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ANTICIPATORY POSTURAL ADJUSTMENTS DURING STEP INITIATION: ELICITATION BY AUDITORY STIMULATION OF DIFFERING INTENSITIES

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Abstract—Step initiation is associated with anticipatory postural adjustments (APAs) that vary according to the speed of the first step. When step initiation is elicited by a ''go'' signal (i.e. in a reaction time task), the presentation of an unpredictable, intense, acoustic startling stimulus (engaging a subcortical mechanism) simultaneously with or just before the imperative ''go'' signal is able to trigger early-phase APAs. The aim of the present study was to better understand the mechanisms underlying APAs during step initiation. We hypothesized that the early release of APAs by low-intensity, non-startling stimuli delivered long before an imperative ''go'' signal indicates the involvement of several different mechanisms in triggering APAs (and not just acoustic reflexes triggering brainstem structures). Fifteen healthy subjects were asked to respond to an imperative visual ''go'' signal by initiating a step with their right leg. A brief, binaural 40, 80 or 115 dB auditory stimulus was given 1.4 s before the ''go'' signal. Participants were instructed not to respond to the auditory stimulus. The centre of pressure trajectory and the electromyographic activity of the orbicularis oculi, sternocleidomastoid and tibialis anterior muscles were recorded. All three intensities of the auditory stimulus were able to evoke low-amplitude, short APAs without subsequent step execution. The louder the stimulus, the more frequent the elicitation. Depending on the intensity of the stimulus, APAs prior to step initiation can be triggered without the evocation of a startle response or an acoustic blink. Greater reaction times for these APAs were observed for non-startling stimuli. This observation suggested the involvement of pathways that did not involve the brainstem as a ''prime mover''.

Key words: anticipatory postural adjustments, gait initiation, startle, blink, inhibition.

In humans, step initiation is associated with anticipatory postural adjustments (APAs). Foot-off is preceded by co-activation of the tibialis anterior (TA) muscles. This generates a backward displacement of the centre of pressure toward the swing leg. A forward centre of pressure displacement toward the stance leg is then observed. The swing leg's heel-off occurs at the start of the second phase of centre of pressure displacement (a lateral shift toward stance leg) and toe-off (TO) occurs just before the forward centre of pressure displacement (Winter, 1995; Delval et al., 2005). These APAs reduce the load on the swing leg and are necessary for forward progression (Brenière et al., 1987; Brenière and Do, 1991). Although APAs are referred to as ''anticipatory'' (Gahéry and Massion, 1981), they also continue during the movement itself.

The precise origin of APA generation (i.e. the midbrain or the cortex) remains unclear. On one hand, intracerebral recordings in the cat (Drew et al., 2004) and studies in subjects with focal lesions of the supplementary motor area (Viallet et al., 1992) and patients with Parkinson's disease or bipallidal lesions (Gantchev et al., 1996; Krystkowiak et al., 2006) have shown that APAs can be generated in the supraspinal circuits that interconnect the supplementary motor area (SMA), the basal ganglia and the pontomedullary reticular formation. For example, the SMA is thought to contribute to the generation and timing of APAs (Jacobs et al., 2009a,b). Repetitive transmagnetic stimulation over the SMA (but not over the dorsolateral premotor cortex) briefly shortened the APA durations, whereas APA amplitude was not affected. In contrast, the midbrain locomotor region (which may correspond in part to the cuneiform nucleus and the dorsal part of the pedunculopontine nucleus) is thought to be involved in the step initiation process, given its connection with limbic structures and the basal ganglia (Pahapill and Lozano, 2000).

A putative role of the midbrain reticular structures in APA generation has also been evidenced, suggesting the involvement of an automatic process in gait initiation. Midbrain involvement in movement triggering was first explored for the action of rising onto tiptoe. Indeed, Valls-Solé et al. (1999) demonstrated that movement can be produced with considerably shorter reaction times (RTs) than a normal, simple, voluntary reaction when the imperative ''go'' stimulus is replaced by an unpredictable, acoustic startle stimulus. The generalized auditory startle reflex is evoked by an unexpected, strong acoustic stimulus and is typically characterized by a short-latency, bilat-

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Abbreviations: APAs, anticipatory postural adjustments; EMG, electromyographic; MBS, maximum backward shift; OO, orbicularis oculi; pAPA, pre-APA; RTs, reaction times; SCM, sternocleidomastoid; SMA, supplementary motor area; TA, tibialis anterior.

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eral burst of electromyographic (EMG) activity involving the sternocleidomastoid (SCM) (Brown et al., 1991).

