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Review Articles

An Overview of Proprioceptive Concepts of the Human Foot: Morphological, Neurophysiological, and Anthropological Perspectives

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The human foot is increasingly recognized as a proprioceptive organ, integrating morphology, neurophysiology and cultural adaptation to regulate balance and locomotion. Recent studies highlight that plantar mechanoreceptors, intrinsic muscles, and ligamentous structures form an interconnected sensory system that dynamically adjusts to posture, load and environment. Neurophysiological findings demonstrate that cutaneous and muscular receptors redundantly maintain proprioceptive acuity, with plasticity evident through interventions such as robotic training, proprioceptive insoles and minimal footwear. Clinical applications include improved balance, reduced falls, and enhanced rehabilitation outcomes in older adults and neurological patients, while athletes benefit from sharper agility and reduced injury incidence. Anthropological perspectives show that barefoot populations maintain superior acuity compared with shod groups, suggesting an evolutionary role of proprioception in bipedal endurance. Collectively, these findings redefine the foot not as a passive support structure but as a dynamic sensory platform with broad clinical, athletic, and anthropological implications.

Key words: proprioceptive, human, foot, proprioception

Introduction

Proprioception - the ability to perceive body position and movement - is central to motor control and human adaptation. While muscles and joints are widely recognized as major proprioceptive contributors, the role of the human foot as a sensory organ has only recently gained attention [4, 5, 11, 13, 18]. The plantar sole contains one of the highest concentrations of mechanoreceptors in the body, providing continuous feedback about surface interaction, stability, and posture [3, 10, 14, 17]. Recent studies have highlighted three critical dimensions of this phenomenon. First, morphological plasticity allows structural tissues of the foot - including arches, fascia, and intrinsic muscles - to act as both mechanical stabilizers and sensory modulators. Second, neurophysiological adaptability ensures that cutaneous, muscular, joint, and ligamentous receptors work redundantly to preserve function under varying loads and postures. Third, anthropological insights reveal that barefoot populations maintain superior proprioceptive acuity compared with shod groups, illustrating how cultural practices shape sensory pathways [6, 20]. In addition to these natural mechanisms, clinical and athletic interventions now leverage proprioceptive training, robotic devices, and textured insoles to enhance sensory function [7, 15, 16]. By synthesizing these perspectives, the present review provides an updated framework for understanding the foot not as a passive base of support but as an active proprioceptive system with evolutionary, clinical, and medico-anthropological significance.

Systematic approach in proprioception studying

A narrative systematic review was performed with analysis of contemporary literature published between 2019 and 2025. Searches were performed in PubMed, Scopus, Web of Science and Google Scholar databases using the following keywords: foot proprioception, plantar sensitivity, insoles, robotic training, gait biomechanics, barefoot populations, anthropological locomotion.

Inclusion criteria: peer-reviewed studies investigating morphological structures and proprioceptive mechanisms of the foot; experimental and clinical studies evaluating proprioceptive training or interventions; and anthropological research comparing barefoot and shod populations.

Exclusion criteria: works published before 2019 unless essential for conceptual background; case studies unrelated to proprioception; purely mechanical gait models lacking neurophysiological or sensory data.

A total of 23 studies met inclusion criteria. Morphological data included imaging and cadaveric research on fascia, arches, and postural influence [3, 10, 14, 17]. Neurophysiological studies included microneurography, afferent mapping, robotic training, and insole trials [2, 8, 16, 20, 22]. Anthropological works addressed barefoot locomotion, footwear effects, and evolutionary developments [20, 21, 23]. Findings were synthesized across these domains into an integrated account of foot proprioception.

Clinical findings and proprioception relations

Findings demonstrate that the human foot functions as a complex proprioceptive system where structure, receptors, and cultural practices converge. Postural variations alter afferent thresholds: dorsiflexion increases mechanoreceptor sensitivity in the heel and midfoot, while plantarflexion enhances responsiveness in the forefoot [3, 14].

Intrinsic muscles show anticipatory activation before ground contact, stiffening the arch and refining feedback accuracy [9]. The plantar fascia, traditionally considered mechanical, emerges as a sensorimotor bridge where strain deformation correlates with afferent thresholds [10]. Imaging studies reveal uneven distribution of fascial strain, strongest along the medial arch, underscoring its dual stabilizing and sensory role (**Fig. 1**). Minimal footwear studies show that morphology is adaptable: even three minutes of use enhances acuity [4], while long-term adaptation significantly improves plantar thresholds and reduces gait variability [17].

