stationary, it can be perceived to be moving. These findings emphasize that cognitive information about the spatial properties of the environment can influence body orientation and the apparent stability of external objects.

Contact of the hand with a stationary surface also overrides deficient or aberrant proprioceptive signals from the legs. When a subject is standing heel-to-toe, vibration of the right peroneus longus muscle, an ankle evertor, will elicit a reflexive contraction and cause the subject to fall to the right. If the subject is allowed light touch of the index finger, the effect of the vibration will be completely suppressed and the subject will be more stable than when attempting to stand heel-to-toe with neither vibration nor finger contact³³. This overriding influence of the hand on postural control is significant because it is also relevant for enhancing the balance control of astronauts returning from space flight who show post-flight disturbances of posture and locomotion, and of people undergoing rehabilitation for balance disorders³⁴.

Sensory–motor adaptation to gravity

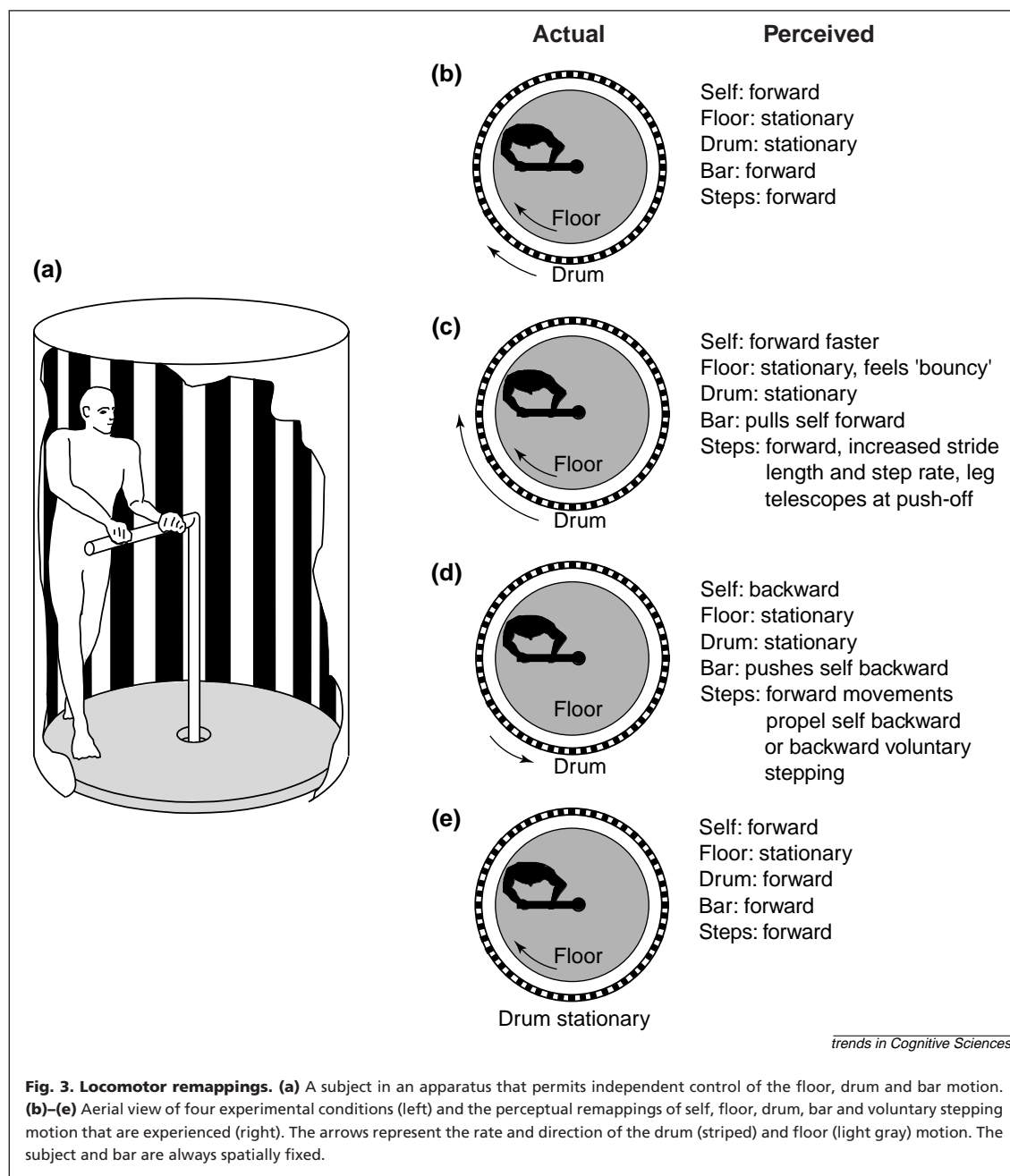
Orientation and sensory–motor control mechanisms are normally dynamically tuned to the background acceleration level of earth gravity¹¹. That is, we have an internal model of gravity and can estimate its influence on our actions. The existence of this calibration is usually 'perceptually transparent' to us so that we are not aware of the sensory and motor accommodations that we make in relation to gravity. As already mentioned, if we shift stance from two feet to one, the force on the sole of the stance foot doubles, yet we perceive little or no change. An even more striking example of

