Proprioception, Tensegrity, and Motor Control
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Movements for breathing, locomotion, and feeding are critical for survival, but how they are controlled by the CNS is poorly understood. It has long been recognized that sensory information from receptors in many tissues is required for accurate movements. Such information may be transduced by receptors in the skin, joint and muscles and their associated connective tissues. Additional information about the body’s relation to the external environment derives from the vestibular apparatus, while the eye and ear provide further data. This information is considered to be compiled into a fluid functional brain map or representation of the body and its parts, a map that is consulted to plan and execute movements. Multisensory inputs and planning are also involved in the deceptively simple task of standing (e.g., Loram, Magnaars, & Lakie, 2005). In their special review, Turvey and Fonseca (2014) tackle the medium of haptic perception on a broad dimensional scale, from subcellular components to the whole organism. They go on to propose that tensileity, a fundamental structural property based on efficient deployment of tension and compression elements, is a unifying concept, again over a broad scale of size.

The review by Turvey and Fonseca (2014) performs the helpful task of suggesting some much-needed linkages across different fields, from structural biology to neuroscience. Not surprisingly, the attempt is fraught with dangers but nonetheless it raises some important questions. I consider briefly some of the linkages and some of the controversies.

Some Peripheral Issues

An important emphasis is the functional relation between the micro and macro properties of the musculoskeletal system, and perhaps, the authors would argue, even the body as a whole. For example, it is good to be reminded that the basic mechanism of hearing should not be viewed solely in a narrow focus from the molecular behavior of the cochlear inner hair cells to the properties of the cochlear nerve fibers and then their central projections. Instead, it is better, at a more ecological level (e.g., Dusenbery, 1992) to consider the properties of the tissues in which the hair cells are embedded from the basilar membrane, back through the bones of the middle ear and the muscles which dampen their effects, to the pinna and ultimately the types of environmental vibration that are being transduced. Of course this concept can be extended to the main classes of proprioceptors. Here the muscle spindle offers some insight. This structure resides within mammalian muscles and has seemingly complex afferent and efferent connections with the central nervous system. It is well known that primary and secondary muscle spindle endings encode length changes and their time derivatives (e.g., Matthews, 1972). Traditionally muscle spindles are considered to be in parallel with the nonspindle tissues (i.e., extrafusal muscle). Hence, they would have a simple path for the distribution of stress and be able to respond faithfully to muscle length changes. Less well known is that some spindles (including in human muscles) are in series with the extrafusal muscle and its connective tissue matrix such that their local deformation, and hence their signaling, must be more complex (see Burke, Aniss, & Gandevia, 1987). Consequently, the encoding of length disturbances by a population of spindle endings does not translate into a ruler-like, Newtonian, measure of the length of the muscle-tendon unit (e.g., Dimitriou & Edin, 2008). If the purpose of spindle populations were to provide such a measure then some additional problems considered to varying degrees by Turvey and Fonseca (2014) require solving.

First, the receptors are not uniformly distributed within the muscle and their distribution and density varies between muscles in ways that have not yet been satisfactorily resolved. Spindle density (expressed as spindle number per muscle weight or number of muscle fibers) is not directly linked to the capacity to perform fine-grained contractions (for details, see Gandevia & Burke, 1992). Whether some other movement parameter is so linked remains a speculation. There is no a priori reason why spindle density should be the primary measure to link to function when theoretically one stretch receptor in parallel with the extrafusal muscle would do. The location of spindles (and other specialized receptors such as Golgi tendon organs) within muscles has also remained a vexed issue. The proposal here that they reside at transitional zones between tissue regions of different viscoelastic properties is testable. Furthermore, if confirmed, it represents a fundamental pattern laid down in development. At least in human skeletal muscle, the idea that spindles may be rich in regions of type 1 (oxidative, low voluntary threshold) muscle fibers is not well supported. In a similar vein, we do not know the fundamental basis for the distribution of tendon organs.

Second, the history dependence of the muscle and connective tissue net (MCS) to stirring reveals its thixotropic properties. While this property resides broadly in the MCS and can be demonstrated to alter human muscle properties (e.g., Lakie & Robson, 1988; see Figure 13 in Turvey & Fonseca, 2014), it is particularly prominent in the actin-myosin interactions within the muscle spindle’s intrafusal fibers (Proske,
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Morgan, & Gregory, 1993). Hence, the fusimotor drive to these fibers that accompanies voluntary activity combined with changes in length of the muscle can leave its muscle spindles in a tight or more loose configuration, despite the muscle-tendon unit staying at the same length. Spindle firing is high under the tight condition and low or absent under the loose condition. This alters proprioception as the muscle will be perceived as long or short depending on the firing rate of its spindles, and it will affect the sensory response of the muscle to perturbations and hence its reflex and volitional output (for a review, see Proske & Gandevia, 2012). Intrafusal thixotropy and the variability in the response of human muscle spindles from the same muscle to a similar length change raises difficulty for the claim that the MCS should be considered a homogenous isotropic medium.