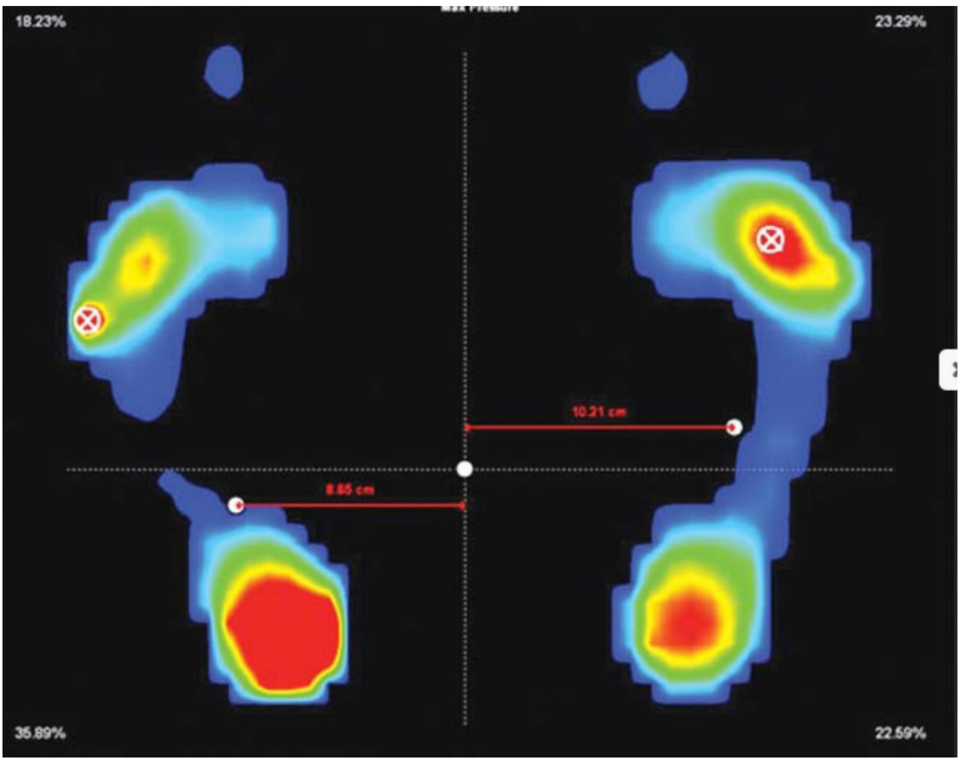

Fig. 1. Evaluation of pressure distribution in orthostatic condition.

Proprioception arises from the integration of multimodal sensory inputs, primarily derived from muscle spindles and Golgi tendon organs, with additional contributions from joint and cutaneous receptors. Muscle spindles are widely considered the dominant source of afferent information for proprioceptive acuity, particularly in fine motor control. Golgi tendon organs complement this by encoding muscle force, while articular and cutaneous receptors serve as modulators, particularly at movement extremes or when muscle spindle input is reduced. The vestibular system, while not strictly proprioceptive, is integral to the central nervous system's construction of body schema and postural orientation (**Table 1**).

Table 1. Major receptor types and their relative contribution to proprioception

Receptor Type	Anatomical Location	Principal Function in Proprioception	Approximate Relative Contribution
Muscle spindles (Ia and II afferents)	Intrafusal fibers within skeletal muscles	Encode dynamic and static changes in muscle length; provide fine-grained information regarding limb position and movement	**50–70%**
Golgi tendon organs (Ib afferents)	Myotendinous junctions	Monitor muscle tension and force generation, contributing to load detection and protective reflexes	**10–20%**
Joint capsule and ligament receptors	Articular capsules and periarticular tissues	Signal extremes of joint movement and contribute to joint position sense, particularly under high strain	**~10%**
Cutaneous mechanoreceptors (e.g., Ruffini endings, Merkel cells, Pacinian corpuscles)	Dermis and subcutaneous tissues surrounding joints	Provide supplementary proprioceptive feedback through skin stretch and pressure changes	**~10%**
Vestibular apparatus (otolith organs and semicircular canals)	Inner ear labyrinth	Supplies information on head position and motion; interacts synergistically with proprioceptive signals but is not classically categorized as a proprioceptor	*Not a direct proprioceptor; ~5% influence in integrated body schema*

