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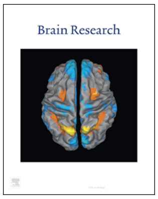

Research report

Synchronised vestibular signals increase the P300 event-related potential elicited by auditory oddballs

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ABSTRACT

The perception of beat within an auditory rhythm can be facilitated when accompanied by synchronised movements. Electrophysiological investigation shows that this facilitatory effect is associated with a larger P300 amplitude. It has remained unclear, however, which movement-related processes drive this P300 effect. To investigate whether vestibular signals play a role, we administered alternating, sub-sensory (mean=.3 mA) galvanic current to the vestibular nerves of participants while they counted the number of oddballs presented in a stream of tones played at a rate of 1 Hz. Consistent with a vestibular effect, the P300 elicited by the oddballs was increased during stimulation relative to a sham condition, but only when the frequency of the alternating current matched that at which the tones were played. This finding supports the general idea that the vestibular system is involved in audio-motor synchronisation and is the first to show by electrophysiological means that it influences cognitive processes involved in beat perception.

1. Introduction

We are all familiar with the urge to nod our head, drum our fingers, tap our foot or even dance to music. This coordination of a repeated physical movement with an auditory rhythm makes it easier to both detect the beat and changes to it (see Todd and Lee (2015)). The present study investigates one mechanism by which this facilitatory effect might occur.

In a previous study we found that auditory-motor synchronization enhances the P300 response to pitch deviants (Schmidt-Kassow et al., 2013). Participants listened to periodic and aperiodic continuous tone sequences and were asked to silently count deviant tones that differed in sound frequency from the standard tones. While performing this task, they either sat still or pedalled on a stationary exercise bike at a rate that matched the frequency of the periodic tones. The detection of pitch deviants in periodic tone sequences while pedalling, compared to sitting still, elicited a larger P300. More so, this amplitude was greater and its latency shorter when the time taken to complete a revolution of the pedals more closely matched the frequency (1 Hz) at which the deviant tones were presented. By contrast, electrophysiological responses to pitch deviants in aperiodic tone sequences were not influenced by whether participants were cycling or stationary. Precise interpretations of the P300 continue to be debated (see Patel and Azzam (2005), Polich (2007)) but the observed effect was taken as support for the idea that synchronised limb movements improve attentionally-mediated aspects of auditory perception and may affect the way we encode and interpret beat (i.e., the basic 'pulse' of music) (see Butler and Trainor (2015), Cirelli et al. (2014), Grahn and McAuley (2009), Manning and Schutz (2013), Morillon et al. (2013), Manning and Schutz (2015)) and metre (i.e., the recurring pattern of stresses and accents in beat over time; see Tan et al. (2010), Chemin et al. (2014), Phillips-Silver and Trainor (2005, 2007) and see also Repp and Su (2013)).

Recent studies have begun to cast light on the source of these facilitatory motor effects, and in particular, on the role of the vestibular system. The vestibular system detects linear, angular and gravitational acceleration of the head and plays an important role in the autonomic control of eye movement, posture, gait and egocentric perception (see Smith and Zheng (2013)). Convergent sources of evidence suggest that vestibular signals may mediate audio-visual synchronisation in humans. At a biological level, the vestibular end-organs are known to respond to specific intensities and frequencies of sound (Colebatch et al., 1994) that, in turn, contribute to both short- (i.e., 10–30 ms) and long- (i.e., 50–250 ms) latency auditory cortical evoked potentials (Todd et al., 2014a, 2014b). Anatomical investigations indicate that the ascending vestibular afferents are closely entwined with those implicated in rhythm perception and tend to terminate in the same cortical association and motor areas (see Bense et al. (2001),

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Bucher et al. (1998), Todd and Lee (2015)). At the psychological level, infants' perceptions of metric structure are altered when they are bounced (i.e., subject to vestibular stimulation) in time with music (Phillips-Silver and Trainor, 2005). In adults, Phillips-Silver and Trainor (2008) demonstrated that while the interpretation of an ambiguous musical metre as a triple or duple metre is not affected by synchronous movement of the lower body (legs and feet), it is affected by the passive, synchronised rocking induced by lying on a moving seesaw. Given that these two forms of movement can be distinguished by the degree to which they activate the vestibular system, the authors tested whether head movements performed while the rest of the body remained stationary that were synchronised to either the second (duple) or third (triple) beat of a metre were sufficient to bias subsequent judgements of auditory tempo. Consistent with a vestibular-based effect, head movements alone were sufficient to bias these judgements.

