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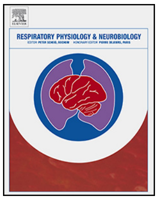

Electroencephalographic evidence for a respiratory-related cortical activity specific of the preparation of prephonatory breaths[☆]

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ABSTRACT

Speech is a major disturbance to automatic breathing control. Speech occurs during exhalation, involving controlled inhibition of automatic inspiration. Additionally, utterances are preceded by prephonatory inspirations that must be prepared to account for prosody and loudness. We hypothesized that the speech-related breathing control activities shaping prephonatory breaths originate in cortical pre-motor areas and should be associated with corresponding EEG evidence. We studied 10 normal subjects (4 men, age 23–27) during spontaneous breathing, sniff manoeuvres, and while reading out loud. Fronto-median inspiratory potentials (Cz EEG derivation) were consistently present before voluntary inspirations and large prephonatory breaths, while these potentials were generally absent during resting breathing or small prephonatory breaths. We conclude that the preparation of prephonatory breaths during speech has a cortical substrate, involving the cortical sources of premotor potentials. These results have important implications to validate whether co-modulation of the pre-motor cortex and breathing during speech are incidental or whether these cortical modulations are necessary for initiation of "speech breathing".

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1. Introduction

Mammalian breathing is peculiar among vegetative functions in that its automatism and regulation (that proceeds from the activity of brainstem central pattern generators projecting to peripheral respiratory motoneurones) are frequently and massively interfered with by competing, non-homeostatic activities. These activities include activities relating to airway clearance (cough, sneezing) or to the need for food ingestion without aspiration (Bartlett and Leiter, 2012). They also include breathing behaviours depending on cortical networks that allow voluntary apnoea (McKay et al., 2008) and the execution of voluntary respiratory manoeuvres that can be complex and very precise (Colebatch et al., 1991; Corfield et al., 1999; Gandevia and Rothwell, 1987; Plotkin et al., 2010; Similowski et al., 1996). In humans, speech represents the most frequent disruption of automatic breathing by a voluntary activity. Speech implies profound alterations of breathing control that can compromise homeostasis (Bunn and Mead, 1971) or generate dyspnoea (Hoit et al., 2007). First, speech only occurs during exhalation: utterances with a duration exceeding "normal" expiratory time require active expiration (Estenne et al., 1990; Hixon et al., 1976) and the temporary inhibition of automatic inspiration. Of note, this inhibition competes with the reflex excitatory inputs that are elicited by lung deflation (Guz et al., 1971) as that build up during interbreaths phonation. Furthermore, most speech activities extend over several breaths, utterances being separated by prephonatory inspirations. Compared to resting inspirations, prephonatory inspirations are shorter and faster, which helps to minimize disruption of discourse (McFarland and Smith, 1992; Winkworth et al., 1995). They also often have larger amplitude, as speech must be initiated at higher lung volumes in order to prolong the length of the utterance and

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increase vocal loudness (McFarland and Smith, 1992; Winkworth et al., 1995).

The neural origins of these speech-related respiratory alterations have not been extensively studied. Several mechanisms may coexist. At the subcortical level, studies in decerebrate animals have shown that a variety of organized vocalizations involving several respiratory muscle groups can be elicited via midbrain stimulation – periaqueductal grey matter – (review in Bartlett and Leiter, 2012; Zhang et al., 1994, 1995). Of note, the inspiratory neurones in the ponto-medullary network are synaptically inhibited by the so called postinspiratory neurons which are controlled by the pontine Kolliker-Fuse nucleus which is in turn closely connected to periaqueductal grey, considered as the final common pathway for vocalization. The ventilatory behaviours elicited by midbrain stimulation can be complex and include sharp and ample prephonatory breaths phenomenologically resembling human interphonatory breaths (Nonaka et al., 1999; Subramanian et al., 2008). In humans, vocalization is also associated with increased periaqueductal grey matter activity (Schulz et al., 2005). Speech is however a voluntarily initiated, modulated, and inhibited action that goes beyond vocalization and that requires elaborate cortical control (Bouchard et al., 2013). Of note, during human speech the periaqueductal grey matter exhibits strong connectivity with neocortical motor regions – medial and lateral premotor structures and elements of basal ganglia thalamocortical circuitry (Schulz et al., 2005). Prephonatory chest wall movements and inspired volumes required for “speech breathing” depend on the length and loudness of the subsequent utterance (McFarland and Smith, 1992; Sperry and Klich, 1992; Winkworth et al., 1995). This indicates anticipation and targeted movement preparation, hence the intervention of cortical processes.