The receptor network of the foot comprises cutaneous, muscular, joint, and ligament receptors. Merkel discs and Meissner corpuscles in the toe pads detect contact and slip, Ruffini endings in the dermis sense sustained stretch, and Pacinian corpuscles respond to high-frequency vibration and micro-slips [3, 11]. Microneurography confirms that the hallux and medial forefoot are sensory "hot spots," while anesthesia studies show postural sway increases 30–50% when plantar sensitivity is partially blocked [18]. Intrinsic muscle spindles monitor toe and arch position, while tendon organs in extrinsic muscles regulate tension for mediolateral stability [8, 9]. Fatigue studies show reduced spindle sensitivity leads to impaired ankle joint sense, confirming their importance. Joint and ligament receptors further secure function, responding at extremes of motion and deformation, with finite element models linking ligament strain directly to afferent activation (**Fig. 2**).

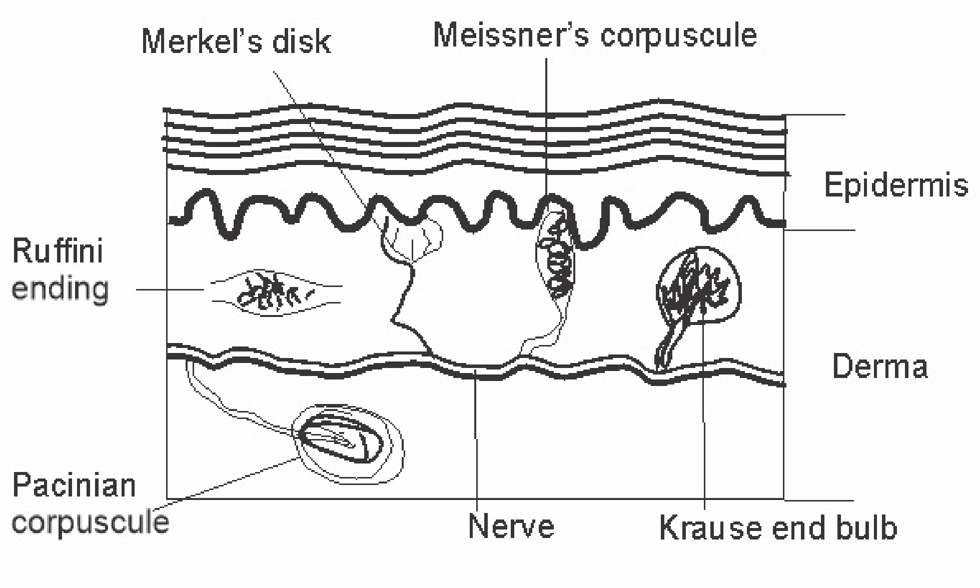

Fig. 2. Primary mechanoreceptors of the skin

Neurophysiological adaptability is supported by experimental modulation. Thermal stimulation of the sole enhances reflex amplitudes in leg muscles [8], whereas electrical stimulation has yielded mixed outcomes [19]. More effective are robotic ankle-foot interventions. Park et al. [16] reported that robot-assisted training improved walking speed by 25% and reduced balance errors by nearly a third in post-stroke patients, with associated cortical reorganization, demonstrating proprioceptive plasticity even after injury.

Proprioceptive insoles represent one of the most practical and effective interventions. Textured or contoured designs continuously stimulate plantar mechanoreceptors during gait. Alfuth et al. [2] documented reduced double-support phase and altered plantarflexion mechanics, while D'Aout et al. [7] showed posture-specific changes in lower-leg muscle activity. Clinical evidence demonstrates improved stability in older adults and enhanced sensory thresholds in neuropathic and post-stroke populations [3, 16]. In athletes, insoles sharpen agility, landing mechanics, and reduce injury incidence (**Table 2**.).

Zech et al. [22] found martial artists improved response times by 15%, while systematic reviews confirm broader reductions in ankle sprains and improved agility [1, 15]. Importantly, individual variability exists: some users benefit immediately, others require habituation. Factors include baseline plantar acuity, footwear history, and neuromuscular conditioning. Insoles should therefore be viewed as active modulators of sensory input; not passive orthotic supports.

