Neuroscience and Biobehavioral Reviews 57 (2015) 142–155

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review

The role of the cerebral cortex in postural responses to externally induced perturbations

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ARTICLE INFO

Article history:
Received 25 April 2015
Received in revised form 9 August 2015
Accepted 25 August 2015
Available online 29 August 2015

Keywords:
Cerebral cortex
Balance
Postural response
Central set
Compensatory balance response

ABSTRACT

The ease with which we avoid falling down belies a highly sophisticated and distributed neural network for controlling reactions to maintain upright balance. Although historically these reactions were considered within the sub cortical domain, mounting evidence reveals a distributed network for postural control including a potentially important role for the cerebral cortex. Support for this cortical role comes from direct measurement associated with moments of induced instability as well as indirect links between cognitive task performance and balance recovery. The cerebral cortex appears to be directly involved in the control of rapid balance reactions but also setting the central nervous system in advance to optimize balance recovery reactions even when a future threat to stability is unexpected. In this review the growing body of evidence that now firmly supports a cortical role in the postural responses to externally induced perturbations is presented. Moreover, an updated framework is advanced to help understand how cortical contributions may influence our resistance to falls and on what timescale. The implications for future studies into the neural control of balance are discussed.

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http://dx.doi.org/10.1016/j.neubiorev.2015.08.014
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1. Introduction

A broadly distributed neural network controls upright stability in humans. While the relative contribution of distinct parts of the nervous system to maintain balance remains unclear it is now well established that even the most advanced regions of the neural hierarchy play some role in balance control. Most remarkable is the accumulating evidence that the cerebral cortex plays an important role in balance including compensatory reactions to unexpected postural challenge. This represents an important departure from the historical framework that placed postural regulation largely in the domain of subcortical networks.

A seemingly effortless ability to stay upright in healthy humans belies the sophisticated mechanisms acting to preserve an elevated centre of mass over a small bipedal base of support. However in many disease states, particularly those involving neurological disruption, the challenge of this task is exposed rendering numerous clinical populations vulnerable to falls. With significant societal and individual costs related to falls (e.g. severe injury and even death) this represents a major health care concern (Baker et al., 2011; Carroll et al., 2005; Kannus et al., 2005). Thus illuminating the underlying neural mechanisms for controlling balance is essential for developing targeted therapies to mitigate fall risk. As expected, considerable effort has gone into exploring factors that impact balance such as the role of different sensory cues in triggering corrective actions (Bolton and Misiaszek, 2009; Macpherson et al., 2007; Stapley et al., 2002) or spinal and brainstem mechanisms acting to stabilize the body (Bolton and Misiaszek, 2012; Honeycutt and Nichols, 2010; Macpherson and Fung, 1999; Mori, 1987). Conversely, much less research has investigated the role of the cerebral cortex in balance. This gap has likely been encouraged by the long-held belief that postural responses are mostly managed sub cortically (Magnus, 1926; Sherrington, 1910). Of course, this view has been reasonable given that reduced animal preparations retain an impressive capacity for generating complex righting reactions (Honeycutt and Nichols, 2010). Moreover, the comparably slow pace of sensory-cued voluntary acts versus the onset of automated postural responses has influenced the assumption that much of the neural processing related to generating balance reactions originates sub-cortically. While subcortical networks are critical in generating compensatory behaviour more recent investigations have demonstrated that the cerebral cortex makes a meaningful contribution to compensatory balance reactions.

The major shift towards recognising an important role for the cerebral cortex in balance control has been discussed previously (Jacobs and Horak, 2007; Maki and McIlroy, 2007) and the reader is referred to these comprehensive reviews. A critical distillation of these past reviews is that the cerebral cortex can: (1) Modulate upcoming potential postural responses via central set based on intention and knowledge of perturbation or environmental characteristics, (2) provide online monitoring of balance status and (3) modulate late-phase or change-in-support responses characteristics perhaps through direct control.

The present review extends upon past work to highlight some of the more recent advances. This includes updated information regarding cortical contributions to the perception (and prediction) of instability as well as a role in shaping the motor response. Where possible an indication of the impact of particular brain regions in responding to external perturbations will be provided. Moreover, compelling evidence now exists that postural threat is associated with accelerated engagement of cortical networks thus challenging previously assumed speed of transmission barriers to why the cerebral cortex could not play a role in rapid postural responses. This review will present the emerging evidence for a cortical role in reactive balance emphasizing research that directly measures cortical neurophysiology in association with externally induced postural responses. Moreover, suggestions for future research are provided. Overall, an updated framework is advanced for how the cerebral cortex may influence both the online generation of compensatory reactions as well as contributing to a priori setting of the central nervous system (CNS) state to influence such control.

2. What is a compensatory reaction?

Compensatory balance responses are highly sophisticated, whole-body reactions rapidly generated by the nervous system to resist a loss of equilibrium. The initial triggered stage of the response, the automatic postural reaction (APR), is intimately linked to the sensory volley from a fall, evident by the direction specificity of the resultant muscle pattern and the fact that the motor response scales with the perturbation magnitude (Macpherson and Horak, 2013). These postural responses are extremely robust in that a variety of sensory inputs, even from separate modalities, can trigger an appropriate corrective action. Furthermore, APRs are highly generalizable in the sense that many different forms of perturbation may elicit a similar direction-appropriate counter response including surface translations or tilts (Moore et al., 1988; Nashner, 1977; Safavynia and Ting, 2012) slips or trips while walking (Eng et al., 1994; Schillings et al., 1996) and perturbations to the torso (Misiaszek and Krauss, 2005). Importantly, these responses are not a simple collection of segmental stretch reflexes but instead represent complex patterns of muscle action organized around the goal of maintaining upright balance (Macpherson and Horak, 2013). This is perhaps most obvious when one considers that many of the muscles engaged in the automated action are often remote from the site of perturbation. For example a perturbation to standing stability can trigger rapid corrective reactions in the upper limbs at similar onset latencies to the early leg responses (McIlroy and Maki, 1995). The fact that these responses even at the remote locations have a direction-specific nature (e.g. early arm responses that aim toward a handle) argues against a generic startle effect but rather suggests a more behaviourally relevant motor command (Gage et al., 2007; Maki and McIlroy, 1997). This last point seems remarkable given that APRs are delayed relative to an autogenic stretch reflex but faster than muscle onsets associated with standard measures of voluntary reaction time, which tends to indicate an important role for fast-acting subcortical networks in coordinating this class of behaviour.

An important feature of APRs is that they persist even when subjects try to supplant these actions with separate motor commands or attempt to suppress them altogether (Burleigh and Horak, 1996; McIlroy and Maki, 1993; Weerdesteyn et al., 2008). Thus, to a certain degree the initial postural response is immutable, at least in terms of the directionally tuned response pattern and onset. However, intention and environmental context can allow some critical modulation in the gain over these early actions. A classic example of contextual modulation in a balance reaction involves the distinct response strategies that subjects adopt when perturbed while standing on a surface that imposes different biomechanical constraints (Horak and Nashner, 1986). Here, it has been shown that when producing a counter reaction to a rapid platform translation subjects will tend to generate an ankle torque to resist the fall. However, when exposed to the same rapid translation but standing on a narrow beam motor reactions are now engaged about the hip to counter the body sway given that the ankle torque is no longer contextually relevant to control balance. Thus, these responses are not entirely hard-wired reactions but rather can be modified in a goal-specific manner.

Although an automated and stereotyped early postural response is critical when recovering balance this must be reinforced with continuing action to eventually secure upright posture. This is

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