

SENSORIMOTOR INTEGRATION

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s0010 SUMMARY

p0010 Sensorimotor integration is central to sustained control of configuration (postural control). This chapter considers postural sensorimotor integration at the level of the whole system, which includes concurrent perceptual, executive and motor processes. These mechanisms provide a basis for physiotherapeutic practice. Multiple sensory modalities are combined with prior personal experience and converged to a set of movement possibilities. From these possibilities, control priorities are selected and passed to the motor system which generates coordinated inhibition and excitation of the entire muscular system. Within a main perception–selection–motor feedback loop, two levels of mechanism work together. The slow intentional system acting through central selection and optimization pathways (e.g. basal ganglia, premotor and prefrontal cortex, cerebellum) allows sequential optimization, selection and temporal inhibition of alternative possibilities up to a maximum rate of two to four selections per second. The fast habitual-reflexive system acting through previously facilitated transcortical, brain stem and spinal pathways implements coordinated responses to environmental stimuli with a latency as low as 50–100 ms. The main perception–selection–motor loop provides a mechanism for amplifying or diminishing maladaptive perceptions and selections. Restoration of maladapted function requires re-education of the central processes of perception and selection.

s0015 POSTURAL CONTROL

p0015 Posture simply means configuration of the body. The human body comprises multiple segments along a kinematic chain which includes feet, shanks, thighs, pelvis, spine, thorax, arms, neck and head. There are many possible configurations. Some configurations require little muscular energy to maintain whereas others require a great deal. In choosing a configuration one is constrained to provide the effort required to balance that configuration. The postural task is to maintain these segments in a desired configuration or choose some other control priority which allows configuration to adjust as required.

p0020 Passive structures, including joint surface, ligaments and inactive muscle, provide some degree of postural control.¹⁻³ For example, muscle naturally becomes stiffer when it is still and that stiffness dispels during movement,^{2,4} thus assisting maintenance of configuration without impeding movement. It is possible to align the

shanks, thighs, pelvis, spine, thorax, neck and head such that standing is temporarily possible with no muscle activity.^{3,5,6} Passive stabilization through alignment, or through contact with external surfaces (e.g. floor, wall, table or chair), reduces the control and attentional demands of maintaining configuration. However, even allowing for passive stabilization, the free-standing upright aligned body is mechanically unstable. In the absence of sensory feedback even small departures from alignment will cause the body to fall.^{2,7-13} During accurate alignment, the active muscular forces required to balance gravity are minimal. The time taken to fall from the aligned configuration increases exponentially with the accuracy of the initial alignment.^{2,14-16} Hence, upright configuration is achieved most economically and most stably when alignment is controlled accurately.

Neural regulation is essential for postural control. p0025 Mechanical instability alone means sensorimotor feedback is required. Furthermore, daily life requires sensory and mechanical engagement with external objects and social engagement with other people: the required configurations are many and difficult to predict beyond a short time scale. Pre-computing motor solutions and storing them in a retrievable fashion is appropriate when the controlled ‘system’ and necessary constraints do not change.¹⁷ Pre-computed building blocks of motor control known as motor primitives are stored within the motor cortex, brain stem and spinal cord. The sensorimotor system retrieves and combines these primitive components in the construction of posture and movement.¹⁸⁻²⁰ However, through fatigue, development and ageing the human system changes. Local pain, injury and irritation cause people to limit the ranges of desired configurations. These altered limits may be required swiftly and may also evolve gradually. Constraints on configuration and control strategy change with the need to catch, pick up and hold objects, look at computer monitors, communicate with other people, evade dangerous objects and generally negotiate the mechanical environment. Pre-computed solutions alone are insufficient. This kind of control, to handle changing constraints, requires flexibility for computing new motor solutions in the moment of activity.²¹ Constructing new motor solutions in the moment of activity requires selection, recombination of existing possibilities and temporal inhibition of non-selected alternatives.²² Thus within a main feedback loop retaining executive control of posture, the human postural system requires two kinds of feedback: a fast loop for implementing pre-computed control, and a slow loop for implementing control which is reconstructed during

activity. The human nervous system has sensorimotor pathways corresponding to both loops.²³ In this chapter these loops are named as habitual-reflexive (fast) and intentional (slow). In control theory, the general paradigm which provides time for selection and optimization within the main feedback loop is known as intermittent control.^{17,23,24} The continuous paradigm (e.g. servo control, continuous optimal control) has been the mainstay of postural and motor control since early physiological investigation into postural reflexes,^{25,26} and since the 1960s from investigation of sensorimotor integration.²⁷ The more recently developed intermittent control paradigm includes and extends the explanatory power of the better known continuous paradigm.^{23,24}

p0030 To summarize, postural mechanisms provide sustained control of an unstable multisegmental structure in known and unpredicted circumstances. This control requires neural integration of multiple sensory modalities with multiple possible goals and constraints.

s0020 **SENSORIMOTOR INTEGRATION**

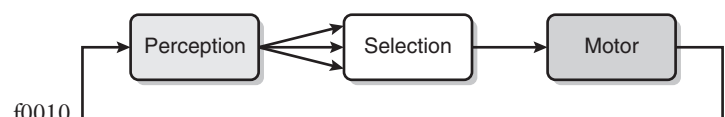
p0035 Sensorimotor integration is central to postural control. Postural control can be understood as a main feedback loop combining concurrent elements of perception, selection and motor control^{23,28} (Fig. 4-1) implemented through a range of neural pathways (Fig. 4-2).

s0025 **Perception**

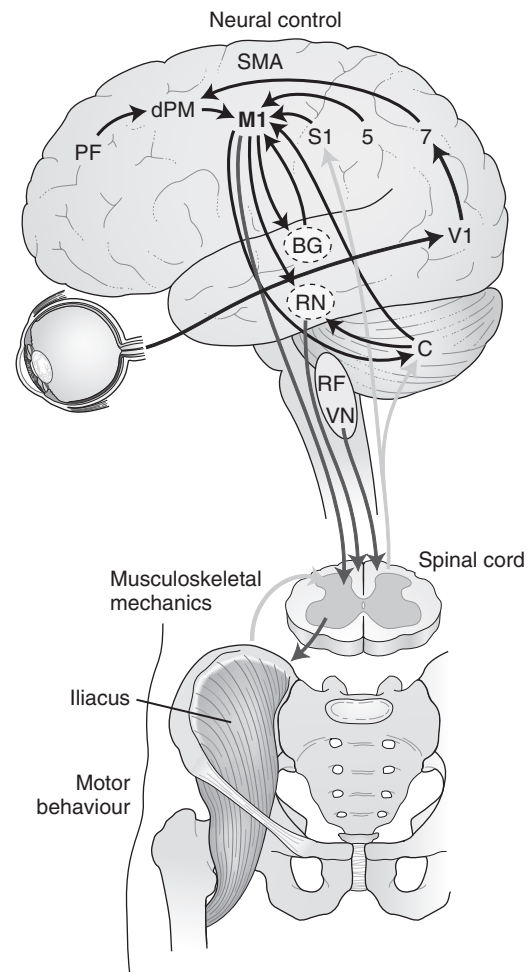
p0040 The person receives multiple channels of information through their eyes, ears, skin, muscles, joints and other internal sources. Perception is the interpretive process of sensory analysis. Sensory information is uncertain and potentially ambiguous. Sensory accuracy and confidence are improved by integrating information between sensory modalities, and by combining sensory information with prior experience in a process described mathematically as Bayesian state estimation.²⁹⁻³⁴ Prior personal experience influences the earliest stages of neural sensory representation through to later stages of perceptual decision making.²⁹ Through integrative analysis all sensory channels are converged to a smaller number of possibilities for movement stored as action representations in the frontal cortex.^{23,35}

s0030 **Selection**

p0045 From the current possibilities, priorities are selected for postural and motor action. This response selection



f0010 **FIGURE 4-1** ■ Perception–selection–motor feedback loop. Sensorimotor integration forms a feedback loop in which selected motor control influences sensory analysis, perception and future selection. This feedback loop provides a mechanism for amplifying or diminishing the consequences of maladaptive selections.



