EEG CORRELATES OF LEARNING IN CLASSICAL EYEBLINK CONDITIONING IN HUMANS

Emmi Rantanen
Pro gradu –tutkielma
Psykologian laitos
Jyväskylän yliopisto
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Ihmisten välillä on suurta vaihtelua oppimissuorituksessa klassisen ehdollistumisen tehtävissä laboratoriokokeissa. Erot kognitiivisissa kyvyissä voivat selittää osan vaihtelusta, mutta luultavampaa kuitenkin on että vaihtelu ihmisen sisäisessä vireystilassa aiheuttaa hajontaa oppimiskyvyssä. Tutkimuksessamme opetimme ihmisiä silmäniskuehdollistamisessa ja mittasimme ihmisten spontaania jatkuvaa aivosähkökäyrää silmät auki/kiinni –tilanteissa opettamisjaksojen välissä. Tarkkailimme erityisesti theta- (3 – 8 Hz) ja alfa- (9 – 13 Hz) taajuuksia nähdäksemme, selittääkö toinen näistä ihmisten välisiä suorituseroja. Theta-aktiivisuus liitetään usein oppimis- ja tiedonkäsittelyprosesseihin sinänsä, kun taas alfa-taajuuden väistyminen silmät avattaessa (alpha blocking) liittyy vireystilaan vaihteluun. Kokeessamme hyvien ja heikkojen oppijoiden välillä oli suuri ero suorituksessa. Hyvillä oppijoilla alfa-taajuuden väistyminen pysyy tasaisena koko kokeen ajan, kun taas heikoilla oppijoilla alfan määrä silmät auki –tilanteessa oli lähes yhtä suuri kuin silmät kiinni –tilanteessa kokeen loppupuolella. Tämä tarkoittaa siis sitä, että hyvillä oppijoilla vireystila pysyy korkeampana kuin heikoilla oppijoilla. Theta-aktiivisuudessa hyvillä ja heikoilla oppijoilla ei ollut tilastollisesti merkitseviä eroja. Näyttäisi siis siltä, että ihmisen sisäisen vireystilan muutokset vaikuttavat oppimiseen tämän kaltaisissa tehtävissä.

There are big differences in learning between subjects in classical conditioning in laboratory experiments. These differences can be explained by variation in the cognitive abilities or in the inner state, such as in arousal, of individuals. In our study we recorded the EEG of subjects during classical conditioning. Especially, we examined the theta (3 – 8 Hz) and alpha (9 – 13 Hz) frequencies in order to see if one of them could explain the differences between subjects. Theta-band activity is usually connected with cognitive functions, whereas alpha blocking response to eye opening refers to the state of arousal. In our study, there was a great difference between the group of good and the group of poor learners in their performance. In the group of good learners, the amount of alpha blocking stayed at the same level throughout the whole experiment, whereas in the group of poor learners, the amount of alpha was nearly as big in the eyes open condition as in the eyes closed condition in the end. In other words, the state of arousal stayed higher in the group of good learners than in the group of poor learners as time passed by. There were no statistically significant differences in the amount of theta between the two groups. All in all, it seems that the changes in the mental alertness affect learning in conditions like these.

Avainsanat: klassinen ehdollistuminen, theta, alfa, vireys

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INTRODUCTION

Human eyeblink classical conditioning provides a useful paradigm for examining learning. Although it is a motor skill, there are cognitive processes modulating the learning rate. In our previous study, we found that the relative magnitude of pre-existing theta-band (3-9 Hz) EEG activity predicts learning rate in subsequent human trace eyeblink conditioning (Rantanen, 2008). In classical conditioning, a conditioned stimulus (CS, usually a tone) is followed by a biologically significant unconditioned stimulus (US, a mild airpuff directed towards the eye). At first, the CS does not cause any behavioral response whereas the unconditioned stimulus (US) elicits a reflexive eyeblink (unconditioned response, UR). After repeated pairing of the CS and US, the CS begins to elicit a conditioned response, a tone-evoked eyeblink before the onset of the US. In *delay* conditioning, the CS co-terminates with the following unconditioned stimulus (US), whereas in *trace* conditioning the stimuli are separated by a brief silent interval. Delay conditioning is suggested to be unrelated to awareness, whereas for the trace conditioning, awareness of the connection between the CS and the US is required (Clark & Squire, 1999) because learning is not automatic or reflexive due to the trace interval (Clark, Manns & Squire, 2001). Thus, trace classical eyeblink conditioning requires declarative memory, which is dependent on the hippocampus (Manns, Clark & Squire, 2000). On the contrary, delay eyeblink conditioning is hippocampally independent (Knuttinen, Power, Preston & Disterhoft, 2001).

