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Theta phase locking across the neocortex reflects cortico-hippocampal recursive communication during goal conflict resolution

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Abstract

EEG theta coherence, EEG theta power and subjective levels of response were examined in a continuous monitoring target detection task where periodic goal conflicts were introduced as 34 participants progressed through a stimulus sequence leading to response. EEG theta coherence revealed increases in phase locking between cortical areas at specific task stages involving goal conflict. Theta power also increased at points of goal conflict. The temporal characteristics of subjective response (measured continuously throughout the task) indicated a delay between participants actually experiencing goal conflict and overt indications of conflict. The starting point for the study was based on a specific aspect of Gray and McNaughton's [Gray, J.A., McNaughton, N., 2000. The Neuropsychology of Anxiety: An Enquiry into the Functions of the Septo-Hippocampal system, 2nd ed. Oxford University Press, Oxford] *behavioural inhibition system* model—namely, *septo-hippocampal system involvement in the resolution of goal conflicts*. We drew on Gray and McNaughton's [Gray, J.A., McNaughton, N., 2000. The Neuropsychology of Anxiety: An Enquiry into the Functions of the Septo-Hippocampal system, 2nd ed. Oxford University Press, Oxford] suggestion that septo-hippocampal involvement in this process is reflected by EEG theta. While their theory explains many of our findings, we also drew upon Given's [Givens, B., 1996. Stimulus-evoked reseting of the dentate theta rhythm: relation to working memory. Neuroreport 8 (1), 159–163] proposal that the dentate theta rhythm is reset by behaviourally relevant stimuli. We made further proposals based on Makeig et al.'s [Makeig, S., Westerfield, M., Jung, T.-P., Enghoff, S., Townsend, J., Courchesne, E., Sejnowski, T.J., 2002. Dynamic brain sources of visual evoked responses. Science 295, 690–694] view that specific stimulus events invoke concurrent phase resetting and transient frequency domain coherence across different areas of neocortex. Relations with Go/NoGo event related potentials (P300 and N2; e.g., [Bokura, H., Yamaguchi, S., Kobayashi, S., 2001. Electrophysiological correlates of response inhibition in a Go/NoGo task. Clin. Neurophysiol. 112 (12), 2224–2232]) were also discussed, as well as parallels between our data and interpretation, and other theoretical models of theta (e.g., [Kahana, M.J., Selig, D., Madsen, J.R., 2001. Theta returns. Curr. Opin. Neurobiol. 11, 739–744]). Suggestions for further research were made.

Keywords: Septo-hippocampal system; Goal conflict; Theta power; Theta coherence

1. Introduction

In many real life situations we are required to either respond or withhold response. Such situations involve conflict, in which excitation and inhibition are opposed. The theoretical basis for the present study is the elaborate neurological system controlling motor behaviour during approach and avoidance described by Gray and McNaughton (2000).

Drawing on the behavioural effects of experimental lesions and administration of anxiolytic drugs, Gray and McNaughton (2000) place special emphasis on the septo-hippocampal system. As potential threats are approached, the special role of the septo-hippocampal system is to resolve goal conflicts. The septo-hippocampal system assesses current goals, detects conflicts in cases where other possible goals become active, inhibits behaviour, and then acts to resolve the goal conflict.

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Information received by the hippocampus from brain areas involved in coding goals provides a basis for the detection of concurrently active goals. When information is received about only one goal the hippocampal formation stays in *just checking* mode, but when information is received about a second goal, and a conflict is detected, it switches to *control* mode. In control mode hippocampal formation output consists of information return to the brain areas associated with the two conflicting goals. This process is supported through recursive loops operating between the septo-hippocampal system and brain areas supporting each side of the conflict. The recursive loops represent a cyclical series of calculations.

The idea of recursive communication between the septo-hippocampal system and the neocortex was first proposed by Miller (1989). The aim was to explain the ability of neurons to make sufficient connections when global cell assemblies need to be formed in order to represent different large-scale environments. Loops of connectivity between the hippocampus and the neocortex, resonating at the frequency of the hippocampal theta rhythm, overcame this problem by carrying neural activity associated with the definition of global cell assemblies (Miller, 1989).