f0015 **FIGURE 4-2** ■ Sensorimotor pathways through the central nervous system. The central nervous system is conventionally viewed as having a hierarchical organization with three levels: the spinal cord, brainstem and cortex. The spinal cord is the lowest level, including motor neurons, the final common pathway for all motor output, and interneurons that integrate sensory feedback from the skin, muscle and joints with descending commands from higher centres. The motor repertoire at this level includes stereotypical multijoint and even multilimb reflex patterns, and basic locomotor patterns. At the second level, brainstem regions such as the reticular formation (RF) and vestibular nuclei (VN) select and enhance the spinal repertoire by improving postural control, and can vary the speed and quality of oscillatory patterns for locomotion. The highest level of control, which supports a large and adaptable motor repertoire, is provided by the cerebral cortex in combination with subcortical loops through the basal ganglia and cerebellum.³⁶ Motor planning and visual feedback are provided through several parietal and premotor regions. The primary motor cortex (M1) contributes the largest number of axons to the corticospinal tract and receives input from other cortical regions that are predominantly involved in motor planning. Somatosensory information is provided through the primary somatosensory cortex (S1), parietal cortex area 5 (5) and cerebellar pathways. The basal ganglia (BG) and cerebellum (C) are also important for motor function through their connections with M1 and other brain regions. RN, Red nucleus; V1, Primary visual cortex; 7, Region of posterior parietal cortex; dPM, Dorsal premotor cortex; SMA, Supplementary motor area; PF, Prefrontal cortex. For colour version see plate section. (Reproduced with modification from Scott.³⁸)

process acts through central selection and optimization pathways such as those within the basal ganglia and cerebellum^{22,36} and allows sequential optimization, selection and temporal inhibition of alternative possibilities up to a maximum low rate of two to four selections per second.^{23,28,37}

s0035 Motor Control

p0050 Using parameters passed from the selection process, the motor system produces coordinated inhibition and excitation of the entire set of muscles joints and implements control of configuration. These selections are executed through the slow and fast pathways working together within the main perception–selection–motor feedback loop. The slow intentional pathway provides control which is reformulated and executed sequentially within the main feedback loop with a variable latency of 180–500 ms.^{28,37} Using preselected parameters, the fast loop acting through transcortical, brain stem and spinal pathways implements coordinated habitual-reflexive responses to environmental stimuli with a latency as low as 50–100 ms.⁵

p0055 The results of motor control generate sensory input which is interpreted, thus completing the feedback loop. The feedback loop is a dynamic system. Thus all maladapted features of postural control (symptoms) evolve through time, either constructively or destructively depending on whether feedback is mathematically negative or positive.

s0040 SENSORY INTEGRATION

p0060 Combination of sensory signals with prior expectation occurs centrally in areas including the mid-brain and cerebral cortex.^{30,39,40} For example, the posterior parietal cortex receives input from the three sensory systems that enable localization of the body and external objects in space: the visual system, the auditory system and the somatosensory system. The posterior parietal cortex also receives input from the cerebellum which is increasingly thought to generate expected sensory signals from known motor commands²⁰ (Fig. 4-3). Much of the output of the posterior parietal cortex goes to areas of the frontal motor cortex.²⁰

p0065 For postural control, the visual, vestibular, proprioceptive and cutaneous modalities work together to estimate where parts of the body are in relation to one another and the external world. These senses are commonly stated to be redundant, since postural control is possible with one or more modalities missing. However estimation is more accurate and more robust when different senses are combined (see Chapters 4, 40, 42). A weighted combination of signals from all sensory modalities is combined with copies of motor signals passing through central neural networks trained by prior experience to produce equivalent expected sensory signals (Fig. 4-3).^{20,41,43-45} This integration enables the nervous system to use all its available information and knowledge to resolve potential conflicts of interpretation.^{43,44} For example, when you move your eyes causing the image of

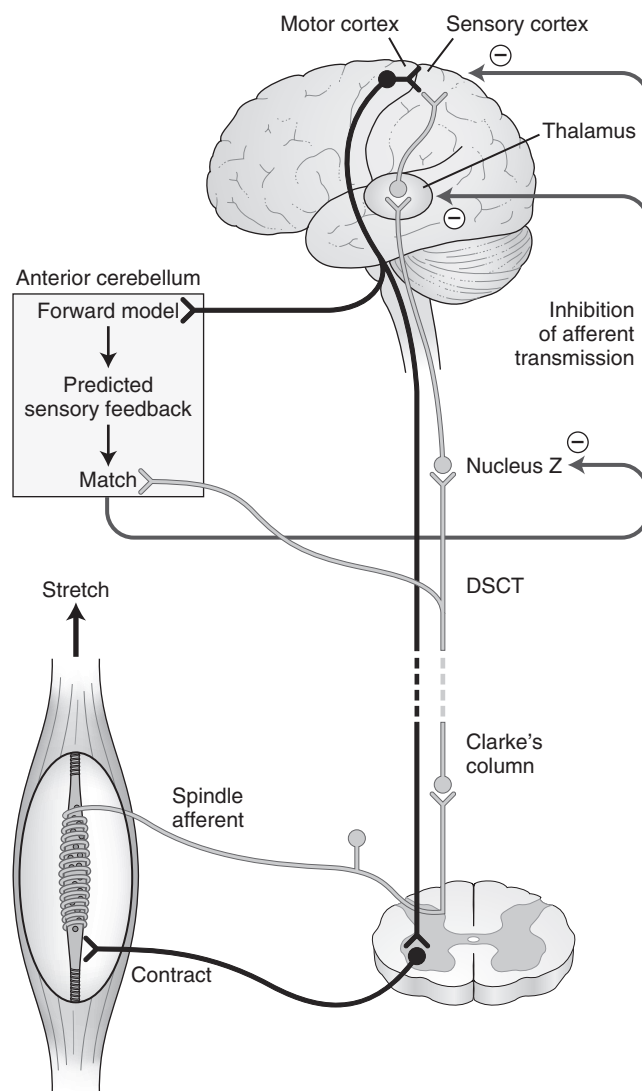


FIGURE 4-3 ■ Neural pathways estimating position from sensory and motor information. Integration of muscle spindle afferents with expectations generated from motor output. When the muscle is stretched, spindle impulses travel to sensory areas of the cerebral cortex via Clarke's column, the dorsal spino-cerebellar tract (DSCt), Nucleus Z, and the thalamus (shown in red). Collaterals of DSCt cells project to the anterior cerebellum. When a motor command is generated, it leads to co-activation of skeletomotor and fusimotor neurons (shown in blue). A copy of the motor command is sent to the anterior cerebellum where a comparison takes place between the expected spindle response based on that command and the actual signal provided by the DSCt collaterals. The outcome of the match is used to inhibit reafferent activity, preventing it from reaching the cerebral cortex. Sites of inhibition could be at Nucleus Z, the thalamus, or the parietal cortex itself. For colour version see plate section. (Reproduced from Proske and Gandevia.⁴¹)

the world to move across your retina, the world appears stationary because your nervous system knows that you are stationary relative to the ground and knows that you have moved your eyes rather than believe the external world has moved.⁴⁶