Table 2. The effects of proprioceptive insoles across populations

Population	Reported Effects	Key Studies
Older adults / fall risk	Reduced sway, improved symmetry, enhanced stability	Altfuth et al. (2); D'Aout et al. (7)
Neurological patients	Better balance, faster walking, cortical reorganization	Park et al. (16); Alshehri et al. (3)
Athletes	Improved agility, faster responses, reduced injury incidence	Zech et al. (22); Meng et al. (15); Acar (1)
Habitually shod adults	Enhanced plantar feedback, reduced double-support time	Liu et al. (12); Park et al. (19)
Habitually barefoot groups	Already high acuity, little added benefit	Mace et al. (14); O'Neill et al. (18)

Anthropological research reveals the role of culture in proprioception. Barefoot populations outperform shod groups in balance and sensitivity, exhibiting 25% less postural sway [6, 20]. Minimal footwear restores some of this acuity in industrialized populations [12]. Fossil evidence suggests that the development of the medial arch and hallux alignment represented not just mechanical innovations but sensory refinements for endurance locomotion [21, 22]. Cultural practices such as barefoot running and martial arts maintain this evolutionary heritage, sustaining high proprioceptive capacity even in modern contexts.

Conclusion

The evidence reviewed here positions the foot as an organ of proprioception as much as of locomotion. Morphologically, its structures adapt continuously, transforming load-bearing tissues into sensory mediators. Neurophysiological, redundancy among receptor classes ensures robust input even when one pathway is compromised. Anthropologically, the evolution of the arch and hallux, and the persistence of barefoot practices in recent time, highlight the deep roots of proprioception in human adaptation.

Clinical implications are substantial. Proprioceptive enhancement through training, insoles, and robotic devices consistently improves balance, gait efficiency, and cortical reorganization in older adults and neurological patients [2, 3, 16]. These non-invasive interventions address fall risk, stroke rehabilitation, and neuropathy. Athletic populations demonstrate parallel benefits: improved agility, sharper reaction times, and reduced injuries [1, 15, 22]. Proprioceptive conditioning therefore links rehabilitation and performance optimization, bridging medical and sports domains.

Anthropologic insights reveal that cushioned footwear diminishes sensory capacity, while barefoot and minimal practices preserve it [6, 12, 14].

Future research must prioritize personalized interventions, wearable technologies, and longitudinal cross-cultural studies to assess proprioceptive trajectories over the lifespan (**Fig. 3**).

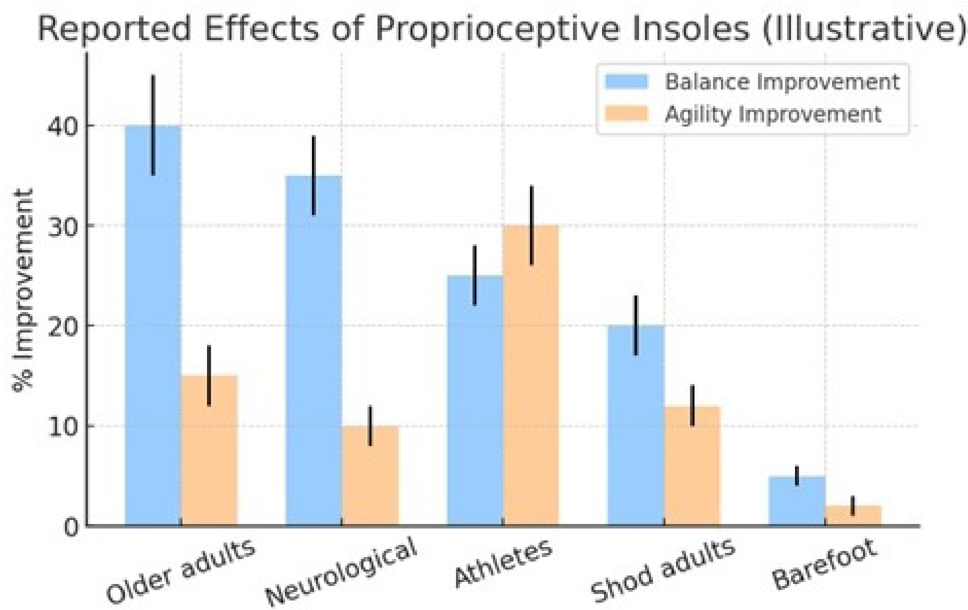

Fig. 3. Boxplot comparison of postural sway in barefoot vs shod groups

The conceptual shift is evident: the foot should not be regarded merely as a mechanical support structure, but rather as a dynamic sensory organ. This reconceptualization carries significant implications for rehabilitation, athletic training, and anthropological analysis, ensuring that one of humanity's most fundamental anatomical structures is appreciated in its full functional and adaptive complexity.

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