Frequency distribution of spontaneous EEG can be used to monitor subject's state and its effects on cognitive performance. The relative amount of oscillatory activity of different frequency bands can be linked to different psychological states and phenomena. In the context of learning and memory trace formation, the theta-band oscillation (3 – 8 Hz) has been found important in storing new information (Gluck, Mercado & Myers, 2007), in the coordination of neuronal networks (Buzsáki, 2002) and in enhancing a slowly developing plasticity of hippocampal neurons, which may help the subject to learn faster (Griffin, Asaka, Darling & Berry, 2004). Also, increased hippocampal theta activity recorded with intracranial electrodes implanted on epilepsy patients during successful encoding predicts recall (Sederberg, Kahana, Howard, Donner & Madsen, 2003). Berry and Thompson (1978) studied the spontaneous hippocampal EEG activity of rabbits immediately before classical conditioning and found a predictive relationship between theta activity and the rate of learning. Even though the exact structures responsible for generating theta oscillations are still unclear, it has been established that the medial septum/diagonal band of Broca and the hippocampus are the main structures involved (Buzsáki, 2002). It has also been suggested that the human scalp EEG theta might reflect the interaction of the hippocampus and related cortical areas (Miller, 1991). All in all, theta band activation is mostly connected with cognitive modulation.

On the other hand, simple arousal may affect learning. Alpha oscillations (9 – 13 Hz) have been traditionally connected with a relaxed state. They can be detected on anyone sitting quietly with eyes closed but as soon as the eyes are opened or the subject becomes mentally or physically active, the alpha activity disappears or at least decreases to the degree that the subject is alert (e.g. Chen, Feng, Zhao, Yin & Wang, 2008). This phenomenon, first discovered by Berger (1929), is called alpha blocking. Alpha oscillations have been thought to reflect idling and to occur especially during the default mode brain state (Raichle & Snyder, 2007). However, today, alpha frequency band oscillations are thought to be important also in cognitive processes, for example in attention, working memory and consciousness (Palva & Palva, 2007). Alpha synchronization occurs during mental inactivity and blocks information processing because great populations of cortical neurons oscillate synchronously (for a review see Klimesch, 1999). In contrast, alpha desynchronization reflects cognitive processes as the neuronal networks start to oscillate with different phases and frequencies. Chen et al. (2008) suggest that these changes from eyes closed to eyes open state are intrinsic. It has been assumed that there is a distributed alpha system rather than a unique source (Basar, Schürmann, Basar-Eroglu & Karakas, 1997). All in all, alpha rhythm, and its modulation as a function of extent of visual input, can be considered an index of the subject’s vigilance state (Karakas, 1997).

Given that different oscillations are involved in different states, this leads to the question of whether there is a difference between good and poor learners in their oscillatory activity in classical conditioning. The purpose of our study was to examine the connection between EEG indexes of attentions and learning. Especially we wanted to see if there were any factors predicting learning. Our hypothesis is that good learners, that is, the participants who learn the CS-US connection faster, also have a stronger theta ratio in the beginning than the poor learners. A connection between learning in classical conditioning and theta oscillations has already been verified (Berry & Seager, 2001, Berry & Thompson, 1978, Seager, Johnson, Chabot, Asaka & Berry, 2002, Sederberg et al., 2003). Furthermore, it may be that theta is a sign of increased attention towards the critical events/objects in the subject’s environment, which can lead to better performance in tasks such as trace conditioning (Griffin et al., 2004). If the subject pays more attention to learning relevant features in the surroundings in the beginning of the session, he/she learns faster, in other words, a greater amount of spontaneous theta oscillation could improve the learning rate by indicating participant’s selective attention towards the stimuli in the experiment (Nokia, Penttonen & Wikgren, 2010). Alternatively, state of general arousal, as indexed by the degree of alpha blocking, could be related to learning performance. In this case good learners should have stronger alpha blocking.