Vision provides powerful sensory input to posture and balance,⁴⁷⁻⁴⁹ illustrated by its famous ability in 'moving room' experiments to make young children fall over.^{50,51} Vision signals movement of the external world relative to

the eye via optic flow of the visual field across the whole retina.^{52,53} Estimation of body movement from retinal information requires knowledge of eye-in-head movement, knowledge of head-on-neck movement and other joint movement down the kinematic chain.^{54,55} For example, when fixing the fovea on stationary targets, together rotation of eye-in-head and head-on-neck signal movement of the head and trunk relative to the external target. Visual sensitivity to postural sway is high, allowing detection of sway about the ankle joint of only ~0.1 degree,^{52,56} but this sensitivity decreases as distance to the visual target increases.^{52,53} Closing one's eyes illustrates both an immediate reduction in stability and also that normally postural control without vision is possible.

p0075 *Vestibular* organs including the semicircular canals and otoliths register rapid rotation and translation of the head, respectively.⁵⁷⁻⁵⁹ While commonly thought to sense acceleration, these organs contain substantial internal viscous damping, which means they measure damped acceleration that more closely resembles velocity.⁴⁶ Vestibular sensitivity to postural sway is an order of magnitude lower than vision and requires postural rotations about the ankle joint of approximately ~1 degree. Similar to vision, extraction of body motion from sensed head movement requires knowledge of head orientation with respect to the trunk.⁵⁷⁻⁶⁰ Similar to vision, postural control is possible with vestibular loss, but balance is less robust and falls are more likely.⁶¹⁻⁶⁴ However, vestibular organs provide compelling sensory input of larger, faster head movements relevant to falls and balance. Most importantly, whereas vision alone cannot distinguish motion relative to the ground (self-motion) from motion of external objects relative to the eye (world motion), vestibular sensation alone provides an absolute measure of self-motion albeit motion of the head in space. Vestibular sensation is important for resolving ambiguity resulting from visual and proprioceptive sensation.⁴⁴

p0080 *Proprioception* provides the sense of relative position and movement between neighbouring parts of the body. The sensory information derives mainly from sensory receptors associated with skeletal striated muscles (spindles, Golgi tendon organs), less so from joints, and is combined with cutaneous receptors signalling skin stretch and pressure.^{41,43} Proprioception does not provide any particular sensations, but provides knowledge of the position and movement of our limbs and body.⁴¹ If there is any sensation, this usually relates to a difference between what is expected and what has actually occurred.⁴¹ In contrast to vision and vestibular sensation, loss of proprioception is instantly devastating for motor and postural control.⁶⁵ For example, in a rare case of large-fibre sensory neuropathy, the individual (I. W.) has no sensation of cutaneous light touch and no movement/position sense below the neck: without vision he has no knowledge of where his limbs and body are in space.⁶⁰ Following this loss, motor control, posture, movement and learning new control have only been possible when deliberately using direct vision of the limbs for guidance and forward planning.^{65,66}

p0085 Estimation of body configuration and motion is a multimodal process integrating proprioception, vision and vestibular input.⁵⁴ The proprioceptive organs,

particularly the muscle spindles, form a 'proprioceptive chain' crossing all articulations between the eyes, feet and hands which functionally links the eye muscles to the foot and hand muscles.^{43,67-69} Along the proprioceptive-kinematic chain, information accumulates from the source of sensory information to the mass segment whose location needs to be controlled. For postural control, the head and ground (or other supporting surface) source two lines of accumulating sensory information:

- Head referenced information: Proprioception is essential for extracting body motion from visual and vestibular sensation of head movement.⁵⁴ The main mass of the body lies within or close to the trunk and the primary articulation defining trunk location from the head is the neck. Proprioception of the neck is substantial and well connected with the vestibular and visual system^{68,70-73} and provides the first, most predictive estimate of body location. This estimate of body location is improved through proprioception of additional joints along the extended proprioceptive-kinematic chain.
- Ground referenced information: Proprioception alone can extract body motion relative to the ground or other supporting surface. When supported only on the ground through the feet, the primary articulation defining body location is the ankle joints, and during free standing, ankle rotation alone provides a good estimate of centre of mass location,^{7,8} which is improved through adding knowledge of articulations further along the chain from the ground reference. Consequently, proprioception of ankle rotation is highly sensitive (~0.1 degree).⁵⁶ Single joint muscles crossing the ankle such as the soleus and to a lesser extent the tibialis anterior are richly endowed with muscle spindles.^{7,74,75} To summarize, vision (with eye proprioception) and vestibular sensation give movement of the head, and movement of the body requires measurement of neck rotation. Movement of the body can be measured directly relative to the ground. For both of these proprioception is vital.

Pressure registered through the feet signals the mean location and strength of the contact support force. During free-standing postural control, accelerations are low and the ground contact force position signals the anterior-posterior and mediolateral location of the gravitational force vector and thus of the whole body centre of mass position. Thus, under normal conditions, sensation through the sole contributes to estimation of the centre of mass location relative to the foot. This estimate is important, since balance requires maintaining the centre of mass within the base of support.⁷⁶

Proprioception provides knowledge of the kinematic chain. In unconstrained movements, proprioceptive information provides relatively accurate estimates of limb position. So-called active proprioception, in which the person moves their own limb, does not provide better estimates of limb position than passive proprioception in which the limb is moved for the participant.⁷⁷ During multijoint movement,⁷⁸ proprioceptive information is thought to be used in the translation of higher level

movement goals into joint based motor commands⁵⁵ and also to provide local reflexive stabilization of joints.⁷⁹⁻⁸¹

p0105 However, there are limits to the accuracy of proprioception, particularly for slow changes in position.⁴¹ Muscle spindles are highly sensitive to change in muscle length and like most sensory cells tend to habituate to constant conditions that limit their capability to sense absolute values of joint angles (Fig 3).⁴¹ Tendon compliance, which is high under postural conditions of low forces, and muscle slack, dependent on the previous history of contraction, both mean that muscle length and change in muscle length can be poorly related to joint angle.^{6,7,41,74,82,83} Thixotropy, namely the tendency of muscle to become stiff when still,^{84,85} means that joint rotation transmits less effectively into muscle length change under postural conditions, and this is compounded by the changes in muscle length caused by fluctuating muscle activity which can be an order of magnitude larger than those caused by joint rotation.^{6,74} The sense of position, as identified by position matching tasks, shows that proprioception can be substantially disturbed by the previous history of movement, contraction, muscle slack, thixotropy and exercise (Fig. 3).⁴¹ Proprioception becomes markedly less sensitive during co-activation across joints (Fig 7)⁴¹ and passive spindles are more sensitive to movements than when fusimotor neurons are contracting.^{41,74,86} During voluntary muscle contraction skeletal-motor and fusimotor neurons contract together (α - γ co-activation). Hence these findings are at odds with the common view that proprioception is more accurate under active than passive conditions.⁴¹ These factors, very well reviewed by Proske and Gandevia,⁴¹ highlight three main facts: (a) proprioception provides limited absolute accuracy; (b) sense of limb position is more complex than simple measurement of joint angles through sensory organs; and (c) accuracy of proprioception is influenced by motor control (e.g. co-activation, activity). To illustrate (b), the perceptual sense of ownership (i.e. distinguishing our own body from the external world) depends primarily on proprioception, but is also highly plastic given appropriate stimuli.⁴¹ Expectation of position through central sense of effort and prior experience are integral to the sense of position.⁴¹ The effect of (c) is that the current postural control strategy has consequences for the quality of position sense, which thus influences motor planning, translation of higher level movement goals into joint based motor commands and therefore motor control. This is a feedback loop, a dynamic system, in which quality of position sense can be amplified or diminished over time.