The fact that this rapid triggering of a movement sequence only occurs when the task is known in advance suggests that a planned motor sequence is involved (Carlsen et al., 2004). Furthermore, (Valls-Solé et al., 1995, 1999) concluded that the RT that they observed was too fast for the cerebral cortex to be involved. This prompted researchers to consider that startle-evoked reductions in the RT are due to interaction between the brainstem-mediated startle response and a subcortically stored motor program, causing early release of movement (Rothwell, 2006). Moreover, Carlsen et al. (2007) also demonstrated that the shortening of the RT for arm movements varies with the auditory stimulus' intensity and dramatically decreases when associated with a startle response. When an acoustic startle stimulus is delivered at the same time as the imperative ''go'' signal for step execution, the latency of all gait initiation-related events decreases and the bursts of EMG activity are greater in amplitude (Queralt et al., 2010).

During step preparation, an acoustic startle stimulus delivered at various intervals before the imperative ''go'' signal can also result in the early elicitation of the APA-stepping sequence (MacKinnon et al., 2007). In the latter study, APAs could be triggered when an acoustic stimulus was presented as much as 1.4 s before the imperative ''go'' signal. However, only loud startling stimuli (115 dB) were used. The APA sequences appeared in only about 40% of these trials and were not associated with early step initiation. McKinnon et al. considered that elicitation of these early APAs specifically involves reticular structures.

Even automated postural responses (known to be controlled by the brainstem) can be elicited by non-startling auditory stimuli. This presumably involves transcortical pathways (Campbell et al., 2009). The elicitation of APAs during step initiation may variously involve either midbrain structures (Queralt et al., 2010), diencephalic structures or cortical structures (such as the SMA) (Jacobs et al., 2009b). The aim of the present study was to better understand the mechanisms underlying APAs during step initiation. We hypothesized that the early release of APAs by low-intensity, non-startling stimuli delivered long before an imperative ''go'' signal would indicate the involvement of structures other than the reticular neurons of the brainstem (e.g. networks following integration of the auditory stimulus and involved in decision-making or inhibitory control). We also wonder whether or not the characteristics of these APAs would differ according to the stimulation conditions (i.e. startle reflexes or not). We further hypothesized that APAs could be elicited by an acoustic stimulus through several different mechanisms. The APAs' characteristics might also differ according to the intensity of the stimulus. Indeed, APA release as the subject is preparing to step could be provoked either by a stimulus that evokes a startle-like response or by a low-intensity stimulus (i.e. in the absence of a startle response or an auditory blink response).

EXPERIMENTAL PROCEDURES

Subjects

Fifteen young adult subjects (8 males, 7 females; median age: 23; 1st quartile: 22; 3rd quartile: 27) were included in the study. None had a history of medical treatment, drug abuse or any pathology that could have interfered with gait. All gave their written, informed consent to participation. The study was approved by the local independent ethics committee.

Data collection

Auditory tone bursts (frequency: 1000 Hz; duration: 40 ms; intensity: 115, 80 or 40 dB, rise/fall time: 0.1 ms) were delivered binaurally through earphones (TDH39). The delivery of sound and visual stimuli was managed by a PC-based system (Gentask from Compumedics Neuroscan, Charlotte, NC, USA). The inten-

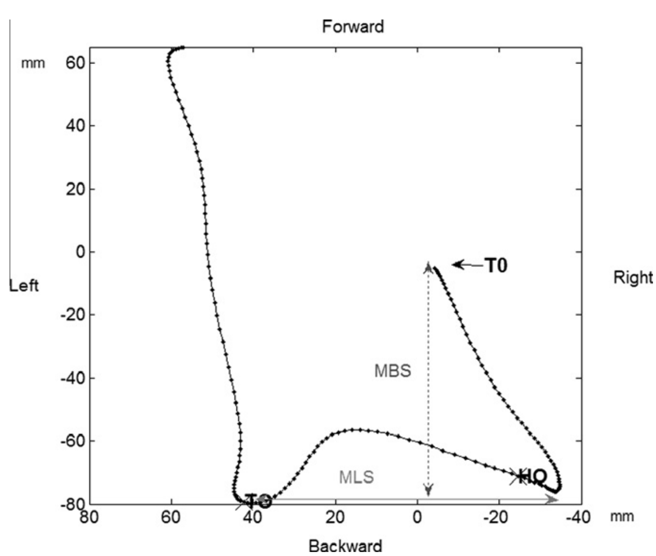

Fig. 1. Trajectory of the centre of pressure for a control subject during gait initiation with the right foot (visually-triggered gait initiation). Note the backward centre of pressure shift toward the swing leg, followed by a lateral shift toward the stance leg. Heel off (HO) and toe-off (TO) times are noted. MBS: maximum backward shift, MLS: maximum lateral shift. T0: start of the anticipatory postural adjustments.