METHODS

Participants and recording

The participants were volunteers between 19 and 30 years. They were both men and women. The data was collected during the autumn of 2009 and the measurements were done in the laboratory of the University of Jyväskylä. EEG data was recorded while participants were seated in a comfortable chair doing nothing for about 45 minutes. A 21 channel cap with Ag/AgC1 cup electrodes was used to record the EEG from scalp electrodes (Fp1, Fp2, Fz, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T3, T4, T5, T6, Cz, FPz, Pz, Oz). All recording electrodes were referenced to linked mastoids and an electrode on the forehead was used as the ground. Signals were sampled at a 1000Hz sampling rate.

Conditioning

To obtain baseline EEG indexes, six minutes of spontaneous activity was measured in the beginning. The subjects were instructed to keep their eyes open for 3 minutes and closed for 3 minutes in random order. The instructions were written on a computer screen and a brief tone signaled the moment when eyes were to open. During the eyes open condition, participants were instructed to visually fixate on a small cross below the computer screen. Then nine CS-tones were presented alone at 15 to 25 s intervals. The CS was a 85-dB tone delivered through a speaker placed above the subject. The conditioning session consisted of five blocks of nine trials. Each block was preceded by a 6 minute period (3 minutes eyes closed and 3 minutes eyes open in random order) of measuring the spontaneous activity.

We used the long delay paradigm with a 1100 inter stimulus interval. The CS was presented for 1200 ms. The US was a 100 ms airpuff of 0.5 bar in source pressure to the corner of the right eye. The airpuff was delivered through a vinyl tube attached to goggles. Eyeblink responses were measured with EMG electrodes placed below the right eye. In the end, a trial of nine CS alone was presented again preceded by a six minute period of measuring the spontaneous activity as described earlier. The intertrial interval (ITI) was between 15-25 seconds, with the average being 20 seconds.

Statistical analysis

Behavioural data

The subjects were divided in two groups, good and poor learners, on the grounds of the CR percentage in the fifth conditioning block (20 participants with the least and 20 participants with the greatest amount of CRs). A repeated measures analysis of variance (ANOVA) was used to examine the differences in the CR percentages between the two groups and/or across conditions (eyes open/closed) across the seven blocks of nine trials.

EEG data

EEG data were averaged in 3 regions: frontal (Fp1, F3, F7, Fz, Fp2, F4, F8), central (T3, C3, Cz, T4, C4) and posterior (T5, P3, O1, Pz, T6, P4, O2).

Alpha

By monitoring the EEG signal, we searched for interference-free periods from all the six-minute periods of spontaneous eyes closed and eyes open activity. To determine the relative power of alpha activity during these periods, Fast Fourier Transform was run on them using a Hamming window. – Then the power of alpha (9-13 Hz) and the power of the surrounding frequencies (delta: < 4 Hz, theta: 4-8 Hz, beta: 14-29 Hz) were calculated. Next, the alpha ratio was determined by dividing the power of alpha activity by the sum of the power of alpha and the power of the surrounding frequencies and multiplying it by 100 ((alpha/(alpha+reference))*100). The alpha ratio shows the percentage of alpha (9-13 Hz) of the power of the whole band. The mean alpha ratio values of each group of channels (frontal, central, posterior) were determined separately for each subject. Then the alpha blocking was calculated by dividing the alpha ratio of the eyes open period by the alpha ratio of the eyes closed period and by multiplying this by 100 ((alpha ratio eyes open/alpha ratio eyes closed)*100). A repeated measures of analysis (ANOVA) was used to study the amount of alpha blocking in the two groups in the posterior region (Chen, Feng, Zhao, Yin & Wang, 2008). A general linear model was used to study the effect of the segment, that is, the effect of time passing by, on the groups separately. An independent samples T-test was used to study whether there was a significant difference in the amount of alpha between eyes open and eyes closed conditions in all the segments in the two groups separately.