s0045 Perception

p0110 The main point of this section is to emphasize the increasingly accepted idea that prior personal experience influences sensory analysis of sensory information.^{87,88} The postural task is to control configuration appropriately with respect to perception of the environment and the current intentions of the person within that environment. Perception is not solely determined by the input from our senses but it is strongly influenced by our expectations.²⁹ As introduced by Kok and colleagues,²⁹ many

perceptual illusions are explained as the result of prior knowledge of probable external sensory input influencing perceptual inference: we expect light to come from above rather than below, faces to be convex and not concave, and objects in the world to move slowly rather than fast. Illusions aside, we easily forget that our perception does not provide an absolute impression of the sensory world. We cannot tickle our self because our prior knowledge of our action cancels the self-generated sensation of tickle.⁸⁹ If we support the dead weight of an external body part such as arm or leg, these are surprisingly heavy, yet we do not sense our own weight which is cancelled by our prior expectation. Perhaps only when emerging from the swimming pool when our expectation has partially adapted, do we partially sense our weight. We tend to perceive difference from expectation rather than sensory information directly.^{41,89}

It might be thought this Bayesian process of combining prior belief with sensory input to create a perception is confined to higher-order neural areas. However, data shows that prior expectations can modify sensory representations in the early visual cortex²⁹ and even in the retina.⁹⁰ Prior expectations modify sensory processing at the earliest stages by affecting not only the amplitude of neural responses or their sharpness, but also by changing the contents of sensory representations.⁹¹ In other words, prior expectations affect what is represented, rather than just how well things are represented.²⁹

With respect to the control of posture, perception of the current environment concerns more than configuration alone. This element is missed in analyses that view postural control as only a low-level dedicated control of configuration isolated from wider perceptual factors. Asking people to stand 'naturally' for a photograph is an easy way to demonstrate the influence of perceptual factors on postural control. In an increasingly established paradigm,⁹²⁻⁹⁶ the effect of these perceptual factors are illustrated by experiments in which the perceived risk to life is manipulated by comparing postural control at exposed height with control at ground level. At exposed height, the altered visual environment changes the visual input necessary for the control of balance: the distance to visual targets increases, decreasing visual sensitivity of postural sway with the consequence that postural sway increases.^{47,52} However at height, awareness of risk also influences visual input even to the extent that spatial dimensions perceived as dangerous are perceived to be greater than they are.⁹⁷⁻⁹⁹ Experiment has shown that in response to postural threat, knowledge of danger rather than current visual environment was the dominant cause of cautious gait and elevated physiological arousal.⁹⁵ The disturbing control of locomotion, balance and autonomic response occurred at level that integrates cognition and prior experience with sensory input.⁹⁵ This disturbed control results in changes of sustained postural configuration as well as higher levels of co-activation and greater restriction of movement.^{94,95,100}

However, while sensory input through vision and proprioception are both modifiable by perceptual factors, the same appears not to be true for the vestibular system.⁹⁴ Galvanic vestibular stimulation of participants who were highly motivated to minimize sway because they were

perturbed at height, showed no change in the initial, pure vestibular response, even though there were strong differences in the later response that integrates balance-relevant sensory feedback from all modalities. Pure vestibular sensory input and the immediate reflexive response appears to lie outside of cognitive and emotive control.¹⁰¹ Unlike somewhat ambiguous signals from the other senses (e.g. vision, proprioception), the semicircular canals provide an unambiguous signal of head rotation.⁵⁸ It is probably important for survival that these vestibular-balance reflexes cannot be interfered with. The reflexive vestibular-balance responses can be trusted even though fearful participants may not trust their own mechanisms.⁹⁴

which are maintained weakly within the prefrontal and premotor cortex (Fig. 4-4).^{22,35,106,107} If selected for expression, these parallel action possibilities have the possibility of being amplified by corresponding columns within the thalamus (35).

Selection

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Consistent with all vertebrates,^{103,109} the human nervous system contains centralized mechanisms for switching between alternative possibilities for motor control. Anatomically and functionally, there is convergence of analysed sensorimotor input, contextual perceptual and motivational input into and through the basal ganglia.¹⁰⁹ Input to the basal ganglia from all major sources, the cerebral cortex, limbic structures and the thalamus are topographically ordered.^{109,110} Inputs to ventromedial sectors come from structures in which competing behavioural goals may be represented (prefrontal cortex, amygdala, hippocampus), while the connections of dorsolateral sectors are from regions that guide movements (e.g. sensory and motor cortex) (Fig. 4-4). As summarized by Redgrave,¹⁰⁹ basal ganglia outputs contact regions of the thalamus that project back to those regions of cortex providing original inputs. Similarly, basal ganglia outputs to the brainstem tend to target those regions that provide indirect input to the basal ganglia (Fig. 4-5). Projections from the basal ganglia output nuclei to the thalamus and brainstem are also topographically ordered. Neurons in the basal ganglia output nuclei have high tonic firing rates (40–80 Hz). This activity ensures that target regions of the thalamus and brainstem are maintained under a tight and relatively constant inhibitory control. Reduction of inhibitory output releases associated target regions in the thalamus and brainstem (e.g. superior colliculus) from normal inhibitory control.^{23,35,109} Topologically, in a spiral architecture using successive connections between the

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s0050 Generation of Action Possibilities

p0130 Sensory analysis provides the information needed to regulate motor output. In the context of postural control, people normally think of reflexes as being the underlying and primitive mechanism that transforms sensory input into motor output. Reflexes provide rapid, environmentally triggered responses similar in kind and easily mistaken for habitual automated habitual responses.¹⁰² The biological process of decision making and adaptation involves generation of multiple possibilities, selection, and reinforcement of selections which are rewarded by valued outcomes. Mechanisms implementing this process of decision making extend through vertebrates,¹⁰³ invertebrates,¹⁰⁴ even to the level of individual cells.¹⁰⁵ Thus biological mechanisms of decision making are just as primitive as reflexes.¹⁰⁴ Neurophysiological recording shows that sensory analysis converges to the simultaneous, active representation in the frontal cortex of multiple possibilities for action.^{106–108} Action possibilities include representations for movement, thought, simple or complex action, control priorities or cognitive processes