sensory–motor adaptation to earth gravity becomes apparent when one attempts to move during exposure to greater or less than 1 g background gravito–inertial acceleration levels. On earth, when we lower our body in a deep knee-bend we feel self-displacement downwards in relation to the stationary surface. However, if the same movements are attempted during exposure to increased or decreased background acceleration levels in an aircraft performing parabolic maneuvers, a different pattern will be experienced³⁵.

In 2 g acceleration levels, lowering the body in a deep knee-bend elicits the sensation of having moved downwards too rapidly and of the support surface moving upwards under the feet. Visually, the aircraft will also be seen to displace upwards as the body moves downwards. Rising up requires greater than normal effort, and the body will feel as if it is moving too slowly and as if the deck is being pushed downwards; simultaneously, the aircraft will be seen to move downwards. (The reverse pattern is experienced at less than 1 g background force levels.) With additional movements, subjects adapt so that their actions again seem normal. However, on return to 1 g acceleration level, they experience aftereffects: their movements feel abnormal, and the substrate of support and the visual world seem unstable when they move until re-adaptation to 1 g is achieved.

Astronauts who return from space travel experience similar instability of the ground and of their bodies when moving about. When lowering their body in a deep knee-bend, they seem to move downwards too rapidly, and feel and see the ground move upwards³⁶. This pattern is precisely that experienced by subjects during exposure to high force levels in parabolic flight. These observations show that sensory–motor control of our body movements and perception of the spatial properties of the support surface are dependent on and dynamically interpreted in relation to the background force level of earth gravity. Recently, we studied movement control in an aircraft flying parabolic maneuvers to simulate Mars' gravity – 0.38 g instead of 1 g. If, under this circumstance, one switches from a two-legged to a one-legged stance, a decrease in force is felt on the stance foot. This reflects the persistence of a calibration to 1 g and the 'expectation' of a much larger increase (0.5 g) in force on the stance foot than actually occurs (0.19 g). Perceived stability of an actually stable base of support during body movement is dependent on spatial constancy mechanisms, internal models of self and the background acceleration level, which subserve voluntary movement control of the entire body and relate patterns of afferent feedback to those expected for the patterns of efferent commands issued to the musculature. These spatial constancy mechanisms are recalibrated or updated on the basis of multimodal inputs. For example, in the parabolic flight experiments that involve deep knee-bends, the illusory felt and seen motion of the aircraft will be virtually eliminated and the subject's movements will seem more normal if the subject is allowed light touch of the hand with a stationary surface while making the deep knee-bends³⁷.