Theta

The theta ratio was also determined by dividing the power of theta activity by the sum of the power of theta and the power of the surrounding frequencies and multiplying it by 100 ((theta/(theta+reference))*100). A repeated measures analysis of variance (ANOVA) was used to study the differences between the two groups and/or conditions across the seven segments of measuring the spontaneous activity.

RESULTS

Behavioural data

The twenty participants with the greatest percentage of conditioned responses in the fifth conditioning block were categorized as good learners while the twenty participants with the lowest CR percentages constituted the group of poor learners. The remaining eight participants were omitted from further analyses. A repeated measures analysis of variance (ANOVA) showed a significant change in the amount of CR percentages across the seven blocks, $F(6,228) = 48.89$, $p < 0.05$. The interaction of the segment and the group was statistically significant, $F(6,228) = 34.91$, $p < 0.05$. There was also a significant difference between the two groups, $F(1,38) = 180.47$, $p < 0.05$.

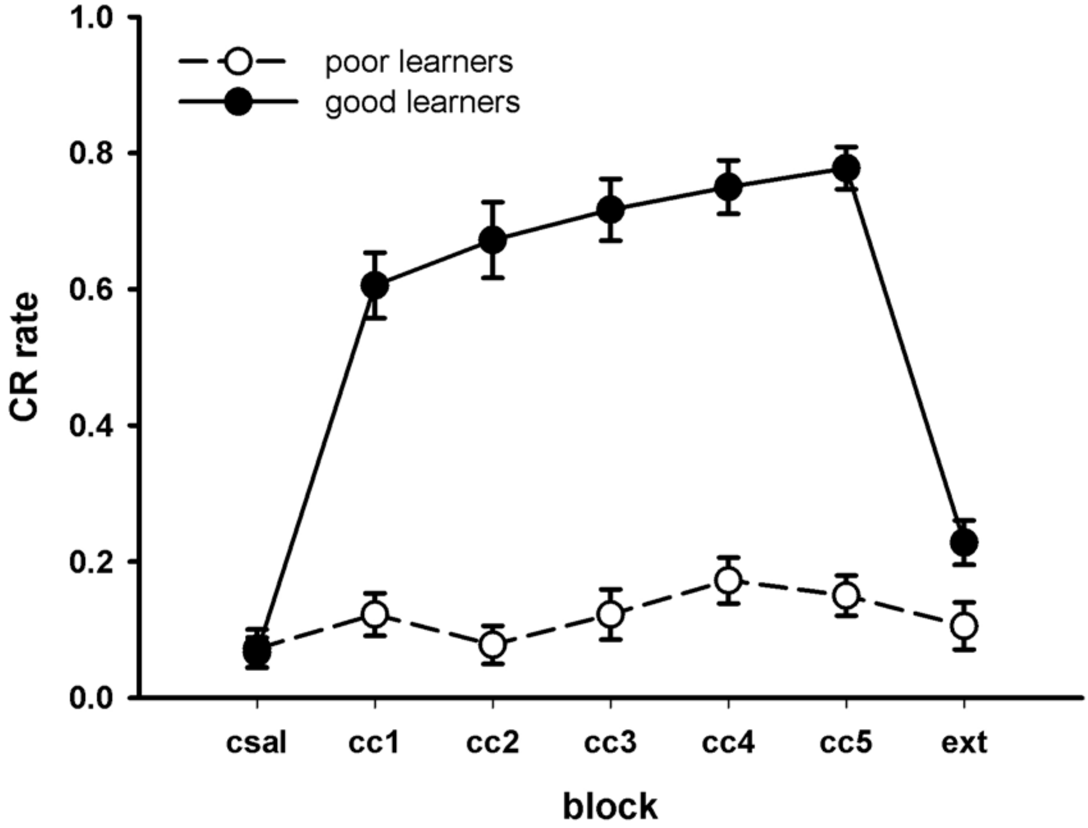


Fig. I CR percentages of the two groups as a function of trial block. As seen, the CR percentage started to increase immediately at the outset of training (CC1) in good learners whereas the poor learners barely showed any increase.