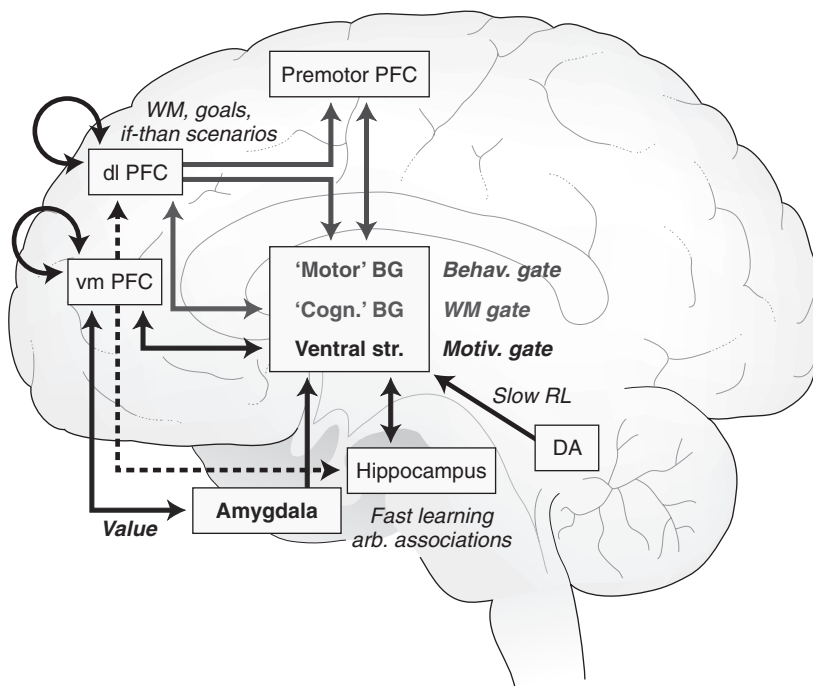
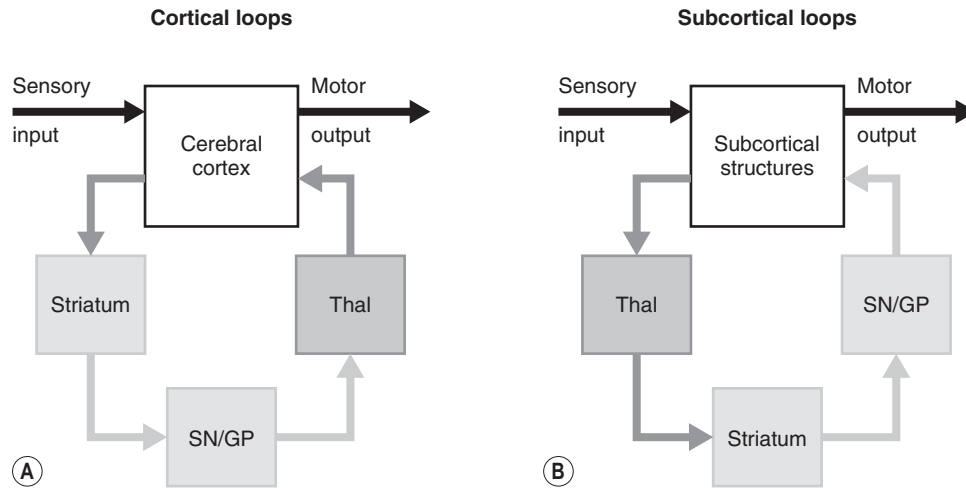


FIGURE 4-4 ■ Access of basal ganglia to motivational, cognitive and motor regions for selection and reinforcement learning. The basal ganglia are a group of interconnected subcortical nuclei that represent one of the brain's fundamental processing units. Interacting corticostriatal circuits contribute to action selection at various levels of analysis. Coloured projections reflect subsystems associated with value/motivation (red), working memory and cognitive control (green), procedural and habit learning (blue), and contextual influences of episodic memory (orange). Sub-regions within the basal ganglia (BG) act as gates to facilitate or suppress actions represented in frontal cortex. These include parallel circuits linking the BG with motivational, cognitive, and motor regions within the prefrontal cortex (PFC). Recurrent connections within the PFC support active maintenance of working memory (WM). Cognitive states in dorsolateral PFC (dlPFC) can influence action selection via projections to the circuit linking BG with the motor cortex. Dopamine (DA) drives incremental reinforcement learning in all BG regions, supporting adaptive behaviours as a function of experience. For colour version see plate section. (Reproduced from Frank.²²)

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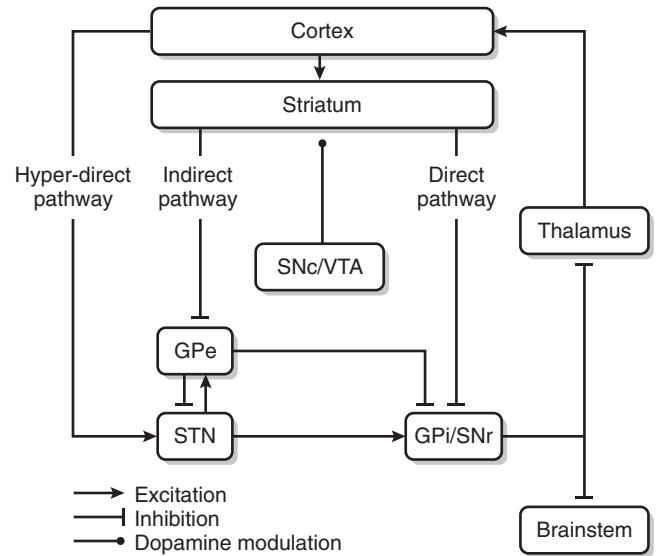
FIGURE 4-5 ■ Cortical and subcortical sensorimotor loops through the basal ganglia. (A) For corticobasal ganglia loops the position of the thalamic relay is on the return arm of the loop. (B) In the case of all subcortical loops the position of the thalamic relay is on the input side of the loop. Predominantly excitatory regions and connections are shown in red while inhibitory regions and connections are blue. Thal, Thalamus; SN/GP, Substantia nigra/globus pallidus. For colour version see plate section. (Reproduced from Redgrave.¹⁰⁹)

limbic, associative and sensorimotor territories, the basal ganglia are organized to allow progressive selection of overall goal, actions to achieve a selected goal and movements to achieve a selected action.^{103,109,111}

p0140 The basal ganglia act as a system that dynamically and adaptively gates information flow in the frontal cortex, and from the frontal cortex to the motor system.^{35,36,109}

The basal ganglia are richly anatomically connected to the frontal cortex and the thalamocortical motor system via several distinct but partly overlapping loops.^{22,35} Through hyper-direct, indirect and direct pathways, this system provides centralized mechanisms for generalized inhibition, specific inhibition and specific facilitation of action possibilities represented in the frontal cortex (Fig. 4-6).^{22,35,103,112} As described by Cohen and Frank,³⁵ the basal ganglia system does not directly select which action to ‘consider’, but instead modulates the activity of already active representations in cortex. This functionality enables the cortex to weakly represent multiple potential actions in parallel; the one that first receives a ‘go’ signal from basal ganglia output is then provided with sufficient additional excitation to be executed. Lateral inhibition within thalamus and cortex act to suppress competing responses once the winning response has been selected by the basal ganglia circuitry.^{22,35}

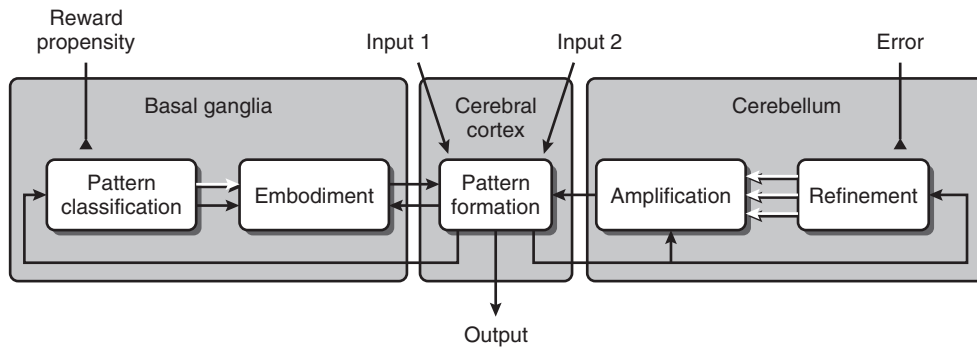
p0145 Mechanisms of response selection also lie within the prefrontal and premotor cortex.^{113,114} While these mechanisms are the subject of much current research, a general conclusion is that together, these striatal (basal ganglia) and prefrontal systems provide both selection and reinforcement learning (i.e. progressive facilitation of those responses which achieve valued outcomes and progressive inhibition of those responses which achieve undesired outcomes).^{22,35,102} While selection and reinforcement of rewarded selections is associated with the basal ganglia system, refinement and adaptation of the possibilities available for selection is associated with the cerebellum within cortico–cerebellar–cortico loops that match equivalent cortico–basal ganglia–cortico loops (Fig. 4-7).³⁶