To address the possibility raised by the studies above (e.g., Phillips-Silver and Trainor, 2005, 2008) that the beneficial effects of head movement on auditory perception may reflect increased proprioceptive and visual, rather than vestibular, stimulation, Trainor and colleagues tested the effect of galvanic vestibular stimulation (GVS) on auditory disambiguation. GVS involves the delivery of transcranial current to the mastoid processes which are situated near the underlying vestibular nerve and peripheral organs (see Fitzpatrick and Day, 2004). Importantly, GVS modulates the firing rates of the vestibular (but not proprioceptive, visual or cochlear) afferents in a manner similar to natural head movement, and thereby elicits a comparable range of compensatory cortical and sub-cortical responses (Cevette et al., 2012; Lobel et al., 1998; Stephan et al., 2005). Trainor et al. (2009) asked their participants to listen to an ambiguous metric pattern (an auditory sequence that could be interpreted as duple or triple metre), while they were stimulated with super-sensory alternating current (AC) galvanic vestibular stimulation (GVS). At super-sensory levels, AC GVS induces an illusory perception of side-to-side rocking which, by manipulating the AC frequency, enabled Trainor and colleagues to match the illusory rocking sensations to the tempo (duple or triple time) of an auditory beat. As predicted, participants' interpretation of the ambiguous metre as either duple or triple was strongly determined by the frequency of the coincident vestibular stimulus; if the GVS frequency corresponded to the temporal structure of a duple metre then participants interpreted the ambiguous sequence as duple metre, while the same held for the triple metre condition. This outcome was taken as further evidence that the vestibular component of bodily movement exerts an independent influence on the perception of auditory sequences.

The outcome of the Trainor et al. (2009) study is compelling. In the current study we went a step further by investigating how sub-sensory, rather than super-sensory, GVS affects electrophysiological markers of auditory cognition. By applying a sub-sensory GVS signal we could test whether activation of the vestibular system without an experimentally-induced movement illusion is sufficient to influence auditory processing. One drawback of such an illusion is the corresponding activation of premotor regions and the supplementary motor area (Lobel et al., 1998; Stephan et al., 2005). A second problem with super-sensory currents is that they usually elicit itching/tingling underneath the electrodes. This can make it difficult to disentangle vestibular influences from those that are somatosensory in origin. Trainor and colleagues sought to mitigate this problem by employing a control condition in which the stimulating electrodes were fastened to the elbows. Although this helped confirm that the observed effects could not be attributed to non-specific alerting, it could not address whether they might arise from cutaneous sensations emanating from the mastoid processes. By contrast, sub-sensory currents do not elicit illusory rocking or cutaneous sensations and therefore constitute a purer vestibular stimulus.

To gain insight into how the vestibular system might be affecting detection of pitch deviants, we employed an auditory oddball paradigm that enabled measurement of the P300. As discussed later, controversy surrounds the precise functional significance of the P300 waveform although there is general agreement that it is mostly driven by infrequent or unexpected stimulus change and reflects context-updating (Polich, 2007). Our specific aim was to build on the earlier finding that pedalling in time to a beat enhances the P300 response to pitch deviants (Schmidt-Kassow et al., 2013). If this effect is at least partly vestibular in origin then it should still be evident when, instead of pedalling, sub-sensory GVS is administered in time with pitch deviants.

We administered a 2-tone oddball auditory paradigm similar to that used by others to investigate the influence of stimulus timing on pitch perception (Kim and McAuley, 2013; Schmidt-Kassow et al., 2009, 2013; Schwartze et al., 2011). Participants were seated and asked to silently count deviant tones that appeared within strings of non-deviant tones while receiving either active or sham stimulation. There were three stimulation conditions, all of which featured tones that were temporally spaced apart at a frequency of 1 Hz: (1) a sham condition in which subjects wore inactive GVS electrodes, 2) a condition in which the frequency of sub-sensory AC-GVS (1 Hz) matched the temporal frequency at which the tones were presented (stim1 condition), and 3) a condition in which the frequency of sub-sensory AC-GVS (0.8 Hz) did not match the temporal frequency at which the tones were presented (stim08 condition).

We reasoned that if the detection of pitch deviants is facilitated by coincident vestibular activation then the P300 elicited by auditory deviants should be amplified when the GVS signal is synchronised to the frequency at which the auditory stimuli are presented. By contrast, neither asynchronous nor sham stimulation should exert a comparable effect. Alternatively, if the mere copresence of vestibular activity, regardless of its temporal frequency, is sufficient to influence processes concerned with deviant detection then, relative to the sham condition, the P300 amplitude should be affected by both asynchronous and synchronous GVS. Such an outcome might be predicted given that general movement of the head up-regulates metabolic activity across auditory, motor and multi-modal cortices and may therefore sharpen neural response (see Lopez et al. (2012)).

Finally, we should point out that the auditory tones were presented at a frequency (600/700 Hz and 75 dB A) that fall outside the range typically associated with the induction of vestibular evoked myogenic potentials (Todd et al., 2014a). This is relevant because, under certain conditions, VEMPs can modulate short- and long- (i.e., N1 and P2) latency auditory cortical potentials. In the present experiment, even if (contrary to expectation) auditory tones constituted vestibular stimuli then there should be no net effect on the P300 because the tones are common to all three experimental conditions.

2. Results

2.1. Behavioural data

On average, participants made fewer than four errors in deviant tone counting per stimulation block (*sham:* 2.9 errors, SE =0.6; *stim08:* 2.5 errors, SE =0.6; *stim1:* 2.4 errors, SE =0.7), indicating that they paid attention to the pitch changes. A one-way ANOVA revealed no significant difference between blocks, $F(2,16)=0.29$, $p=0.75$, $\eta_p^2=0.02$.

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