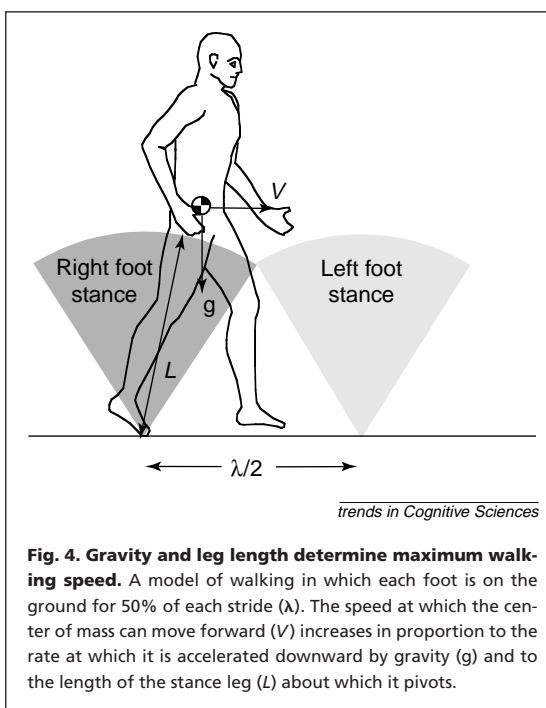
The calibration of locomotory movements involves a dynamic interplay of vision, proprioception, haptic contact cues, efferent control and internal models. Figure 3 shows an apparatus by which the relationship between stepping



movements, body displacement in space, and visual feedback can be rearranged. The subject, while walking on a circular treadmill inside a large optokinetic drum, grasps a handle that can be fixed in position or free to move. If the bar is fixed in place and the floor rotated backwards, the subject must walk in place making forward stepping movements. Under these conditions, if the optokinetic drum is rotated in the same direction as the floor and at the same rate, the subject will experience forward walking in a circle on a stationary floor in a stationary visual surround³⁸, while pushing a freely moving bar. In reality, the subject is walking in place, the bar is spatially fixed and the drum is rotating. If the speed of the optokinetic drum is doubled, the subject will feel as if he is moving twice as fast and that the bar he is grasping is pulling him forwards, so that he has to move faster to hold on to it. The subject will simultaneously perceive either that he has increased his stepping frequency so that he is walking twice as fast or that as he pushes off

with his foot, his leg lengthens telescopically to displace him double the normal stride length through space³⁹.

Other remappings can be demonstrated by reversing the direction of the optokinetic drum motion, then a forward-stepping subject can perceive himself to be making voluntary backward-stepping movements. The bi-directional nature of these remappings is revealed when the optokinetic drum is slowly brought to rest while the subject is walking forwards in place on the moving floor. Then, the subject will continue to experience circular self-displacement through space on a stationary floor, but he will perceive the physically stationary optokinetic drum to be rotating and keeping pace with his self-displacement³⁹. Thus, the perceived visual motion is 'driven' by the stepping movements of the legs. These bi-directional interactions show that self-calibration includes internal models that involve assumptions about environmental constraints, for example, the ground underfoot and the visual scene are usually connected



and not independent. Locomotion usually occurs in situations in which there is sight of the ground and ground-fixed scenery as well as haptic contact with the feet and often the hands. This allows accurate perceptual–motor calibration to be achieved and maintained.

The perceived step frequencies that can be generated by abnormally high visual flow patterns using the ‘walking in the drum’ paradigm can be much higher than the step frequencies that are physically possible on earth. Walking step frequency is constrained by V^2/gL (the Froude number, which is about 1 in humans) where V is the velocity of forward motion, g is the acceleration of earth gravity, and L is leg length⁴⁰. During walking, unlike running, one foot is in contact with the ground at all times and it is the acceleration of earth gravity acting on the body pulling it downwards that makes walking possible (see Fig. 4). The maximum walking velocity possible with straight legs before breaking into running is about 3 m/s for an individual with a leg length of 0.9 m. (On the moon, which has one sixth the gravitational acceleration of earth, the maximum velocity is only 1.2 m/s, hence the spontaneous switch to ‘bounding’ that the Apollo moon astronauts adopted.) With a stride length of 0.7 m, the maximum possible step frequency is just over 4/s. The nervous system, however, is not limited by these physical constraints in assigning perceptual representations of stepping frequency. Similarly, in representing the dimensions and configuration of the body, the nervous system does not respect physical constraints or possibilities. For example, during the Pinocchio illusion, the nose can be perceptually experienced as a foot long or more. This means that the perceptual and cognitive worlds that can be experienced are not limited by the physical one in which we evolved (Box 1).