EEG data

Alpha

A repeated measures analysis of variance (ANOVA) showed a significant change in the amount of alpha blocking across the segments of spontaneous activity F(4,105) = 2.77, $p < 0.05$. The interaction of the segment and the group was statistically significant, F(4,105) = 2,72, $p < 0.05$ There was no difference between the groups F(1,26) = 0.47, p = 0.50. In other words, the eyes open alpha's percentual share of eyes closed alpha in the poor learners was big, that is, they had almost as much alpha in the eyes open condition as in the eyes closed condition in the end.

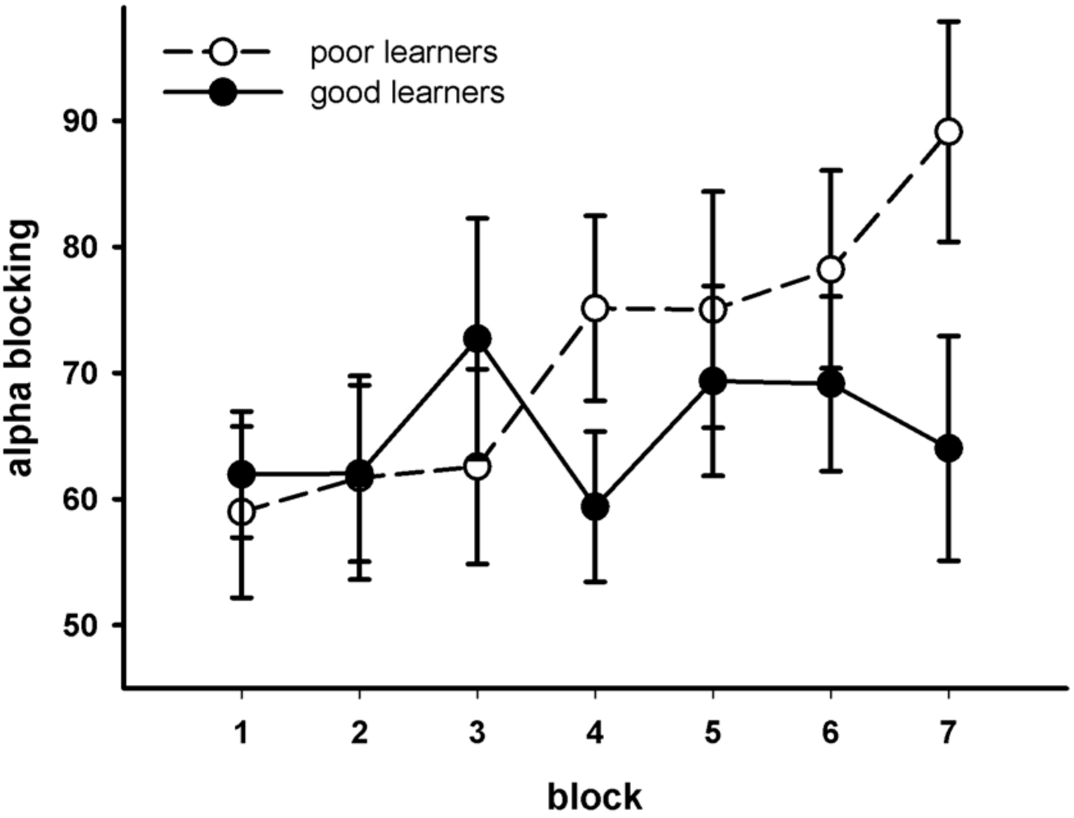
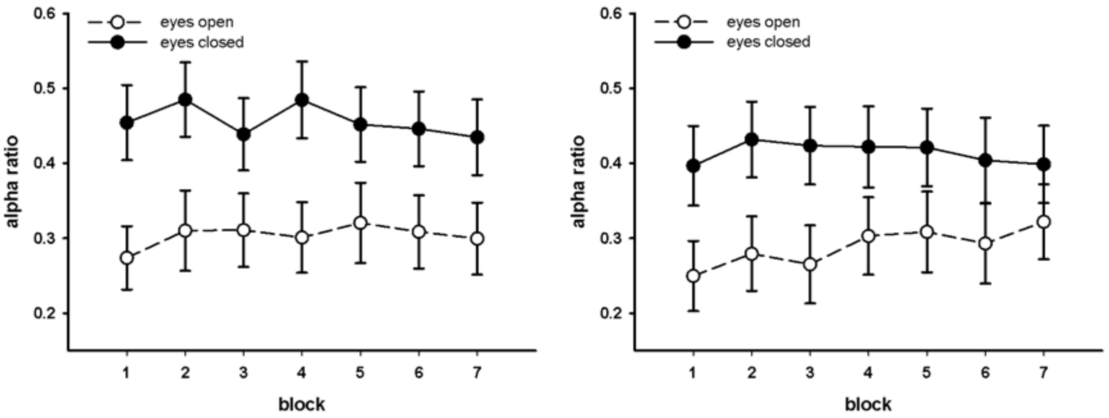


