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Sensory attenuation of self-initiated sounds maps onto habitual associations between motor action and sound

Nathan G. Mifsud*, Thomas J. Whitford

School of Psychology, UNSW Australia, Sydney, New South Wales, Australia

A R T I C L E I N F O

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A B S T R A C T

Sensory attenuation refers to reduced brain responses to self-initiated sensations relative to those produced by the external world, a distinction that is vital for dynamic motor control and our sense of agency. Typically, willed vocalizations elicit larger N1 reduction of the auditory evoked potential compared to indirectly evoked sounds, such as tones generated by button-presses, which is attributed to the prediction and cancellation of incoming signals enabled by speech motor commands. However, physical confounds exist, including different stimuli and the increased motor artefact associated with mouth vs. finger movements. The present study investigated N1 attenuation to physically identical sounds evoked by hand, eye, and mouth-initiated movements. Twenty-eight healthy participants had their electroencephalogram (EEG) recorded as they blew into a microphone, pressed a button, or moved their eye to generate a pure tone. We found that N1 and P2 response was most reduced in the blow initiation condition, and that both blow and button-press but not saccade initiated tones elicited significantly reduced N1 and P2 amplitude compared to external initiation. This indicates that the eliciting motor action markedly influences ERP response to auditory stimuli. Given that saccades are never associated with sounds, finger movements sometimes are, and mouth movements often are, the pattern of results suggests that N1 attenuation to self-initiated sounds may depend on existing associations between the initiating action and resultant sensation.

1. Introduction

A central aspect of everyday experience is that sensations caused by our own actions are easily distinguishable from those with an external origin. This fundamental distinction is believed to play a central role in establishing our sense of agency (Engbert et al., 2008). It is accounted for by a motor control framework in which the central nervous system uses a forward model to anticipate the sensory effects of movement based on internal motor commands (Wolpert et al., 1995). Modulatory signals, referred to as corollary discharges (Sperry, 1950) or efference copies (Von Holst, 1954), contain the predictions and attenuate incoming sensory input accordingly, such that residual sensory activity represents deviation from what was expected on the basis of the outgoing motor command. Sensory attenuation due to forward prediction may explain why we cannot tickle ourselves (Blakemore et al., 1998). The phenomenon also comports with the inhibition of auditory neurons during vocalization to prevent self-induced desensitization, widely observed in crickets (Poulet and Hedwig, 2002), bats (Suga and Shimozawa, 1974), primates (Eliades and Wang, 2003; Müller-Preuss and Ploog, 1981), and humans (Curio et al., 2000; Ford et al., 2001; Houde et al., 2002; Paus et al., 1996).

The event-related potential (ERP) literature on sensory attenuation has dramatically expanded over the past two decades. Ford et al. (2010) detailed a typical paradigm involving vocal production, where participants first utter a series of basic syllables (self-initiated condition) and have this recording played back to them (externally initiated condition). Healthy individuals have consistently been shown to exhibit attenuated response of the N1/M1 for self-initiated vocalizations (e.g., Behroozmand et al., 2009; Curio et al., 2000; Ford et al., 2007; Houde et al., 2002). As the N1 (i.e., the negative peak in the EEG that appears around 100 ms after transient onset of an auditory stimulus) is sensitive to volume and known to originate from the auditory cortex (Näätänen and Picton, 1987), this pattern of results suggests that the auditory cortex is adjusting its sensitivity and lowering its response to self-initiated vocalizations.

There are, however, significant limitations to these willed vocalization studies. Most problematic is that there are physical differences in the auditory signal between conditions. For instance, self-initiated vocalizations will always have the confound of bone conduction (Stenfelt and Goode, 2005). Even if an online recording is played simultaneously through headphones during vocalization, the eardrum will receive a

* Correspondence to: School of Psychology, Mathews Building, UNSW Australia, Sydney, NSW 2052, Australia.
E-mail address: nathan.mifsud@unsw.edu.au (N.G. Mifsud).

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combination of air-conducted sound and bone-conducted sound, such that the heard sound in the self-initiated condition will be qualitatively different from the heard sound in the externally initiated condition. Moreover, speech production may lead to contraction of the middle ear stapedius muscle, which alters transmission of the sound signal (Horvath and Burgyan, 2013). Such confounds make it difficult to determine to what degree differences in the ERP amplitudes of each condition are associated with forward prediction as opposed to merely between-condition differences in the auditory signal. These issues are mitigated in button-press paradigms, in which participants press a button to initiate artificial stimuli such as tones, avoiding both bone conduction and muscle contraction (as the mouth is not used for stimulus production). In line with the findings of vocalization paradigms, several research groups have reported auditory N1 suppression to button-press elicited tones (e.g., Baess et al., 2008; Martikainen et al., 2005; Mifsud et al., 2016a; Schafer and Marcus, 1973; Sowman et al., 2012), as well as abnormal N1 suppression of tones in patients with schizophrenia (Ford et al., 2013; Whitford et al., 2011).