Reaching during real and virtual rotation

Together the observations that have been described point to the key roles of proprioception and of hand and leg movement control in the calibration of the body schema, the main-

tenance of postural stability, the perceptual stability of the visual world and the apparent stability of the support surface during whole-body movements. These same factors allow sensory–motor adaptation to different background acceleration levels, to changes in body dimensions, and to changes in muscle efficiency over time. Muscle spindle receptors are key components in such adaptation as can be seen from recent experiments involving adaptation to rotating artificial gravity environments. Movements made during rotation generate unusual forces. For example, if a forward-reaching movement is made during counterclockwise rotation, a Coriolis force will be generated on the arm displacing its path and endpoint rightward (see Fig. 5). The Coriolis force is a transient inertial force that is proportional to the cross-product of the angular velocity of the rotating environment and the velocity of the arm relative to the rotating environment. Before and at the end of the arm movement, the Coriolis force is thus zero.

Individuals who make reaching movements in a rotating environment initially show large deviations of movement path and endpoint, missing the target position. However, when they make additional movements, their reaching paths become straighter and their endpoints more accurate. Within 20 or 30 movements, even in the absence of visual feedback, they again reach in straight paths to the goal position^{41,42}. This means the nervous system has modeled and compensated precisely for the influence of the Coriolis forces on movement. When this adaptation is complete, pointing movements again feel completely normal, the Coriolis forces, although still present during movements, are no longer felt; the nervous system has rendered them perceptually transparent. Muscle spindle receptors are an important component in the adaptive process because when a reaching movement is perturbed by a Coriolis force, the resulting patterns of muscle spindle feedback and Golgi tendon organ activity are inappropriate for the intended movement (see also Fig. 6). Compensations are automatically introduced in subsequent movements to restore accurate control. Box 2 explains how exposure to Coriolis forces differs from exposure to mechanical perturbations.

In everyday life, we commonly reach for objects while simultaneously rotating our trunks. Such rotary movements of the body can typically have peak velocities as high as 200°/s and generate Coriolis forces on the arm that can be much higher than those studied with passive rotation in the laboratory where velocities greater than 60–120°/s are rarely used. In ongoing experiments, we have demonstrated that the nervous system anticipates and compensates for these self-generated Coriolis forces because subjects are able to reach accurately while simultaneously turning their body^{43,44}. Self-generated Coriolis forces are also perceptually transparent: we do not feel them. A simple way of demonstrating that we anticipate and compensate for Coriolis forces associated with our body motion is shown in Fig. 7. A head-mounted display is used to induce compelling illusory self-rotary displacement in a subject who then makes pointing movements to a target⁴⁵. The subject’s initial reaches will be curved and miss the target instead of being straight. The error pattern shows that the subject’s nervous system, in programming the reach, is anticipating that a Coriolis force will be generated and is compensating for it. The subject will

Box 1. Perceptual remappings are complex

The experiences reported by subjects walking in the apparatus illustrated in Fig. 3 (see main text) demonstrate that multiple perceptual-motor remappings can occur, many of which are physically impossible. The existence of these phenomena reveals the complex, layered, mutually dependent representations involved in spatial orientation and motor control. Even simple sub-systems do not operate independently of these representations.

Sensory convergence is a simple concept that has been used to account for many aspects of movement control and spatial orientation. For example, there are similarities in the response of vestibular nucleus cells that receive both vestibular and visual inputs, and the speed of apparent self-motion induced by a concentrically rotating surround (Refs a–d). Inputs to nodal vestibular nucleus cells from motor and somatosensory systems have been invoked to explain the patterns of self-motion and eye movement elicited by walking in place on a circular treadmill (Ref. e) or by brachiating in relation to a revolving cylinder (Ref. f). Recently, convergence of efferent signals onto vestibular nucleus cells has been found (Ref. g).

