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What startles tell us about control of posture and gait

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ABSTRACT

Recently, there has been an increase in studies evaluating startle reflexes and StartReact, many in tasks involving postural control and gait. These studies have provided important new insights. First, several experiments indicate a superimposition of startle reflex activity on the postural response during unexpected balance perturbations. Overlap in the expression of startle reflexes and postural responses emphasizes the possibility of, at least partly, a common substrate for these two types of behavior. Second, it is recognized that the range of behaviors, susceptible to StartReact, has expanded considerably. Originally this work was concentrated on simple voluntary ballistic movements, but gait initiation, online step adjustments and postural responses can be initiated earlier by a startling stimulus as well, indicating advanced motor preparation of posture and gait. Third, recent experiments on StartReact using TMS and patients with corticospinal lesions suggest that this motor preparation involves a close interaction between cortical and subcortical structures. In this review, we provide a comprehensive overview on startle reflexes, StartReact, and their interaction with posture and gait.

Contents

1. Introduction

All of us have experienced the startling sensation of unexpected stimuli. Startling stimuli can result in a startle reflex, which is the fastest generalized motor reaction in humans and animals (Valls-Sole et al., 2008). Startling stimuli also have the ability to accelerate motor responses, a phenomenon termed StartReact (Carlsen et al., 2004b; Valls-Sole et al., 1999). Recently, there has been an increase in the number of studies evaluating startle reflexes and StartReact, many in tasks involving postural control and gait. These studies have helped to improve our understanding on the neural mechanisms underlying startle reflexes and StartReact, and also provided

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insight into the neural control of posture and gait. Here, a comprehensive review on startle reflexes, the StartReact effect, and their interaction with posture and gait is provided.

2. Startle reflexes

2.1. Neural pathways and characteristics of the startle reflex

A startle reflex is an involuntary motor reaction to unexpected sensory input and consists of a generalized flexion response that follows a rostro-caudal progression (Brown et al., 1991a; Chokroverty et al., 1992; Wilkins et al., 1986). Startle reflex activity is most prominently seen in the sternocleidomastoid muscle. Subsequently, the descending volley may activate more distal muscles in the trunk and upper and lower extremities. A pure generalized startle reflex is not always seen in both proximal and distal muscles (Brown et al., 1991a). Startle reflex activity is thought to result from the activation of reticulospinal motor tracts in the pontomedullary reticular formation (pmRF), which in the case of auditory startle, is triggered by direct synaptic activation from the cochlear nucleus (Koch, 1999; Yeomans and Frankland, 1995). Importantly, neurons of the pmRF are not modality specific, and therefore respond to different types of afferent information (Wu et al., 1988). For example, startle reflexes can be elicited by acoustic stimuli (Brown et al., 1991b), tactile stimuli (Gokin and Karpukhina, 1985), high intensity visual stimuli (Bradley et al., 1990), and by stimulation of the vestibular system via unexpected vertical drops of the body (Bisdorff et al., 1995; Gruner, 1989). Startling stimuli do not only result in startle reflexes, but also in blink responses due to activation of the orbicularis oculi muscle. Pathways underlying blink responses are thought to be different from startle reflexes, involving neurons of the inferior colliculus and mesencephalic reticular formation (Hori et al., 1986).

Habituation and prepulse inhibition are important characteristics of startle reflexes. Habituation of startle reflexes is observed when startling stimuli are given in repetition. Startle reflexes decrease in amplitude with repeated exposure, and eventually only the blink response will remain (Brown et al., 1991b). Habituation occurs most often after two to six presentations of a startling stimulus, and is presumably the result of synaptic depression at the pmRF (Chokroverty et al., 1992). Prepulse inhibition is the inhibitory effect of a weak sensory signal given 30–500 ms prior to the startling stimulus (Graham, 1975; Koch et al., 1993; Swerdlow, 2013). The neural pathways involved in prepulse inhibition likely include the pedunculopontine nucleus (PPN) (Inglis and Winn, 1995; Koch, 1999), as studies in rats showed that PPN-lesions abolish prepulse inhibition (Swerdlow and Geyer, 1993). For more detailed information about prepulse inhibition and habituation of startle reflexes, we refer to excellent reviews by Valls-Sole et al. (2008) and Carlsen et al. (2011).