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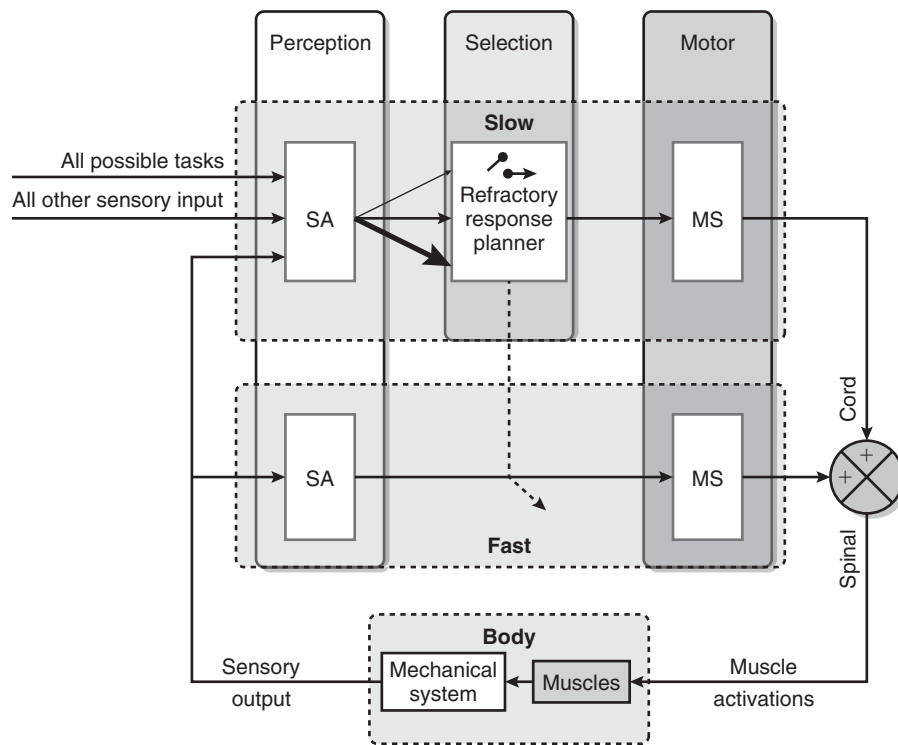
FIGURE 4-6 ■ Simplified illustration of basal ganglia anatomy based on a primate brain. The basal ganglia comprise two principal input nuclei, the striatum and the subthalamic nucleus (STN), and two principal output nuclei, the substantia nigra pars reticulata (SNr) and the internal globus pallidus (GPi) (primates). The external globus pallidus (GPe) is principally an intrinsic structure that receives most of its afferents from and provides efferent connections to other basal ganglia nuclei. Finally, dopaminergic neurones in substantia nigra (pars compacta) (SNc) and the adjacent ventral tegmental area (VTA) provide other basal ganglia nuclei, principally the striatum, with important modulatory signals.¹⁰⁹ The hyper-direct, direct and indirect pathways from the striatum have net effects of generalized inhibition, specific disinhibition and specific inhibition on the cortex, respectively. (Reproduced with modification from Yin and Knowlton.¹⁰²)

During learning, humans select responses flexibly p0150 depending on whether the anticipated outcome is desirable. With reinforcement of selections that are rewarded, responses can become habitual. With sufficient facilitation, corticocortical associations can become sufficiently strong to elicit automatized transcortical responses even



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FIGURE 4-7 ■ Complementary basal ganglia and cerebellum loops for selection-reinforcement learning and optimization. An individual cortical area together with its loops through basal ganglia and cerebellum form a powerful computational structure that has been dubbed a distributed processing module (DPM).¹¹⁵ DPMs communicate with each other via the cortical-cortical connections. There are on the order of a hundred DPMs in the human brain, forming a large-scale neural network. The figure shows the selection (classification) and refinement operations posited for each DPM. Net excitatory pathways are shown with closed arrows, net inhibitory pathways with open arrows and the grey diamonds signify neuromodulatory and training inputs. (Reproduced from Houk et al.³⁶)