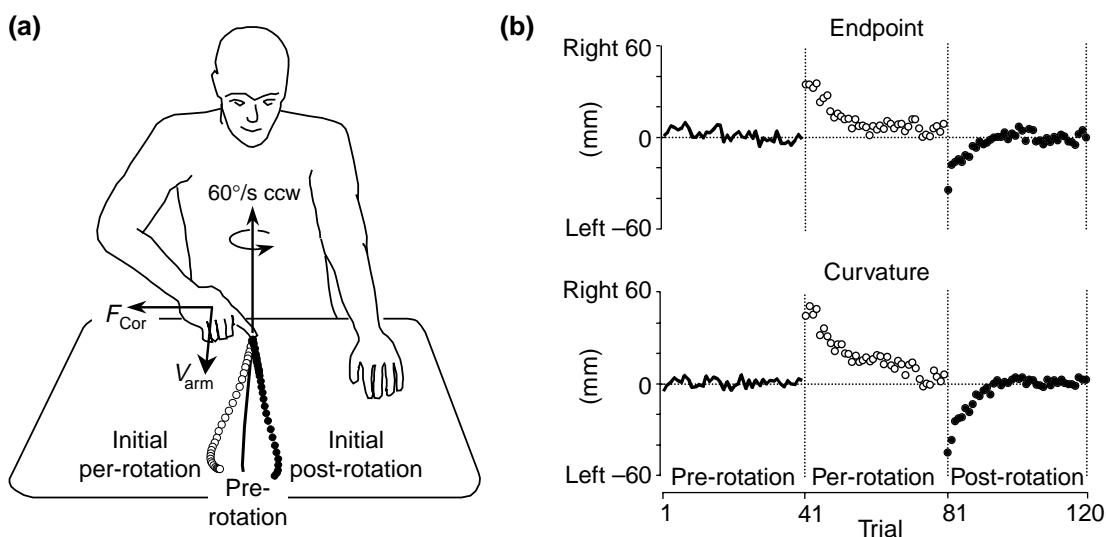
Adding inputs to a sensory convergence model makes it sensitive to more outside influences but at the same time decreases the information content of its output. When the experimental paradigm only offers a two-choice sensory or neural response, such as discrimination between self-motion or motion of the entire environment while seated, the ambiguity seems resolvable by a convergence mechanism that reinterprets prolonged motion of the external world as self-motion. By contrast, the commands issued to generate locomotory movements and the resulting ground reaction forces, visual feedback and body motion through space are not related in any simple way. For example, forward-stepping movements are associated with forward ground reaction forces on level ground but with backward ground reaction forces when walking down an incline. In experimental situations where movement of one's limbs, inertial movement of the whole body, visual flow, a moving substrate and other moving surfaces are all possible, the unitary signal from a nodal cell cannot explain why subjects experience multiple interpretations many of

which involve violation of different physical constraints (Fig. 3d, main text).

The way in which environmental constraints are violated is an important cue to the organization of internal representations. For example, it is possible for a subject walking in place on a circular treadmill to experience forward progress over a stationary floor and to experience the entire visual world as moving apace (Fig. 3e, main text). Research reports never explicitly mention that when stationary seated subjects experience visually induced illusory self-rotation, they not only feel the chair they are sitting in to be rotating but that it is rotating in relation to the floor of the experimental room, which is perceived to be stationary. Our perceptual experiences are more layered than can be explained by simple convergence models. Contact cues and cognitive information govern the hierarchy of internal constraints about stability of the visual world and the substrate of support.

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Fig. 5. Reaching in a rotating room. (a) A subject in darkness experiences no self-motion after 2 min of constant velocity counter-clockwise (ccw) rotation, 60°/s, because the semicircular canals are only stimulated by a changing rotation speed. In the subject's initial per-rotation attempt to reach forward, his hand is deviated rightwards (open symbols) by a transient rightward Coriolis force (F_{Cor}) that arises when the arm is in forward motion (V_{arm}). $F_{Cor} = -2m(\omega V_{arm})$ where m is the mass of the arm, ω is the velocity of rotation in radians/s and V_{arm} is the velocity of the arm in m/s. After 10–15 reaches, the subject's movements become as straight and accurate as pre-rotation (unbroken line). The first post-rotation reach (filled symbols) is a mirror image of the initial per-rotation one. (b) The endpoints and path curvatures of 40 reaches made during pre-, per- and post-rotation periods.

Box 2. Failure of equilibrium point theories

Coriolis force perturbations in a rotating environment are a powerful tool for studying motor control and self-calibration. These transient forces are absent when a movement is first initiated and vanish when it terminates. No sensory cue precedes their evocation by a body movement. Subjects seated at the center of a fully enclosed rotating chamber feel completely stationary after 60–90 s at constant velocity, because this situation is the sensory equivalent of a normal stationary environment. Transient Coriolis forces enable us to test different models of motor control.