2.2. Modulation of startle reflex expression by posture and gait

Studies that evaluated startle reflexes during gait and various postures have shown that the expression of startle reflex activity is modulated by afferent input. During gait, a phase dependent modulation of startle reflexes is observed, with more prominent startle reflexes in the stance leg compared to the swing leg (Nieuwenhuijzen et al., 2000; Schepens and Delwaide, 1995). Startle reflexes in lower leg muscles are more prevalent while standing compared to sitting, whereas rates of occurrence of reflex EMG activity in the sternocleidomastoid muscle do not differ between both postures (Brown et al., 1991a; Delwaide and Schepens, 1995). Moreover, shorter latencies of reflex EMG activity in leg muscles are observed while standing (70–95 ms) compared to sitting (120 ms) (Brown et al., 1991a; Delwaide and Schepens, 1995). Finally, a recent study found that more subtle changes in posture, such as weight-bearing asymmetry, also influence startle reflex expression in leg muscles (Nonnekes et al., 2013d). It has been suggested by these authors that afferent loading information plays a critical role in the observed modulation of startle reflexes. Such information is provided by Ib-afferents from Golgi tendon organs and cutaneous mechanoreceptors in the foot soles (Dietz and Duysens, 2000; Duysens et al., 2000; Kavounoudias et al., 2001). Modulation of startle reflex activity by afferent loading information likely takes place at the spinal cord, as studies in cats indicated that symmetrical volleys from the pmRF are gated at premotoneural level by spinal interneuronal networks (Drew, 1991b; Schepens and Drew, 2006).

2.3. Modulation of posture and gait by startle reflexes

Startle reflexes likely contribute to the large amplitude postural responses that are observed when balance is perturbed unexpectedly or for the first time in a series of perturbations (Campbell et al., 2013; Siegmund et al., 2008). Amplitudes of postural responses to balance perturbations are significantly larger during the first trial compared to subsequent trials involving the same postural stimulus, a phenomenon known as first trial effect (Allum et al., 2011). First trial effects are observed in whole body postural responses that occur when standing balance is perturbed (Allum et al., 2011; Bloem et al., 1998; Chong et al., 1999; Keshner et al., 1987; Oude Nijhuis et al., 2009, 2010; Tang et al., 2012), but also in postural responses in neck and trunk muscles that occur during seated perturbations (Blouin et al., 2006, 2007). These first trial effects have been suggested to result from summation of startle reflex activity on the basic postural response (Blouin et al., 2006; Campbell et al., 2013; Nanhoe-Mahabier et al., 2012; Siegmund et al., 2008). This hypothesis is supported by three observations. First, postural responses habituate after the first trial in a series of repeated perturbations, just like habituation of startle reflexes (Campbell et al., 2013; Oude Nijhuis et al., 2010). Habituation of postural responses could as such consist of the extinction of startle reflexes, leaving only the postural response (Siegmund et al., 2008). Second, early masseter activity after first trial perturbations might be indicative of a startle-like component contributing to balance responses (Visser et al., 2010), as early activation of this muscle is indicative of the presence of a startle reflex (Brown et al., 1991b). A third observation in support of startle-like components contributing to balance responses relates to coherence in EMG activity between bilateral neck muscles during rear-end perturbations (Blouin et al., 2006). An increased coherence in the 10–20 Hz bandwidth is observed after startling auditory stimuli, and is thought to represent increased reticulospinal activity (Grosse and Brown, 2003). During rear-end forward perturbations, an increased coherence in the 10–20 Hz bandwidth was seen during the first trial (Blouin et al., 2006). During subsequent habituated trials the synchrony between bilateral neck muscles decreased significantly, but reappeared when a startling acoustic stimulus was superimposed on the whiplash-like perturbation. Hence, these results also indicate a superimposition of startle reflex activity on the postural response during first trial perturbations.

The above observations raise the question whether the summation of startle reflex activity on the basic postural response results in functional benefits. The function of the startle reflex could lie in the rapid accomplishment of a defensive posture (Brown et al., 1991a; Nonnekes et al., 2013d), yet in modern life, summation of startle reflexes and postural responses might have disadvantages as well. The expression of startle reflexes following rear-end collisions has been suggested to contribute to increased forces and strains in neck tissues, leading to whiplash injuries (Mang et al.,