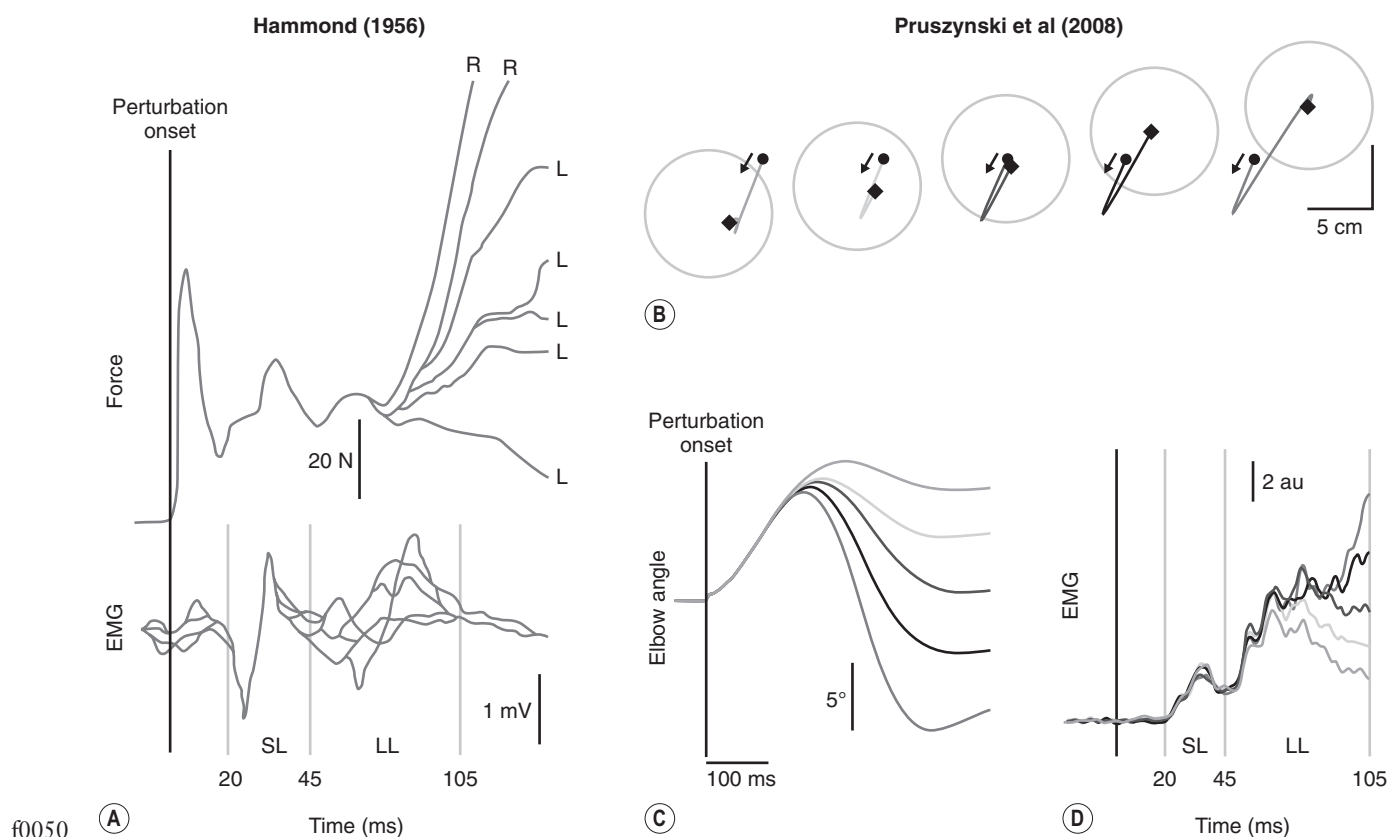


f0045

FIGURE 4-8 ■ Overall scheme of sensorimotor integration. For postural control there is an overall feedback loop relating perception, selection and motor control. Perception requires sensory analysis integrating all sensory modalities with prior experience (SA). Acting through central pathways such as the basal ganglia loops, selections are made. Recent evidence suggests selection converges to a serial process with maximum rate of two to four selections per second (Refractory Response Planner).²³ The motor system (MS) translates selected goals, actions, movements and control priorities into coordinated motor output. Within a slow feedback loop restricted to the voluntary bandwidth of control (2 Hz) the motor system generates coordinated motor responses sequentially from each new selection. With a fast loop restricted to a higher bandwidth (>10 Hz) acting through transcortical, brain stem and spinal pathways, the motor system uses selected parameters to modulate habitual-reflexive feedback.^{23,37,123}

before striatal gating signals occur thus bypassing the basal ganglia loop (see Fig. 4-5).^{22,102,116-119} Functionally, physiological reflexes, reflexes formed through operant conditioning, and habitual responses share the same characteristic of being elicited rapidly by environmental stimuli without regard to the current value of the outcome. Hence these are described collectively as habitual reflexive^{22,102} and in the overall scheme of sensorimotor integration are implemented through the fast feedback loop (Fig. 4-8).

Selection represents executive function. This executive p0155 function is required for choosing postural goals, control priorities and movements required to maintain those goals.²⁸ The configuration to be maintained, or parameters such as peripheral feedback thresholds which determine the resulting configuration, are selected. Implicit or explicit choices are made between different control priorities. For example, does the selected control allow flexible adjustment of configuration, or does it minimize movement at the ankle, knee and hip joints?



18 **FIGURE 4-9** ■ Modulation of fast motor response by prior subject intent. **(A)** Example of how subjects can categorically modulate the long-latency (transcortical) stretch response according to verbal instruction. Subjects were verbally instructed to respond to a mechanical perturbation with one of two verbal instructions ('resist'/'let go'). The upper panel depicts force traces from individual trials aligned on perturbation onset and labelled according to the instruction. The bottom panel is the corresponding muscle activity, which shows modulation in the long-latency stretch response (LL) but not the short-latency (spinal) stretch response (SL). **(B)** Example of how subjects can continuously modulate their long-latency stretch response in accordance to spatial target position. Subjects were instructed to respond to an unpredictable mechanical perturbation by placing their hand inside one of the five presented spatial targets. Each plot represents exemplar hand kinematics as a function of target position. Subjects began each trial at the filled black circle, and the black diamond indicated final hand position. The small arrows indicate the approximate direction of motion caused by the perturbation. **(C)** Temporal kinematics for the elbow joint aligned on perturbation onset. **(D)** Pooled EMG aligned on perturbation onset and normalised to pre-perturbation muscle activity. Note that the long-latency stretch response exhibits graded modulation as a function of target position. For colour version see plate section. (Reproduced from Pruszynski and Scott.²⁷)

Evidence supports a normal tendency is to allow sway within safe limits and minimize muscular effort.⁹ However, normal standing conceals a large inter-individual range in leg control strategies. Commonly, leg configuration is maintained stiffly.¹²⁰ Less commonly, a bilateral, low-stiffness, energy-absorbing strategy utilizing the available degrees of freedom is shown.¹²⁰ These inter-individual differences indicate the range of possibilities available for progression with development and skill acquisition, and also for decline with age, disease, injury, and fear. Consistent with feedback around the perception–selection–motor loop (see Fig. 4-1), it is suggested that the individual coordination strategy has diagnostic and prognostic potential in relation to perceptual–posture–movement–fall interactions.^{100,120}

5 Recent emerging evidence shows how executive function is required for ongoing adjustments in the maintenance of posture. Experimentation demonstrates substantial refractoriness up to 0.5 seconds in the implementation of postural tasks such as adjusting the position of the body and maintaining balance.^{25,28,121}

Refractoriness is the increased delay in selecting and forming one response before the previous selection and formation of the previous response has been completed.²³ The implication is that for postural control, sensory input converges to a sequential single channel process involving optimization, selection and temporal inhibition of alternative responses prior to motor output.^{23,28} In the overall scheme of sensorimotor integration (Fig. 4-8), refractoriness (selection) occurs through the slow loop. This evidence highlights the fact that control of posture requires operation of the slow intentional feedback loop.²³

MOTOR CONTROL

s0060

The executive selection process produces parameters p0165 which relate to the chosen tasks (e.g. standing, standing and looking, standing, looking and pointing, or standing, looking, pointing and talking). The motor system generates coordinated patterns of muscle inhibition and

activation through approximately 700 distinct muscles or muscular regions acting across multiple joints.¹²²

p0170 As shown in Figure 4-8, the motor system operates through fast and slow feedback loops.^{22,102,119} The slow, intentional feedback loop is characterized by refractoriness.^{23,28,121} To reiterate this key point, refractoriness is the increased delay in selecting and forming one response before the previous selection has been completed.²³ Refractoriness is absent from the fast, automatic feedback loop.

s0065 The Fast Loop

p0175 Much accumulated evidence summarized Pruszynski and Scott²⁷ demonstrates the power and sophistication of transcortical reflexes which are a class of fast acting responses, of latency (~60–120 ms), triggered by integrated environmental stimuli including joint rotations, visual, cutaneous and vestibular sensations. Pathways mediating these responses pass through the cortex and are influenced by many brain regions, including the cerebellum, posterior parietal cortex and frontal cortex.²⁷ These responses are modulated by preceding factors, including explicit external instructions, the implicit behavioural context including the current posture and task goals, and by the external environment including the direction of the gravitational-acceleration vector and location of objects.²⁷ These responses are environmentally triggered, without taking consequences into account within the feedback loop: they are reflexive in the sense of having environmental causality according to previously made choices. These response are coherent with environmental stimuli to a frequency of 10 Hz or more.¹²⁴ The fast loop corresponds to automated, habitual and reflexive control.^{22,35,102} Although functional, the fast loop alone is not adequate to reject disturbance, is highly variable and is not fully sustained.¹²⁵ Fully adequate, accurate and sustained control requires the combined operation of both fast and slow feedback loops.