Normal human head and arm movements have been shown to act like mass-spring systems when mechanically perturbed by contact forces (Refs a,b). This has led to theories that voluntary movements evolve from control of muscle stiffness (the α -equilibrium point theory of Bizzi and colleagues; Ref. c) or the positional bias of muscle length–tension characteristics (the λ -equilibrium point theory of Feldman and colleagues; Ref. d). The fundamental prediction of both theories is that transient perturbations will not affect the movement endpoint. In contrast to these theories, Coriolis force perturbations produce large endpoint and path deviations of normal reaching movements, illustrated in Fig. 5 (main text). Blind subjects and individuals who lack vestibular function show the same Coriolis force deviations of their reaching movement as normal controls.

This disparity between inertial and contact force perturbations points out a major confound in previous experiments and an important clue about sensory–motor control. The absence of contact force on the limb is a unique feature of Coriolis forces perturbations. An inertial Coriolis force is distributed over every atom of the reaching arm; all other perturbation methods are applied to a region of the cutaneous surface. When 10–20 consecutive reaches to a target are made during rotation, there is a complete return to straight movement paths and accurate endpoints, despite the continued inertial Coriolis force perturbations. By contrast, it takes many hundreds of movements for a subjects to regain normal control when they have to push or pull a robotic arm programmed to deliver a force field very much like the Coriolis force (Ref. e). After 10–20 reaches during rotation, inertial perturbations are no longer sensed – the Coriolis force becomes perceptually

transparent. By contrast, contact force perturbations delivered by a manipulator are still detected even after many hundreds of trials, although they feel less intense than initially. Thus, motor self-calibration is rapid, whereas learning the properties of external machines and tools is slow. Cutaneous, muscle spindle, Golgi tendon organ and efferent signals are crucial for segmenting the force environment into functionally significant units and they affect the form and rate of sensory–motor recalibration.

Cutaneous stimuli that arise when the finger lands on a surface at the end of a reaching movement also influence proprioception and motor adaptation (see Fig. 6, main text). Reaching deviations due to transient Coriolis forces in a rotating room are adaptively reduced to zero, even in the absence of visual feedback if the reaches end on a smooth surface. However, if the reaches end with the finger in the air above the surface, movement paths will become straight again but endpoint errors will only be reduced by about 50%. This indicates both a muscle spindle and a cutaneous contribution to adaptation.

The Coriolis force paradigm has shown that position control models of movement control are inadequate. Muscle spindle and efferent signals related to velocity control are much more important than previously thought. Continuous spindle and efference copy signals during movement and terminal contact cues are essential for position and velocity control and self-calibration.