Fig. II. Alpha blocking. Higher percentual share ((alpha ratio eyes open/alpha ratio eyes closed)*100) designates lower alpha blocking. The amount of alpha increased in the group of poor learners towards the end where they had almost as much alpha in the eyes open condition as in the eyes closed condition. There was no such change in the group of good learners.

A general linear model shows that the effect of the segment, in other words time passing by, is significant in the group of poor learners F(3,40) = 5.27, $p < 0.05$. There is no such effect in the group of good learners F(6,72) = 0.80, $p = 0.57$.

An independent samples t-test shows that there is a significant difference between eyes open and eyes closed conditions in the alpha ratio in every segment in the group of good learners ($p<0.05$). On the contrary, in the group of poor learners, there is a significant difference in alpha ratio only in the three first segments ($p < 0.05$). After the second conditioning block, the difference in no longer significant ($p > 0.05$).

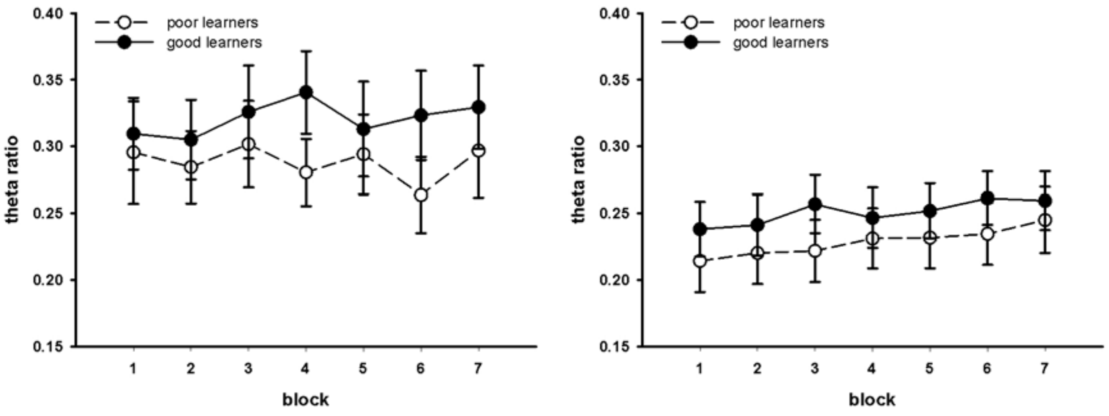


Good learners Poor learners

Fig.III. There was a significant difference between eyes open and eyes closed conditions in the alpha ratio in every segment in the group of good learners but only in the three first segments in the group of poor learners.