p0180 *The slow loop* corresponds to intentional control limited to the low bandwidth of 1–2 Hz.^{13,28,37,121,123,126} Within this bandwidth there is flexibility within the feedback loop to reselect the control priorities, goals internal and external constraints at a maximum rate of two to four times per second.^{15,23,28,37,121,123,127} There is recent evidence that reselection and execution of postural goals proceeds as a sequential process along a single channel of control.^{28,121} The slow loop ensures that control of posture can be voluntarily reprogrammed whenever necessary. For example, when balance is challenged unexpectedly precipitating a fall, the fast system provides response within 60–120 ms, and the slow system allows intentional response within 180 ms.^{23,126} When habitual control is perceived to have undesirable consequences, habitual control can be inhibited and reprogrammed.¹²⁸ It is hypothesized that this slow loop passes through the basal ganglia.^{22,23,28,119} The relative contribution of the slow and fast loops is currently a matter of research and debate, though evidence is emerging that the slow loop is dominant in postural balance as well as visually guided manual control.^{23,28,37,121,129} The hallmark of the slow loop is that it explains power within motor output signals coherent

with unpredictable disturbances limited to below 1–2 Hz and this accounts for the majority of power in postural control.^{13,23}

The motor system receives integrated sensory input p0185 from the vestibular nuclei and different sensory areas of the cerebral cortex such as the posterior parietal cortex. From the selection processes, the motor system also receives the task-related parameters which tell the motor system what kind of coordination, feedback control and muscles synergies to generate. The motor system includes more preliminary organizing function within motor parts of the basal ganglia system, the supplementary motor area, the premotor cortex and cerebellum, and influences muscle activations through the pyramidal and extrapyramidal systems.¹³⁰ The pyramidal motor system transmits directly from the motor cortex, through upper motor neurons within the corticospinal tract. Upper motor neurons terminate within the anterior horn of the spinal cord mostly on interneurons and to a lesser extent directly on lower motor neurons. Lower motor neurons directly innervate muscles as motor units. The pyramidal system is concerned specifically with discrete voluntary skilled movements, such as precise movement of the fingers and toes. The more ancient extrapyramidal motor system includes all motor tracts other than the corticospinal (pyramidal) tract, including parts of the rubrospinal, reticulospinal, vestibulospinal and tectospinal tracts. The rubrospinal tract, small in humans compared with primates, is responsible for large muscle movement as well as fine motor control, and it terminates primarily in the cervical spinal cord, suggesting that it functions in upper limb but not in lower limb control. The reticulospinal tract descends from the reticular formation in two tracts, medullary and pontine, to act on the motor neurons supplying the trunk and proximal limb muscles. It functions to coordinate automatic movements of locomotion and posture, facilitate and inhibit voluntary movement and influence muscle tone. The vestibulospinal tract originates in the vestibular nuclei, receives additional input from the vestibulocerebellum, and projects down to the lumbar spinal cord. It helps to control posture by innervating extensor muscles in the legs and trunk muscles.¹³⁰

While the motor system is complex, there is structure p0190 and organization to the generation of motor output. Firstly, while motor output is executed through multiple muscles crossing multiple joints, the motor output achieves a small number of concurrent goals: thus motor output is organized along a small number of synergistic patterns of muscle activation related to the small number of concurrent task goals.^{28,131–133} There is increasing evidence that motor output is constructed from a repertoire of motor primitives which are stored in the cortex, brain stem and spinal cord for retrieval and use in the generation of movements.^{19,20,108,132,134–137} Secondly, there is temporal organization to motor output. Activation of muscles proceeds sequentially from proximal reference or stabilizing segments to distal segments. This principle is observed in the so-called anticipatory postural adjustments where, for example, activation of leg and trunk muscles precedes activation of arm muscles in reaching movements.^{138–140} The ground provides the reference or stabilizing segment. During reaching movements

activation proceeds temporally from the trunk to end of the arm.¹⁴¹ The trunk-head axis provides the reference-stabilizing segment. During balance perturbations involving sudden translation of the floor, activation proceeds temporally from the leg to the trunk,¹⁴² and in this case the ground provides the reference or stabilizing segment. These observations support the idea that posture is prior to movement. Posture is prior to movement both temporally and hierarchically in that control of the reference segment precedes and sets the boundary conditions for control of the end segments. Thus for control of the hands, head, vocal organs and internal respiratory muscles there is a kinematic basis to the observation¹⁴³ that control of the trunk-head axis is primary. For balance relative to the ground, there is a basis in which control of the legs is primary.

p0195 To summarize (Fig. 4-8), two levels of mechanism work together within a main perception-selection-motor feedback loop. The slow system acting through central selection and optimization pathways (e.g. basal ganglia, premotor and prefrontal cortex, cerebellum) allow online sequential planning, selection and temporal inhibition of alternative possibilities up to a maximum rate of two to four events per second. The fast system acting through transcortical, brain stem and spinal pathways allows implementation of coordinated habitual, reflexive responses to environmental stimuli with a latency as low as 50–100 ms according to preselected goals.

s0070 PRINCIPLES APPLICABLE FOR PHYSIOTHERAPEUTIC PRACTICE

p0200 Sensorimotor integration occurs at the level of the whole system. While understanding of sensorimotor integration is still evolving, we can consider principles relevant to preventing decline and improving function.

p0205 Postural control can be considered as a perception-selection-motor feedback loop (see Fig. 4-1). Perception relevant to postural control integrates prior personal experience with sensory information from the eyes, ears, proprioception and skin. Prior experience biases sensory information: thus postural control is sensitive to expectations including fears of what is required. Furthermore, postural control is likely highly facilitated, proceeding automatically from environmental stimuli without current evaluation of the consequences of the control adopted.

p0210 The selected postural control has consequences. For example, increased co-activation limits proprioceptive sensitivity.⁴¹ Reduced quality of position sense will impair the translation of higher level movement goals into joint based motor commands. Increased joint stiffness limits possibilities for adjusting balance such as when required to prevent a fall.^{120,144} Restriction of joint movement 6 limits the amount, variability and asynchronicity of information gained through joint movement, and thus limits motor learning including the possibility for learning highly differentiated, skilled and economical control.¹⁴⁵ Unvaried, repetitive, synchronous control in which attention is paid to the task is known to cause poor even harmful adaptation within the nervous system, including reduced differentiation of sensory receptive fields and

eventually symptoms of focal dystonia.^{146,147} If the biomechanical loading on bone and soft tissue are inappropriate, then wear, tear, compression, stretch, inflammation and inappropriate regeneration are likely.¹⁴⁸⁻¹⁵⁰ These consequences are subject to feedback through the perception-selection-motor-perception feedback loop. Feedback acts to cumulatively amplify or diminish consequences (symptoms). This process can explain the evolution through time of postural problems, fear of falling and problems consequent on poor postural control. If the individual believes their *inappropriate* control is the right solution (misconception), they increase their inappropriate response to worsening symptoms: that provides destructive (mathematically positive) feedback. Thus two factors determine the progression of symptoms: (a) the concept the person has of their own control; and (b) whether that control is highly facilitated (automatic) or flexible (intentional).¹²⁸

Within the sensorimotor loop (see Fig. 4-1), the motor and sensory processes proceed automatically. Thus there are two possibilities for re-education leading to improved function. First, individuals can be given new information. External feedback of postural and motor control can provide new input, either verbally, by educative manipulation, or using visual-audio-haptic technology.¹²⁸ Discussion and reformulation of perceptions can generate new possibilities for thought and movement. However, if postural control is so facilitated that selection proceeds automatically before striatal selection processes can intervene, then change is unlikely. Hence transfer of control from the fast to the slow loop is required to allow postural control to reformulate along more constructive lines.¹⁴³ This transfer requires training targeted at improving inhibition of highly facilitated postural control.¹²⁸ This training may be more effective if it targets areas early in the natural temporal kinematic progression of control.

To summarize, restoration of function related to sensorimotor integration requires that neurophysiological and neuromuscular mechanisms are working, and beyond that requires re-education of the central processes of perception and selection which drive postural control. p0220

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