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CORTICAL ACTIVITY AND PHASES OF THE RESPIRATORY CYCLE *

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Brain functional states are determined by close interaction between (a) afferent signals and their evaluation by the sensory systems, including comparison with memory content, and (b) internal periodic changes of system state. The dramatic periodicity between sleep and wakeful states is well known, although still poorly understood. However, within major functional states which one may range on a scale of vigilance or consciousness levels, minor fluctuations are detectable. In the periodicity range of seconds, performance fluctuations are absorved which are correlated with phases of the respiratory cycle (1). Tendon reflexes (2) and sensory-motor performances (3) are most efficient during the inspiratory phase, and worst during expiration. To what extend are changes of cortical activity involved? Several authors reported on the correlation of occurrance of various cortical EEG events with phases of the respicatory cycle in animals and man (e.g. 4, 5, 6, 7, 8, 9). In a study on seven healthy volunteers (8) we demonstrated a relationship between amplitude of EEG alpha waves and respiratory cycle (Fig. 1). Alpha was lowest during inspiration, indicating increased arousal. This finding is in good agreement with the observation of lowered sensory threshold during low amplitude alpha (10), and with the observation of shortened reaction times during inspiration (reviewed above). The occurrance of EEG sleep spindles during inspiration (5) accordingly might parallel stimulus-induced sleep spindles after K-complexes.

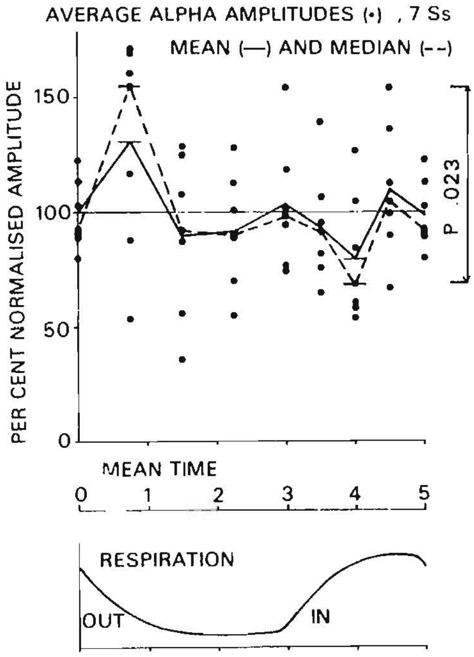

Fig. 1 Alpha EEG amplitude (upper half) during the respiratory cycle (lower half) in humans. The envelope of alpha amplitude was sampled at 8 points during the respiratory cycles (n = 80), and normalized between subjects (n = 7). Dots indicate values of individual subjects. Significance of difference between lowest and highest amplitude was tested with Wilcoxon test (from Lehmann, in preparation).

What are the mechanisms which connect respiratory and cortex EEG events? It is reasonable to assume that the periodic activity changes of the respiratory brain stem centers irradiate to the ascending reticular activating system, and thus modify cortical activity. We examined possible other routes in 54 acute and 8 chronic cat preparations (7, 8). Cortical augmenting responses to 5 - 7/sec chiasmatic stimuli, recruiting responses to repetitive centre median stimuli, spontaneous spindles, and Nembutal-induced spindles served as indicators of levels of cortical excitability and activity. The control of cortical function by afferent information about induced respiratory events can be demonstrated by lung inflation after interruption of the respirator in flaxidilized cats.

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The procedure triggers typical waxing of the augmenting responses (Fig. 2). The relationships between respiratory phases and cortical activity levels clearly persist in flaxidelized artificially ventilated preparations after disconnection of the vagus nerves, and after encephale isolé transsections (see also 6). Although brain stem centers may be the mediating structures in this case, conventional afferent pathways do not appear to be necessary.

