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SUMMARY The time of appearance of an EEG-pattern typical of anaesthesia was correlated with the time of appearance of increased motor activity usually seen during CO₂-exposure. Both 80% and 95% CO₂-concentration were used. The most prominent finding of these studies was that an EEG (electroencephalogram)-pattern typical of anaesthesia had developed in all swine a few seconds before the appearance of increased motor activity, indicating that the swine were unconscious before the appearance of the increased motor activity.

The effects of CO₂-inhalation were also studied after amygdectomy. The bilateral destruction of this, for emotional reactions essential part of the brain, did not visibly change the time of appearance, the duration, and the strength of the muscular reactions.

After 15 seconds of CO₂-exposure, pronounced arterial hypercapnia, hypoxia and acidemia had developed. These dramatic changes in the blood-gas parameters and blood pH were incompatible with consciousness.

The integrated result of these studies suggests that the increased motor activity temporarily observed during CO₂-exposure is a manifestation of neocortical disinhibition of subcortical motor centres.

INTRODUCTION In the ethical debate of pre-slaughter CO₂-anaesthesia in swine, the occurrence of increased muscular activity has been under discussion for many years. A crucial question has been if the increased motor activity is a manifestation of emotional stress or occurs first when the animals are unconscious. The uncertainty on this point has stimulated research on behavioural, neurophysiological and systemic effects of high concentration CO₂-exposure. In a recent study (FORSLID, 1987) it was demonstrated that a neocortical pattern typical of anaesthesia precedes the appearance of increased motor activity during exposure of swine to 80% CO₂ under laboratory conditions. In this situation a slow-wave EEG pattern, typical of anaesthesia appeared some seconds before the jerks were observed, about 25 s following start of CO₂-exposure. However, during slaughter-house CO₂-exposure the transient motor activity usually appears earlier, after about 15 s of CO₂-exposure. A possible explanation for this discrepancy might be that the animals usually are exposed to a CO₂-concentration higher than 80% during slaughter house conditions.

The results, presented in this paper include behavioural and EEG studies in swine during one minute exposure to 95% CO₂, under laboratory conditions, and a comparison between normal and amygdectomized animals during one minute exposure to 80% CO₂.

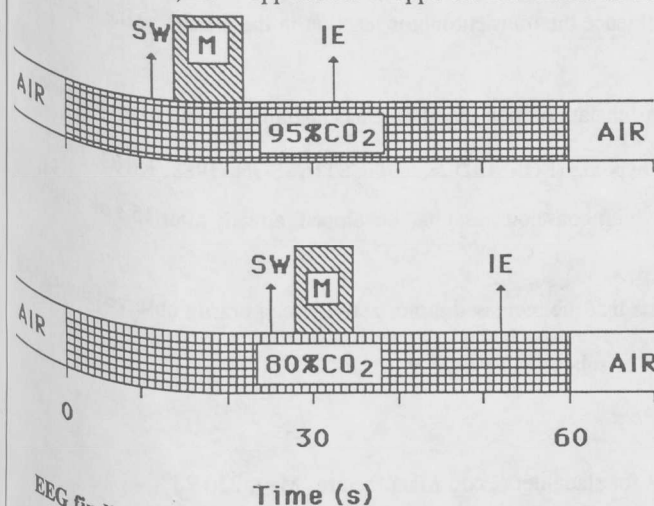
MATERIALS and METHODS EEG: Four Yorkshire swine (body wt 50-60 kg) were used. Electrodes for recording of the EEG were mounted bilaterally over the neocortex. The four animals were exposed to 95% CO₂. Two of the animals were exposed twice with an interval of two days. For technical reasons the remaining two animals were subjected to one exposure only. During continuous recording of the EEG the animals were emersed into 95% CO₂ for one minute. For details regarding anaesthesia, surgical procedures, EEG recording, and exposure technique, reference is made to our earlier papers (FORSLID, 1987, FORSLID *et al.*, 1986, FORSLID & AUGUSTINSSON, 1988).

Amygdectomy: Six Yorkshire swine (body wt ~ 50 kg) were exposed to 80% CO₂ for one min. Three weeks following bilateral radiofrequency destruction of the amygdaloid region of the brain the animals were again exposed to 80% CO₂. During the two exposures the animals were filmed for later assessment of time of appearance, and strength of the increased motor activity (FORSLID *et al.*, to be published). The success of the amygdectomy was controlled by monitoring the levels of catecholamines in the blood before, during and after restraint stress. A histological examination was also performed to verify the result of the amygdectomy.

