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Preface

Thalamo-cortical relations in attention and consciousness ☆

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The spontaneous rhythmic activity in the brain, known as the alpha rhythm, was discovered and described by Hans Berger at the end of the 1920s. Technical developments during World War II made the recording of the electro-encephalogram (EEG) a routine affair in most hospitals during the following decades. Psychologists interested in the psychophysiological aspects of human behavior started to use the EEG as a tool for their investigations. First, only the spontaneous activity was investigated; later the recording of event-related potentials (ERPs) became possible, thanks to the development of computer systems. In the beginning, the electrophysiological measures were mainly used as markers. In case an ERP showed a change in condition A, but not in condition B, the ordinary psychologist was happy to have found a psychophysiological index for a difference between conditions. The origin of the ERP, that is, the brain structure in which the ERP was generated, was not his or her main concern. After all, psychologists were interested in so-called 'higher' processes, and it was sufficient for them to be involved in recording indications of such processes. Since biophysicists have demonstrated indeed that the EEG is, for the main part, a reflection of cortical processes, they provided an argument for psychologists to continue their work as usual. Yet physiologists knew for a long time that the surface EEG depends upon a crucial input from subcortical brain areas. For our understanding of what really goes on in the brain, we have to accept that many subcortical structures are contributing to what we measure at the skull. In order for our work to remain serious, we have to take into account these contributions. Since the development of the single cell recording technique, it became possible to relate the ERPs recorded in the skull to unit activity recorded in very circumscribed brain areas. The spatial precision of unit recordings is absent in the human EEG, but both have the advantage of measuring brain activity in the milliseconds domain. That remains an important aspect in future research, notwithstanding the fact that new imaging techniques (PET, fMRI) have become very important tools for the analysis of behavior, with an admittedly good spatial resolution.

^{*} The present issue of the *International Journal of Psychophysiology* consists of six papers presented at a meeting on *Thalamo-Cortical Relations in Attention and Consciousness* held in October 2000 at Tilburg University. The meeting was supported by the Netherlands Organization for Scientific Research (NWO, Social and Behavioural Sciences), and the Faculty of Social and Behavioural Sciences of Tilburg University.

For all contributors to this symposium it was clear that subcortical structures play an important role in the organization of attention. Writing about thalamo-cortical circuits implies that major inputs from cerebellum and basal ganglia have to be taken into account too. Although 'everybody knows what attention is', to cite the classic William James (1890), there is still sufficient unclarity to continue writing books on this very topic, or to organize a symposium.

The first contribution of David LaBerge is a good example of what I said above. His triangular theory tries to explain the structure of attentional behavior, by taking into account both cortex and thalamus. Since in general, attention is directed to our sensory environment, it is clear that only the sensory nuclei of the thalamus are discussed. The pulvinar is the major node in his triangular networks. Attention is discussed as attention for visual stimuli. Whether or not the other modalities fit into the same framework, has still to be demonstrated. The most important part of his contribution is his claim that for a sustained attention, sufficient time is needed (in the order of 1-2 s) and that the pathway via the thalamus (pulvinar) is needed to realize that. A further extension of his theory (LaBerge, 1995) in the present paper is the underlining of the length of the apical dendrites in relation to that of the basal dendrites. He suggests that the very length of the apical dendrites hampers their possible influence upon the cell bodies they belong to. He suggests that processes in these fibers might be related to consciousness. Measuring consciousness, if at all possible, has puzzled many investigators; LaBerge knows that at present, there is no direct evidence for his statement. Yet as a 'consideration of design', he argues that the phylogenetic thickening of the cortex due to the lengthening of the apical dendrites, is in agreement with his opinion.

In the next contribution Piotr Syffczinsky et al. describe a model of thalamo-cortical networks in relation to the dynamic control of alpha rhythm in relation to focal attention. Their model tries to describe thalamo-cortical circuits much more specifically, because actual neurophysiological signals and changes in rhythmicity were imple-

mented, instead of the more abstractly defined nodes in the model of LaBerge. The model was designed to account for the discovery of Pfurtscheller and Neuper (1994), that the eventrelated desynchronization (ERD) of the 10-Hz activity over a target area is accompanied by an event-related synchronization (ERS) in the neighborhood. The authors were able to model the focal ERD / surround ERS found by Pfurtscheller and Neuper (1994) and confirmed the importance of a thalamic contribution for the emergence of both ERD and ERS. This is the more interesting if one realizes that Fernando Lopes da Silva considered in his earlier work the cortical sources of the alpha rhythm more important than the thalamic sources (Lopes da Silva et al., 1980). This suggests that although the spontaneous alpha rhythm might be generated in the cortex, its attentional modulation could be based upon thalamo-cortical processes. Finally, it should be noted that in an earlier modeling study of LaBerge et al. (1992) arguments were found for an enhancement of activity in target units and an inhibition of activity in distracter units, reminding the results of the modeling study of Piotr Syfficzinsky et al. in this issue.