Nevertheless, the sensory attenuation studies which used tones as auditory stimuli have almost always used button-presses as the initiating motor action (typically via fingers, but see van Elk et al., 2014), and to our knowledge, no studies have used the muscle effectors involved in speech as the initiating motor action. It is possible that differences in the habitual associations between motor actions and corresponding sensory feedback may have an influence on the degree of sensory attenuation. That is, willed mouth movements are very often associated with sounds (e.g., you can hear yourself speak and chew), while willed finger movements are only sometimes associated with sounds (e.g., the tap of keys while typing on a keyboard), and quite often are not (e.g., wiggling one's fingers in the air). Furthermore, the degree of N1 suppression to speech recordings initiated by a button-press has been observed as less strong than the degree of N1 suppression when talking (Ford et al., 2007).

The present study tested the notion that the degree of sensory attenuation, as indexed by auditory N1 amplitude, may map onto the strength of the habitual association between motor action and sensory response. We measured sensory attenuation to physically identical sounds (tones) evoked by three markedly different motor actions, namely mouth movements, finger movements, and eye movements. This study introduces a highly novel self-initiated condition in which participants trigger auditory tones using a soundless blow, which is a movement free of bone conduction in an effector region habitually associated with sounds. This represents the first investigation of an action–sensation contingency that uses a mouth action while comparing truly identical stimuli in the self- and externally initiated conditions. We also compared the blow condition to saccade and button-press conditions to provide a clearer account of quantitative differences in sensory attenuation based on type of eliciting motor action.

We hypothesized that blow initiation would produce the largest degree of auditory N1 attenuation because mouth actions are strongly associated with auditory feedback. Conversely, we hypothesized that saccade initiation would result in the least N1 attenuation, given that eye movements never produce auditory feedback in the natural environment, and consistent with previous results (Mifsud et al., 2016a). Further, we expected that button-press initiation would result in intermediary N1 response between that from blow and saccade initiation, given that the habitual association between finger movements and sounds lies in between those of mouth movements (strongest association) and eye movements (weakest association).

2. Method

2.1. Participants

We recruited 28 participants at UNSW Australia, of whom 18 were female and 24 were right-handed. Their mean age was 22 years (SD = 7). Participants provided written, informed consent and received either course credit (n = 16) or financial imbursement (n = 12, A$30) in exchange for their time. This study was approved by the UNSW Human Research Ethics Advisory Panel (Psychology).

2.2. Procedure

Participants sat 60 cm in front of a computer monitor with integrated eye tracking system (Tobii TX300: 300 Hz gaze sampling rate; 23", 60 Hz, 1920 × 1080 resolution TFT screen; accuracy of .4° visual angle; system latency under 10 ms). Participants completed a demographics questionnaire before being fitted with an EEG cap and electrodes. After a 5-point eye tracking calibration procedure, participants had their EEG continuously recorded as they completed the experimental protocol, which was controlled by MATLAB (MathWorks, Natick, MA) and lasted approximately 50 min. The experiment consisted of seven conditions: three self-initiation conditions (i.e., blow-, press- and saccade-initiated tones), three corresponding motor controls (i.e., motor actions without consequent tones) and an externally initiated condition (i.e., tones initiated without participant input). Each condition was presented as a separate block that consisted of 80 homogenous trials. The order in which blocks were presented was randomized between participants. Each block began with 4 practice trials to ensure that participants understood instructions and, in the self-initiated conditions, were self-pacing their responses. A uniformly distributed random interval (1.5–3 s) preceded the beginning of each trial.

2.2.1. Blow condition

In this novel condition, participants received a tone (30 ms duration, 500 Hz frequency, 70 dB sound pressure level) to their headphones (AKG K77 Perception) immediately following a blow into a microphone (Shure SM58). To assist within-subject consistency of pace between conditions, participants were instructed to respond at will any time after a red fixation dot (.7° diameter) appeared in the center of a black screen, which remained on screen for the duration of the tone. The blowing action, demonstrated by the experimenter for participants to mimic, consisted of a brief, soundless push of the air already in the mouth cavity, which produced a movement of air sufficient for detection by the microphone diaphragm. This soundless blow served to minimize muscle recruitment and eliminate the bone conduction that occurs during speech. To prevent system latency that would result from the master audio device switching between audio capture (detecting the blow) and playback (delivering the tone) in succession, a virtual slave audio device was initialized for each role, and both virtual devices ran in parallel.

2.2.2. Press condition

In this self-initiated condition, participants responded at will any time after a fixation dot appeared (identical to the blow condition) by pressing the space bar on a low-latency keyboard (Ducky Shine 4: 1000 Hz report rate) with their dominant hand, which immediately delivered a tone identical to that in the blow condition. This condition represented a replication of several previous studies (e.g., Mifsud et al., 2016b; Sowman et al., 2012).

2.2.3. Saccade condition

This condition is similar to the saccade initiation condition reported in Mifsud et al. (2016a). This self-initiated condition began with two dots simultaneously appearing on screen: a solid red circle in the center of screen (identical to the fixation dot in previous conditions) and a hollow white circle of equal diameter (17° left or right of center, pseudo-randomly determined to ensure counterbalanced presentation). Participants were instructed to initially fixate on the white circle, which would turn solid to indicate that their gaze had been detected within a 20 ms sample of location recordings. If not detected after 5 s, trials were