BRAIN RESEARCH REVIEWS 54 (2007) 219–232

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BRAIN RESEARCH REVIEWS

Review

Central mechanisms in phantom limb perception: The past, present and future

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ARTICLE INFO

Article history:
Accepted 28 January 2007
Available online 1 February 2007

Keywords:
Phantom sensation
Phantom pain neuromatrix
Mirror neuron
Body schema

ABSTRACT

Phantom limbs provide valuable insight into the mechanisms underlying bodily awareness and ownership. This paper reviews the complexity of phantom limb phenomena (proprioception, form, position, posture and telescoping), and the various contributions of internal constructs of the body, or *body schema*, and neuromatrix theory in explaining these phenomena. Specific systems and processes that have received little attention in phantom limb research are also reviewed and highlighted as important future directions. These include prosthesis embodiment and extended physiological proprioception (i.e., the extension of the body's "area of influence" that thereby extends one's innate sense of proprioception), mirror neurons and cross-referencing of the phantom limb with the intact limb (and the related phenomena of perceiving referred sensations and mirrored movements in the phantom from the intact limb). The likely involvements of the body schema and the body–self neuromatrix, mirror neurons, and cross-callosal and ipsilateral mechanisms in phantom limb phenomena all suggest that the perception of a "normal" phantom limb (that is, a non-painful phantom that has the sensory qualities of an intact limb) is more than likely an epiphenomenon of normal functioning, action understanding and empathy, and potentially may even be *evolutionarily adaptive* and perhaps *necessary*. Phantom pain, however, may be a maladaptive failure of the neuromatrix to maintain global bodily constructs.

Contents

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doi:10.1016/j.brainresrev.2007.01.009

1. Introduction

Phantom limbs are a seemingly curious phenomenon, nevertheless perceived by up to 98% of amputees following amputation (Ramachandran and Hirstein, 1998), nerve avulsion (Melzack, 1992), or spinal cord injury (Bors, 1951; Braun et al., 2001; Le Chapelain et al., 2001; Mikulis et al., 2002; Moore et al., 2000), and by about 20% of children with congenital limb aplasia (Melzack et al., 1997). Phantom pain is experienced by up to 80% of amputees (Kooijman et al., 2000; Sherman, 1994), with pain usually characterised as either (a) burning, tingling, or throbbing; (b) cramping or squeezing; and (c) shocking or shooting (Sherman, 1994). Phantom sensations are perceived immediately after limb loss by most amputees (Ramachandran and Hirstein, 1998); however for some, they may emerge years or even decades after limb loss. The duration of phantom limb perception also varies between individuals, and phantom sensations may be perceived for anything from a few days to weeks, months, years or even decades after limb loss before they fade completely, if at all (Kooijman et al., 2000; Machin and Williams, 1998).

Phantom sensations are reported most commonly following the amputation of an arm or leg, or some part thereof (Ramachandran and Hirstein, 1998), although they have also been reported following removal of the breast (Aglioti et al., 1994; Bressler et al., 1955; Jamison et al., 1979), penis (Fisher, 1999), eye (Sörös et al., 2003), teeth (Marbach, 1993), bladder (Arcadi, 1977; Biley, 2001; Brena and Sammons, 1979) and rectum (Cherng et al., 2001; Farley and Smith, 1968; Ovesen et al., 1991). Phantom sensations following removal of visceral organs may be painful in nature (for example, menstrual pain following hysterectomy or phantom pain that resembles pre-surgical pain) and tend to be characterised by functional sensations; for example, sensations of urination or erection following penis removal (Fisher, 1999; Weinstein, 1998).

The present paper reviews the literature on the perceived "body space" of phantom limbs, their interaction with prosthetic devices, and the evidence that the body schema (Section 4.1, below) plays an integral role in phantom limb perception. Current theories of phantom limb perception are also reviewed, including Melzack's (1990) neuromatrix theory (Section 4.2, below), and the more recently proposed roles of the fronto-parietal mirror neuron system (Brugger, 2006; Brugger et al., 2000), and "pain matrix" mirror system (Giummarra et al., 2006a) (Section 4.4, below). The pain matrix refers to the pain-related network that primarily includes the secondary somatosensory cortex (SII), insular regions, the anterior cingulate cortex (ACC), and the movement-related areas such as the cerebellum and supplementary motor area (Singer et al., 2004). Through the mirror neuron system, amputees with phantom sensations may have a greater "postural empathy" for others such that they are better able to match their own body schema against the observed bodies of others, and are thus potentially more likely to have a bodily experience that resembles that observed in others. The mechanisms of cross-referencing the phantom limb with the opposite limb are also considered (Section 4.5, below). This review proposes that – with the likely involvement of the body schema, mirror systems, and cross-callosal and ipsilateral projections in phantom limb phenomena – the perception of a "normal", non-painful phantom limb is very likely to be an epiphenomenon of normal functioning, action understanding and empathy, and potentially even *evolutionarily adaptive* and perhaps *necessary*.

2. Proprioception of the phantom limb

Phantom limbs are generally perceived to occupy veridical body space – being of a particular size, shape and posture – and may be perceived to be completely paralysed, or under the amputee's volitional control (Roux et al., 2001), or to move spontaneously or reflexively (Ramachandran and Hirstein, 1998). The phantom limb is generally described as adopting a "habitual" position and posture (e.g., partially flexed at the elbow with the forearm pronated), resting at the side of the body, or in a posture that resembles the posture of the limb prior to amputation (Ramachandran and Hirstein, 1998). Spontaneous changes in posture of the phantom limb are also common in amputees (Ramachandran and Hirstein, 1998) and in (normal) patients who are under anaesthesia (Bromage and Melzack, 1974; Melzack and Bromage, 1973). Henderson and Smyth (1948) reported that the phantom tends to be "correctly aligned to the stump with which it moves" (p. 90). Often, however, the phantom limb may be perceived to be stuck in a fixed position (Devor, 1997) and sometimes to