In the model of Gray and McNaughton (2000), through increasing the valence of aversive effects of each of the goals contributing to the conflict, the system progressively increases bias towards one or the other, by suppressing alternative goals, until one goal reaches sufficient prominence to take control. They claim that the discreteness of distinct recursive cycles is maintained through theta frequency, and more specifically, by phase locking. This theta phase locking ensures that inputs from all of the different recursive loops are dealt with concurrently by the various hippocampal comparators, on a consistent basis. Since, this invokes concurrent phase locking between the septo-hippocampal system and distinct areas of neocortex, we have extended this view and speculate that areas of the neocortex should become phase locked in time with each other. Reflecting this, we also take the view that there should be a more orderly neocortical phase structure when the septo-hippocampal system is engaged in resolving goal conflicts, measurable in the degree to which neocortical areas are phase locked with one another. This is an extension of the Gray and McNaughton view regarding phase locking between the septo-hippocampal system and the neocortex but one that we feel has a natural, logical progression.

Gray and McNaughton (2000) place key emphasis on theta activity. They report that theta activity in the hippocampal formation (controlled by pacemaker impulses from the medial septum whose frequency is set by input received from supra-mammillary, hypothalamic nuclei) is an important element in the septo-hippocampal system. Gray and McNaughton were primarily referring to hippocampal theta measured from rodents. In addition, rodent hippocampal theta activity described by Gary and McNaughton was frequently recorded at up to 12 Hz (and actually above 12 Hz in some cases). However, we believe that EEG theta provides the link with human work though it would be premature to assume that human theta activity is the natural analogue of hippocampal theta recorded from rodents. Human theta activity is largely recorded from scalp electrodes, rather than from electrodes implanted in the hippocampus, and typically falls within the lower range of 4–7 Hz. Functional identity between animal and human theta can only be implied where recordings have been made directly from the human hippocampus. Some studies have attempted this and there is some evidence to suggest that theta activity recorded from the human hippocampus oscillates at the same frequency as that traditionally associated with human EEG. For instance, Sano et al. (1970) made direct recordings from the human hippocampus and careful scrutiny of their Fig. 9 shows that hippocampal theta (at 7 Hz) was within the range typically associated with human EEG. Also, Meador et al. (1991) reported differential theta (4–7.75 Hz) response in a task where data were recorded from deep electrodes implanted in the hippocampus of epileptic patients.

Though these data do not strictly confirm that theta activity recorded at the scalp is definitely derived from hippocampal theta activity in humans, they provide evidence that hippocampal theta in humans does coincide with the waveband that has traditionally been associated with human theta activity recorded in the superficial EEG. For this reason, and given the diffuse connections between the hippocampus and the neocortex, our view is that a proportion of theta activity recorded at the scalp is an analogue of hippocampal theta. In the current study we take this view in determining which waveband of the superficial EEG would most likely bear fruit in seeking a physiological indicator of recursive processing during goal conflict resolution, mediated by the septo-hippocampal system.

1.1. Phase-locking and coherence analysis

Coherence analysis is derived from standard EEG recordings and is non-invasive, so it is well suited to studies with human participants. Coherence analysis is an effective way to describe spectral phase at specific electrodes with respect to spectral phase at other electrodes and thus describes coupling (or phase locking) of neocortical cell assemblies (Nunez, 1995). Since spectral power values at specific electrodes are normalised by cross power spectra associated with pairs of electrodes being compared, effects due to differences in power levels associated with lack of topographical homogeneity are eliminated. In essence, coherence analysis is a methodology that is purely concerned with the degree to which two EEG signals show phase synchronisation at specific task stages.

Previous studies where theta coherence has been investigated have often focused on theta's apparent link with working memory operations during cognitive tasks. Sarn-