The preparation of movement involves several premotor cortical regions including the supplementary motor area (SMA) (Nachev et al., 2008). The SMA has respiratory connections and plays a role in breathing control. Transcranial magnetic stimulation studies showed that SMA stimulation induces diaphragm responses (Sharshar et al., 2004). SMA conditioning can be associated with excitatory and inhibitory modulations of the corticospinal control of the diaphragm (Laviolette et al., 2013; Raux et al., 2010). Electroencephalographic studies show that voluntary inspirations give rise to movement preparation potentials that can be recorded over the vertex -Cz- (Macefield and Gandevia, 1991; Raux et al., 2007b). These pre-inspiratory potentials are likely to stem from a group of cortical structures that includes the SMA, as do their locomotor counterparts (Ball et al., 1999; Shibasaki and Hallett, 2006). Functional brain imaging has involved the SMA in voluntary breathing (McKay et al., 2003), and EEG data demonstrate the presence of pre-inspiratory potentials during tidal breathing in patients suffering from defective automatic breathing control when awake (Tremoureux et al., 2014). Finally, pre-inspiratory potentials and increased SMA brain oxygen level-dependent signal are also observed in response to inspiratory loading (Raux et al., 2007b, 2013).

Within this frame, we predicted that some of the speech-related breathing control activities, namely the preparation of large prephonatory breaths markedly differing from tidal breaths, would be associated with pre-inspiratory potentials.

2. Material and methods

2.1. Subjects

Ten healthy volunteers (four males and six females, age: 23–27 years) participated in the study. None of them had previously participated in a respiratory physiology or neurophysiology study protocol. None of them were actors, singers, wind instrument players, yogis, competition swimmers or divers, or free-divers. None were smokers. All subjects were free of heart, lung, neuromuscular or other disease and were not taking any long-term treatment. They were asked to refrain from alcohol and any psychoactive substances for 24 h prior to the experimental session and to avoid sleep deprivation. The study was approved by the appropriate ethical and regulatory authorities. All subjects gave their written informed consent to participate. Of importance, the subjects were unaware of the respiratory purpose of the study, which was only revealed to them post hoc with the possibility to withdraw consent.

2.2. Electroencephalogram

The electroencephalographic signal was obtained by means of a recording cap comprising 12 equidistant electrodes (ActiCap, Brain Products GmbH, Gilching, Germany), according to the conventional “10-20” topographic system, with a reference electrode on *FCz*. The signal was recorded with Recorder V-Amp software (Brain Products GmbH, Germany) at a sampling frequency of 2000 Hz, filtered between 0.01 and 5 Hz (Analyser, Brain Products GmbH, Germany), then stored for subsequent analysis.

2.3. Voice

The subject’s voice was recorded with a microphone (Micpro8, HQ Power, Nedis B.V., Netherlands) connected by a professional low-noise cable to the EEG and ventilation recording equipment in order to obtain synchronous signals.

2.4. Breathing pattern

The ventilatory pattern was recorded with a sampling frequency of 40 Hz by a respiratory inductance plethysmography vest (Visuresp, RBI, Meylan, France) consisting of a sleeveless elastic garment comprising copper wire coils placed around the chest and abdomen with a low voltage power supply (Eberhard et al., 2001). Stretching of the coils in response to breathing movements induces a variation of electrical potential proportional to the volume variations. A mathematical algorithm is used to reconstruct a flow signal that has been validated against a pneumotachographic airflow signal (Eberhard et al., 2001).

2.5. Experimental conditions and protocol

Subjects were seated comfortably in an armchair. They were first asked to perform a series of 100 voluntary sniffs at their own rate (“positive control”, expected to give rise to pre-inspiratory potentials, see Colebatch et al., 1991; Macefield and Gandevia, 1991; Raux et al., 2007b). Subjects then breathed quietly without constraint for 15 min (“negative control”: no electroencephalographic signal related to breathing was expected under these conditions, see Raux et al., 2007b). At a third step of the protocol, the subjects were asked to read out loud, by “projecting” their voice, a text drawn from a classical French play with which the subjects were culturally likely to be already familiar (Molière’s “Le Bourgeois Gentilhomme” Act III, Scene I until Act III, Scene VII, corresponding to a reading time of 15–20 min). Each subject was able to choose his or her own style of reading and volume.

From the three experimental conditions (“sniff”, “tidal”, and “speech”), four categories of inspirations were pre-defined for the purposes of pre-inspiratory potential identification and statistical analysis: tidal inspirations (quiet breathing), sniffs, small prephonatory inspirations (inspired volume similar to that of tidal inspirations in the concerned subject), large prephonatory

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