RESULTS and DISCUSSION Behavioural observations: During the one minute exposure to 95% CO₂ all animals exhibited more or less pronounced motor activity after a latency of 15.3 ± 1.4 s. This temporary period had a duration of 8 ± 1 s (Fig. 1, upper part). At the end of the latter period all swine took a recumbent position and appeared entirely reactionless.

Fig. 1. Illustration of the time relations (mean values) between the periods of motor reactions exhibited by the swine during one minute CO₂-inhalation and obvious changes in the simultaneously recorded neocortical EEG.

Upper part: exposure to 95% CO₂, Lower part: exposure to 80% CO₂, SW = appearance of slow wave neocortical activity, M = motor reactions, IE = appearance of apparent neocortical isoelectricity (FORSLID, 1991).



EEG findings: In all experiments the brief period of increased motor activity was preceded by a change of the desynchronized neocortical EEG (typical for the waking state) into a slow-wave pattern. This change became obvious after a latency of 11.8 ± 0.3 s. After a transient accentuation, the slow-wave pattern gradually faded out and the EEG became flat indicating neocortical isoelectricity. The apparent isoelectricity became manifest 34 ± 2 s after the start of the CO₂-exposure (Fig. 1, upper part). This was about 20 s earlier than in the previous experiment with 80% CO₂ (FORSLID, 1987) (Fig. 1, lower part). For further details regarding the EEG patterns mentioned see FORSLID (1987, 1991).

Amygdalectomy: The analysis of the videofilms taken during CO₂-exposures in swine before and after amygdalectomy did not reveal any differences in the time of appearance, the duration, and the strength of the motor activity between the two experimental series (FORSLID *et al.*, to be published).

It has recently been shown in swine exposed to 80% CO₂ for one minute under laboratory conditions (FORSLID, 1987) that a neocortical EEG pattern typical of the 2nd stage of anaesthesia (PICHLMAYR *et al.*, 1984) occurred a few seconds before the appearance of increased motor activity. It implies that the swine were anaesthetized when the jerks appeared. The motor reactions were interpreted as due to a release phenomenon (FORSLID, 1987). Thus, a likely explanation is that subcortical motor centres may be less rapidly inactivated by severe hypercapnia and hypoxia than neocortical structures, which normally exert an inhibitory effect upon subcortically initiated involuntary movements. Such a release phenomenon has been suggested as the cause of the motor signs that can be seen during the 2nd stage of anaesthesia in humans (PICHLMAYR *et al.*, 1984).

Under slaughter-house conditions the brief period of increased motor activity usually appears about 15 s after start of the CO₂-exposure (BLOMQUIST, 1957, CANTIENI, 1976, HOENDERKEN *et al.*, 1979). This is about 10 s earlier than during inhalation of 80% CO₂ under laboratory conditions (FORSLID, 1987). In Fig. 1 it is demonstrated that an increase in CO₂-concentration from 80% to 95% shortened the latency for the appearance of the slow-wave pattern in the EEG and the jerks by about 10 s. However, a change in the EEG indicating anaesthesia still preceded the period of increased motor activity by some seconds. Hence, a release of subcortical motor centres

from a neocortical inhibition seems to be the most likely explanation also for motor jerks observed during slaughter-house conditions (FORSLID, 1991).

The cerebral amygdaloid nuclear complex, has been found to be responsible for mediation of anxiety and other emotional reactions. It has been shown that bilaterally amygdalectomized pigs do not exhibit any release of adrenalin and noradrenaline during stress (JOHANSSON *et al.*, 1982). If the increased motor activity usually seen under CO₂-exposure was a result of emotional stress an ablation of the amygdaloid nuclear complex (amygdalectomy) would be expected to change the behaviour of the swine during CO₂-exposure. However, the fact that a bilateral amygdalectomy did not visibly influence the transient motor reaction in the present swine supports that the reaction is unconscious and due to a release phenomenon.

Previous studies regarding the effect of high concentration CO₂-inhalation upon blood acid/base parameters and oxygen tension demonstrate a rapid development of acidemia, hypercapnia as well as hypoxia (FORSLID & AUGUSTINSSON, 1988, RING, 1988). These dramatic blood chemical changes (all seemingly incompatible with consciousness) had developed already after 15 s of inhalation (FORSLID & AUGUSTINSSON, 1988).

CONCLUSIONS The integrated result of these studies suggests that the increased motor activity temporarily observed during CO₂ exposure is an unconscious manifestation of neocortical disinhibition of subcortical motor centres.

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