Theta

In general, the analyses of theta activity did not yield any significant results. There was, however, a tendency that the theta band activity was higher in frontal electrodes (of which Fz is shown as an example here) in good learners throughout the experiment. Greater theta power has been previously seen specifically in the frontal and central electrodes (Cummings & Finnigan, 2007). Figure IV suggests that the group of good learners had a stronger theta ratio throughout the whole experiment but the difference did not reach statistical significance.



eyes open eyes closed midline frontal theta

Fig. IV. The difference between the good and the poor learners in their theta ratio was not statistically significant neither in eyes open nor in eyes closed condition.

DISCUSSION

In our study, we found that differing performance in the eyeblink conditioning between good and poor learners can be explained by the amount of alpha blocking across the segments of spontaneous activity. Thus, a link between learning and general state of arousal was established. In the group of poor learners, the eyes open alpha's percentual share of eyes closed alpha was big, meaning that they had almost as much alpha in the eyes open condition as in the eyes closed condition in the end of the experiment. This can be interpreted as loss of mental alertness towards the end of the experiment whereas in the group of good learners, eyes open alpha's percentual share of eyes closed alpha stayed the same across the experiment. In other words, the poor learners became more tired and thus did not stay as focused in the task at hand as time passed by. This finding is in accordance with previous studies where alpha desynchronization was considered to reflect communication between different cortical and thalamo-cortical interactions and by doing this to enhance information processing (Klimesch, 1999). All in all, the amount of alpha blocking is usually positively correlated with cognitive performance. However, there was no statistically significant difference between the group of poor learners and the group of good learners in the amount of spontaneous theta-band activity in the beginning. This finding is not in accordance with previous findings that show a relation between the theta oscillation and learning rate (Berry & Thompson, 1978, Griffin et al. 2004, Seager, Johnson, Chabot, Asaka & Berry, 2002) but we must bare in mind that scalp EEG theta and hippocampal theta might not be directly comparable.

Niedermeyer (1997) states that the alpha blocking response to mental tasks is inconsistent because a higher cognitive task can be solved by using different tactics. Also, alpha frequency varies between subjects as well as in one subject in function of processing capacity (Klimesch, 1997). Even in the resting state, the frequency differs between good and poor memory performers. This is why a fixed range (e.g. 9-13) may be problematic. The alpha frequency decreases as people get older and even subjects of the same age show variability in it. The frequency may also decrease as a result of neurological disorders. It should also be considered that there is no single alpha rhythm but rather a variety of different alpha rhythms. Lower and upper alpha have been thought to operate independently from each other and they might have a different functional significance (Petsche, Kaplan, von Stein & Filz, 1997). For example the alpha desynchronization is more pronounced in the upper alpha band (Klimesch, 1997). The upper alpha band also reflects stimulus related cognitive processes, whereas lower alpha band is linked to attentional processes.

In order to get statistically significant differences between the group of poor learners and the group of good learners in the amount of spontaneous theta-band activity in the beginning, the sample could be larger. Also, we used the delay paradigm of classical conditioning, which does not require awareness (Manns, Clark & Squire, 2000). By contrast, the trace conditioning task requires awareness and declarative memory (Knuuttinen, Power, Preston & Disterhoft, 2001), which is dependent on the hippocampus (Manns, Clark & Squire, 2000) although, just being aware of the stimulus contingencies is not enough for trace conditioning to happen (Clark & Squire, 1999). Then, as the presence of theta may be an indicator of increased awareness to environmental stimuli (Griffin et al., 2004) it might be that this is why there was no strong difference between good and poor learners in the amount of theta activity in our delay conditioning task. Indeed, Griffin, Asaka, Darling & Berry (2004) state that the presence of hippocampal theta in the trace paradigm is more important in early trials, where it can facilitate the formation of the association of the conditioning stimuli, whereas in delay paradigm, the hippocampal theta may be more important in establishing a stable responding. Perhaps this is why we could not find a significant difference between the two groups in the amount of spontaneous theta activity in the beginning. Thus, delay and trace eyeblink conditioning paradigms are different phenomena (Clark, Manns & Squire, 2001).