The contribution of Christa Neuper and Gert Pfurtscheller shows that ERD/ERS analysis holds for both the motor and the sensory system, although the majority of their work is aimed at analysis of synchronization and desynchronization in the motor system. In their recent work they are interested in motor imagery, and in line with findings of others their data suggest that the imaging of a movement seems to activate the same structures as the execution of the actual movement. In the sensory domain there is a problem, though, since if one imagines that a certain stimulus will show up, there is no ascending input from the sense organs to the crucial cerebral structures. In other words the cortex and the thalamus have to be activated from elsewhere. It has to be demonstrated which structures play a major role, and whether the underlying processes are cortical, subcortical or both.

Kees Brunia and Geert van Boxtel continue a line of thought that started in 1992 with a paper of Brunia (1993). Based upon the work of Yingling and Skinner (1977) and Skinner and Yingling (1977) the model of selective intermodal attention was expanded to the motor system. The use of the time estimation paradigm with feedback about a past performance made it possible to separate the preparation of the movement from the anticipatory attention for the imperative stimulus. Recently a modality-specific effect upon the potential distribution of the stimulus preceding negativity (SPN) was found, which asks for an extensive replication with a high density EEG recording, especially since that effect has not always been found in our SPN studies. Compared to the ERD/ERS it seems that the slow potentials have a less well-defined spatial resolution. This too should be investigated further. Brunia and van Boxtel know the recent suggestion of Lamme and Roelfsema (2000) that attention is an affair of re-entrant fibers from 'higher' to 'lower' cortical visual areas. In their proposal the thalamus is not needed. This too asks for further research. The conditions should be defined under which pure cortical activation should be sufficient and under which other conditions the thalamus is needed as well.

Koen Böcker et al. continue their SPN studies in line with an earlier source localization study (Böcker et al., 1994) in which they came up with a possible contribution from the Insula Reili to the SPN, recorded prior to the presentation of a Knowledge of Results (KR) stimulus. Both this localization and the motivational interpretation of the effect of KR stimuli suggested to these authors the existence of a special class of SPN. Their recent experiments combined the use of the startle reflex with the recording of an SPN prior to a threat stimulus. This is an interesting combination because the modulatory pathways upon the startle reflex circuit are for a large part known and since the work of LeDoux (1996), we know that visual emotional stimuli do not have to be processed via the known ventral and dorsal routes to activate the Nucleus Amygdalae. Given the efferent pathways from the amygdala, the authors speculate that the SPN prior to a threat stimulus might be brought about outside a thalamic influence. That statement has to be underpinned further of course, because the authors realize too that there is a connection via the dorsomedial nucleus to the anterior cingulate gyrus.

Marcel Bastiaansen's thesis (Bastiaansen, 2000) analyzed anticipatory attention with the ERD/ERS technique in time estimation paradigms with KR stimuli. The epoch prior to the presentation of the KR stimulus was analyzed, using three different KR modalities. The visual data are clear; there exists indeed, an anticipatory ERD over the occipital areas. Preceding auditory stimuli only the MEG showed in two out of five subjects, a clear ERD. Preceding somatosensory stimuli, a weak indication of a similar process was found. In the latter case, a high resolution EEG will show the results more clearly. The interpretation of the results of Bastiaansen and Brunia is that the anticipatory attention is generated in the prefrontal cortex and that from there, the different thalamo-cortical channels are activated in such a way that the focal ERD / surround ERS is generated. However, this point of view was criticized by Piotr Syffczinsky et al. who noted that the results do not show any similar activation over the prefrontal cortex. In our opinion, the sustained negativity recorded over the frontal cortex in most experiments, suggest that the prefrontal cortex is involved indeed. In order to settle this issue, it should be interesting to implement the prefrontal cortex in a still newer version of the model, presented by Syffczinsky in this issue.

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