The various pathways for force transfer within and between muscles and other structures (i.e., intramuscular, intermuscular, and extramuscular force transmission) are contentious. However, since the pioneering work of Street (1983) on frog muscle and subsequently by Huijing (2003, 2009; for references, see Turvey & Fonseca, 2014) on different mammalian preparations, there can be no doubt of their existence. What remains is to quantify the size of the effects and the circumstances under which they occur. At least for the human triceps surae, with the common insertion of the gastrocnemii and soleus into the Achilles tendon, there is no argument about the presence of intermuscular force transmission between medial gastrocnemius and soleus, but the available evidence suggests that the magnitude of the effect would not produce a big change in the passive length-tension curve of the ankle plantarflexors (Tian, Herbert, Hoang, Gandevia, & Bilston, 2012). In the human upper limb, there are dramatic examples of effective disconnection of muscles from their insertions on the distal phalanx depending on the length of their nearby neighbors (for details, see Van Duinen & Gandevia, 2011) such that the active contraction of flexor digitorum profundus to one finger can generate no force at its insertion. It is an example of “no force” transmission and a dramatic demonstration of the importance of the MCS for movement. However, for the long finger flexors and extensors operating within their common length ranges, the forces produced by their single motor units do not spillover to generate much force via neighboring tendons (for references, see Van Duinen & Gandevia, 2011). This provides some simplification at the level of the periphery for selective force control in the fingers. However, we are only just beginning to tackle some of deeper issues of movement control that are engendered by a realization that there is a spectrum of degrees of nonlinear force transmission.

Some Central Issues

If we accept that the central nervous system has to integrate the neural signals it receives to control movement, both moment-to-moment as well as over short and long time scales (e.g., for learning a skill, for adapting to limb growth), then how is this achieved? This proposition is not necessarily accepted by the authors, and some theoretical limits to the coding are raised. My response is that the brain has evolved methods that do solve the coding complexity for haptic and proprioceptive perception. Thus, the brain can generate a range of possible scenarios and test them for consistency against available sensory information. This scenario-based testing model explains many proprioceptive and visual illusions (e.g., Gregory, 2009). Hence, artificially increased firing of muscle spindles (produced by vibratory or electrical stimulation of say elbow flexors) can produce a sense that the elbow joint is moving into extension, and that it occupies a more extended position, and that the body part that the hand is holding (say the nose) is lengthened. Presumably comparable solutions are available centrally for stimuli, which do not necessarily reach perception (e.g., Luu et al., 2012).

An issue that has been central to many motor control theories since the time of Helmholtz, namely the differentiation of stimuli that are self-generated from those generated by the external environment, was not included in the analysis by Turvey and Fonseca of haptic perception. Clearly, a scenario-based model, or a prediction-based model, of which many have been described is required (e.g., Bays & Wolpert, 2007; Proske & Gandevia, 2012). The variety of ways in which such models need to operate has recently been described for limb movements (Walsh, Taylor, & Gandevia, 2011) and also eye movements (Whitham et al., 2010). It is difficult to see how an overarching tensity-based view of the peripheral structures involved in production of movement (i.e., muscles) and the consequence of movement (i.e., sensory input) can explain the differentiation noted previously. Furthermore, there are major contributions from centrally-generated signals of motor command to proprioception, both for signals of limb position and movement (Gandevia, Smith, Crawford, Proske, & Taylor, 2006; Walsh, Gandevia, & Taylor, 2010) and for signals of force (e.g., Gandevia, 1987; cf. Luu, Day, Cole, & Fitzpatrick, 2011; see also Proske & Gandevia, 2012).

Concluding Comment

The review by Turvey and Fonseca (2014) is stronger in exposing the peripheral mechanisms that are required for haptic, kinesthetic, or proprioceptive judgments than it is in delineating the central processes that must underlie perception and action. This should remind us that for too long the psychologists, physiologists, clinicians, and others have overemphasized the apparently separate perceptual (and other) effects due to activity in one anatomical class of receptor (i.e., those in the skin, joints, or muscles) rather than the orchestrated effects that their usual combination evokes. This likely arose from the anatomists’ natural desire to subdivide musculoskeletal tissues into muscle, joint, tendon, and aponeurosis. Furthermore, we have not broken out from the Sherringtonian terminology of proprioception and its relatives (exteroception, enteroception), Bastian’s earlier but enduring versions of kinesthesia, and the simplistic clinical term joint position.
sense. Hopefully a better terminology will emerge, which could helpfully link with the more encompassing view of the muscle and connective tissue network. Time will tell whether this network is the ultimate medium for haptic sensation.

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**REFERENCES**