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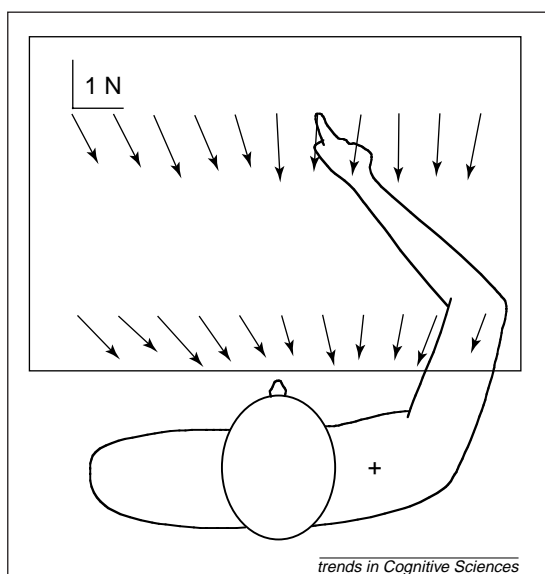
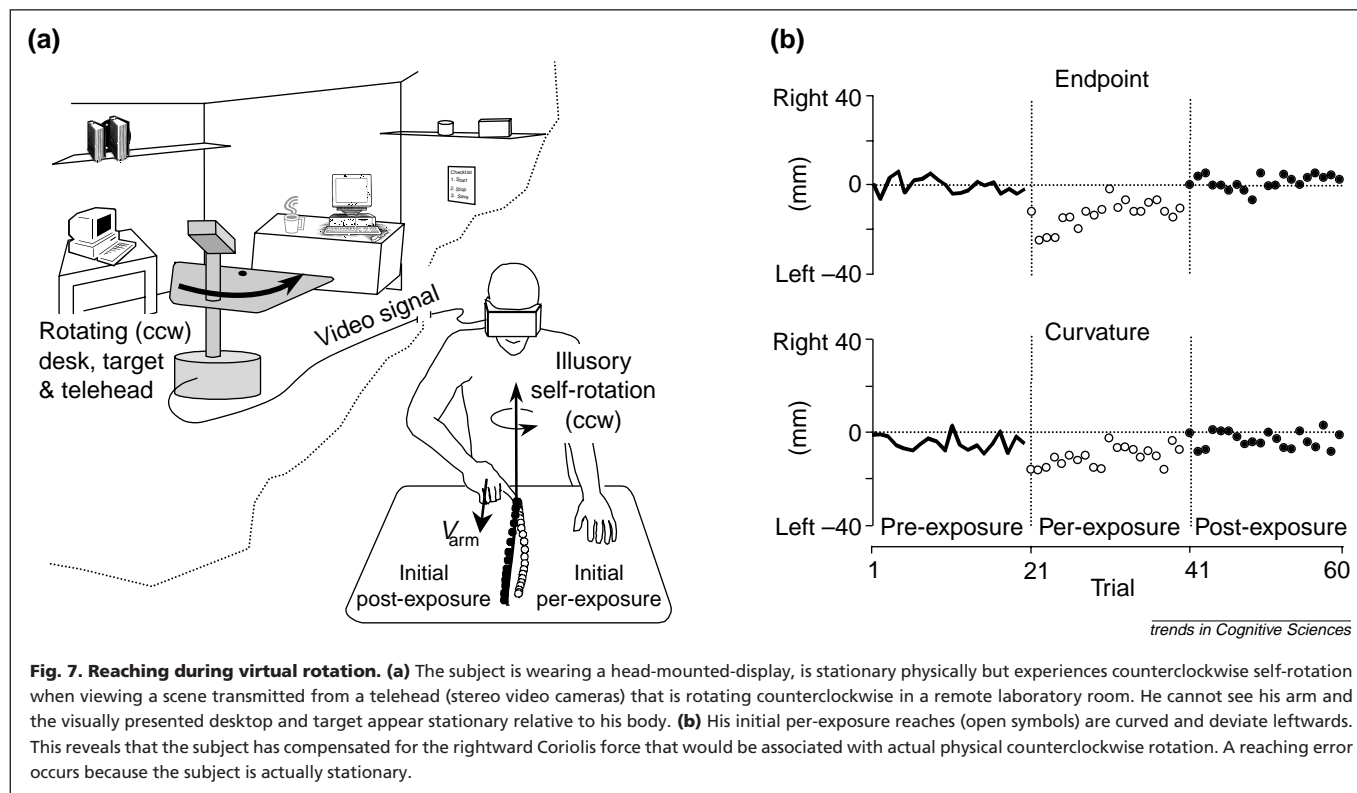


Fig. 6. Fingertip contact forces map-reaching endpoint. When a reaching movement ends in contact with a surface, the shear forces generated during the first 30 ms after impact specify where the hand is relative to the body. The shear reaction force vectors associated with touching different locations on the surface point to the same body relative location near the shoulder (cross). The origin of each vector indicates where the finger made contact with the surface. One newton (N) equals 102 grams of force.

actually feel that an external force has deviated his or her reach!

Conclusions

Sensory–motor control and orientation are dynamically adapted to the force of earth gravity. One consequence of this adaptation is that we do not perceptually experience the actual forces associated with the support and movements of our body in relation to gravity, nor do we experience the Coriolis forces generated by our arm and leg movements during voluntary body turning. Muscle spindle receptors are an important component in the position sense representation of the body and their signals are interpreted in relation to motor commands to the musculature. Spindles also feature prominently in sensory–motor adaptation. The hands are important in the calibration both of auditory and visual spatial localization, and in the perceptual representation of the body surface and its dimensions. Contact of the hand with a stationary surface can greatly enhance postural control and adaptation to unusual force conditions. Multisensory inputs decoded in relation to motor commands and expected patterns of afferent feedback are crucial for orientation and movement control, and the apparent stability of our surroundings. The figure in Box 3 summarizes some of the factors and computations that contribute to this process.