We used a 21 channel cap with cup electrodes to record the EEG from scalp electrodes. This means that these recordings have a low signal-to-noise ratio compared to direct brain recordings. Even so, the oscillations can be perceived as far as they are synchronous widely over the cortex and their amplitudes are high (Kahana, Seelig & Madsen, 2001).

In the future, phase synchrony in the EEG alpha-frequency band in learning could be studied because it is involved in cognitive tasks (for a review, see Sauseng & Klimesch, 2008). Palva and Palva (2007) suggest that it is not the amplitude but the phase dynamics that indicate the functional significance of alpha activity. Alpha frequency band rhythmicity seems to have an important role in attention and in top-down processing. Hanslmayr et al. (2005) found a stronger phase locking in the alpha band for the good performers in a visual discrimination task.

Today, work environments are often cognitively demanding as there is an overload of information due to development of technology. Our attention has to be divided and this multitasking may lead to mental fatigue and human error. This is why we should have methods to estimate the work load of the brain. Holm et al. (2008) studied cognitive load and mental fatigue of the brain after normal sleep and sleep restriction. They used electroencephalography (EEG) to record frontal theta and parietal alpha activity and to calculate the ratio of the absolute power of this frontal theta activity to the absolute power of parietal alpha activity in order to see if this ratio was sensitive to changes of external and internal load. The external load was manipulated by changing the number of tasks the subject had to perform simultaneously. The internal load was manipulated by restricting the subjects' sleep and by controlling the time they spent awake. Both the external and the internal load had an effect on EEG. They used a theta Fz/ alpha Pz ratio and they discovered that the value of this index increased with both the increasing cognitive task demands and time spent awake. Thus, it is indeed theta and alpha activity that should be monitored to estimate mental fatigue.

Among people who have a condition called mild cognitive impairment, there is a proportion that develops Alzheimer's disease. (Jelic et al., 2000). Combined theta and alpha relative power and mean frequency can be used to find these people because there are distinguished changes in the dynamics of their EEG. Especially theta relative power and the decrease in the mean frequency have been found to be most sensitive to the changes occurring over time in those people who progressed to manifest Alzheimer's disease. From the clinical point of view this can be very useful in recognizing the early stages of the disease. Early diagnosis of Alzheimer's disease is crucial for planning interventional strategies. When studying the effects of healthy cognitive aging on theta power, Cummings and Finnigan (2007) found the theta power to be significantly lower in older adults during retention and recognition intervals than in younger adults. The lowered theta power of older adults may be a sign of defective network function, because the theta oscillation is an operational mode of the hippocampus (Buzsáki, 2002). This in turn may be a reason for age-related impairment in cognition (Cummings & Finnigan, 2007). In animal studies, the age-related learning deficits in a hippocampus-dependent learning task have been erased almost completely by training older rabbits during episodes of hippocampal theta activity (Asaka, Y. et al., 2005). Also in humans, a neurophysiological triggering approach could be used to help people to optimize their learning because when subjects' spontaneous theta activity is high, they learn faster (Seager et al., 2002).

In the clinical context, also alpha rhythm is a useful tool to examine the pathological process of different diseases. It seems to be a reliable sign at the beginning of a disease such as in dementia (Samson-Dollfus, Delapierre, Do Marcolino & Blondeau, 1997), trait anxiety (Knyazev, Savostyanov & Levin, 2004) and in HIV brain involvement (Baldeweg & Gruzelier, 1997). Indeed, changes in alpha EEG activity are suggested to be the earliest signs of altered brain activity in patients with HIV. All in all, frequency distribution of spontaneous EEG and the relative amount of oscillatory activity of different frequency bands can be used to both monitor the subject's current state and to look for early signs of brain degeneration.

Conclusions

Our results suggest that the state of general arousal affects learning in classical conditioning. If mental alertness decreases to the point where the amount of alpha in the eyes open condition is as big as in the eyes closed condition, subjects do not learn. These findings should be taken into account when designing a study of classical conditioning and the state of arousal should be standardized between subjects. It would also be interesting to see whether all the subjects, in this case the poor learners, could reach the level of performance of the good learners, if the state of arousal was manipulated.

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