The relations between respiratory phase and various EEG events continue to be detectable even after pretrigeminal cerveau isolé transsections. An example is

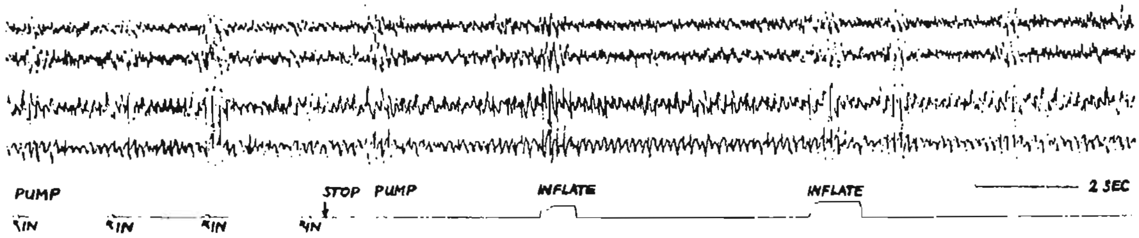

Fig. 2 Waxing of augmenting responses (to repetitive chiasmatic stimulation) induced by lung inflations after respirator stop (flaxidilized cat). Traces 1 & 2: right and left central EEG, traces 3 & 4: right and left occipital EEG. Time makers in 200 msec.

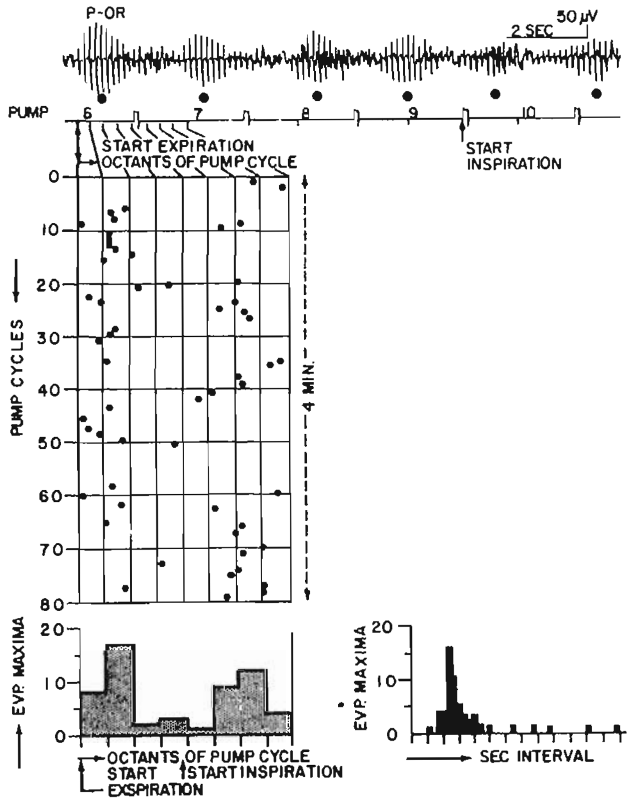

Fig. 3 Maximal amplitude of augmenting responses to 7/sec chiasma stimulation, related to inspiratory and expiratory phase of the artificial respiratory cycle in a pretrigeminal cerveau isolé cat (flaxidilized). Sample record with waxing and waning responses, maxima indicated by dots. Occurrance of maxima plotted as function of time in vertical graph, where time during pump cycle (octants) is horizontal. Sum of maxima occurrance during pump cycle at lower left. Lower right shows maxima intervals.

shown in Fig. 3. Since in this preparation, the telencephalon ist disconnected from the brainstem and all peripheral neural input (olfactory and visual were blocked), we conclude that there are pressure-sensitive elements in the telencephalon which sense respiratory movement via respiration-induced changes of CSF and/or blood pressure.

After pump stop, waxing and waning of EEG events continues. Thus, there is an inherant peridicity of EEG phenomena, independent of respiration. This periodicity may be pulled into an approximate relation with certain respiratory phases in the sense of von Holst's "relative correlation" (11).

There is also an external feed-back route which may contribute to respiratory control of cortical activity: air flow through the nose triggers high frequency (30-50 Hz) olfactory bulb spindles, which can be recorded also from many rhinencephalic areas (12). The rhinencephalon may serve as mediator between respiratory phase and cortical function.

Feed-forward from respiratory centers, internal neural and pressure feed-back, and external air flow feed-back thus provide several routes which contribute to the demonstrated influence of respiratory phase on cortical and behavioral function. It is important that the (basically automatic) respiratory activity can be modulated by voluntary action. Therefore, willed changes of respiration can influence cortical activity, and thereby consciousness. Such observations may well have been the basis of the respiratory exercises which are included in many classical techniques for mental training.

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