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Outstanding questions

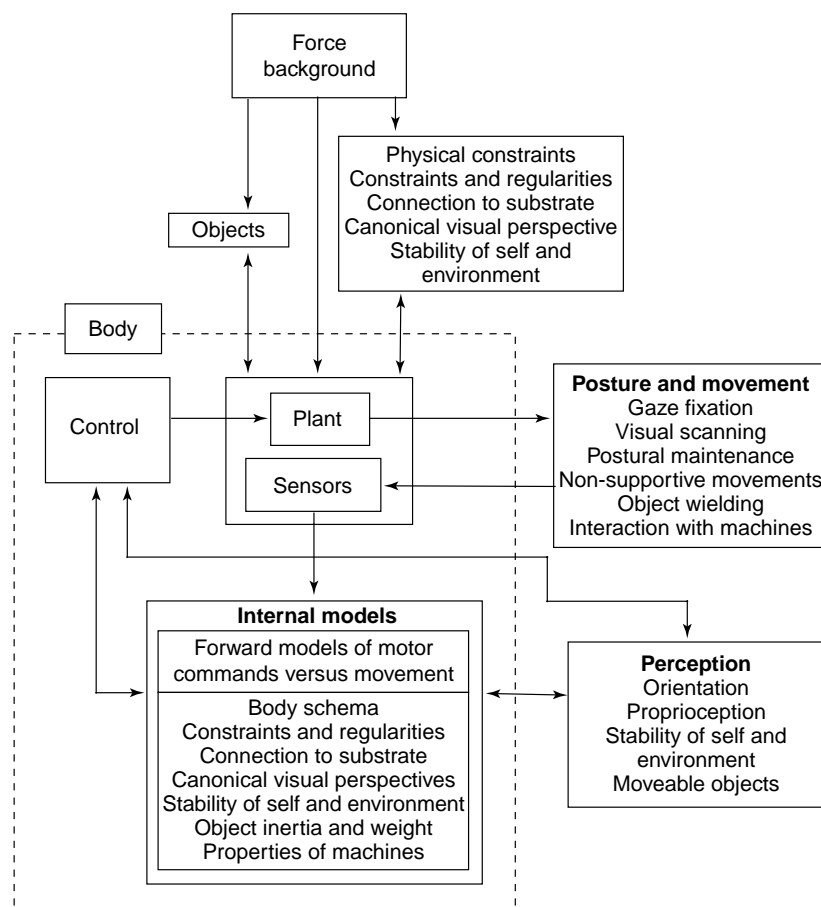
- Why is adaptation to Coriolis perturbations so rapid while adaptation to analogous mechanical perturbations delivered by robotic manipulanda very slow?
- What determines whether forces associated with self-movement and postural control will be perceptually transparent?
- How do tactile contact cues contribute to re-calibration of the body schema and to the perceptual stability of the environment?
- Why is adaptation to altered-force environments so rapid?
- What characterizes sensorimotor environments that humans cannot adapt to?

Box 3. Factors influencing self-calibration

Figure 1 emphasizes the main points of this article. The force background is at the pinnacle because it determines the possible modes and processes of movement and posture. This approach is akin to Henderson's analysis of the physio-chemical basis of life on earth (Ref. a). The gravitational force background creates physical constraints, situations of high probability. For example, the visual perspective during standing is from eye height. The probability of some constraints is context-dependent, for example, inertial stationarity of the entire visual surround is less likely for an aquatic animal surrounded by suspended particles than for a terrestrial animal in clear air. The topography of one's own body is a constraint that must be updated through development. The force environment structures the mechano-receptive signals of the body that influence internal models of the self and of the external milieu. Internal models include forward models (Ref. b) such as predictions about self-generated Coriolis forces during turn and reach movements. Movement and perception are products of current sensory and motor signals in relation to internal representations of constraints and past experiences.

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Fig. 1. Self-calibration process. Block diagram of self-calibration of spatial orientation and movement control.

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