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Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses

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Abstract

Although slow waves of the electroencephalogram (EEG) have been associated with attentional processes, the functional significance of the alpha component in the EEG (8.1–12 Hz) remains uncertain. Conventionally, synchronisation in the alpha frequency range is taken to be a marker of cognitive inactivity, i.e. ‘cortical idling’. However, it has been suggested that alpha may index the active inhibition of sensory information during internally directed attentional tasks such as mental imagery. More recently, this idea has been amended to encompass the notion of alpha synchronisation as a means of inhibition of non-task relevant cortical areas irrespective of the direction of attention. Here we test the adequacy of the one idling and two inhibition hypotheses about alpha. In two experiments we investigated the relation between alpha and internally vs. externally directed attention using mental imagery vs. sensory-intake paradigms. Results from both experiments showed a clear relationship between alpha and both attentional factors and increased task demands. At various scalp sites alpha amplitudes were greater during internally directed attention and during increased load, results incompatible with alpha reflecting cortical idling and more in keeping with suggestions of active inhibition necessary for internally driven mental operations.

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1. Introduction

The human electroencephalograph (EEG) has proven a useful tool in the examination of the

brain’s attentional networks. The purpose of the present study is to help delineate various interpretations of the alpha component of the human EEG in terms of the distinction between internally directed and externally directed attention.

Traditionally it has been argued that the alpha rhythm reflects a generalised idling condition of

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the brain, calm yet alert (Adrian and Matthews, 1934). In support of this many studies have noted a task-related decrease in alpha power, both over occipital sites during visual stimulation and scanning tasks (Berger, 1929, 1930; Mann et al., 1996) and over sensorimotor areas during movement or somatosensory tasks (see Pfurtscheller et al., 1996 for a review).

However, there have been other studies whose observations have been anomalous to the alpha-as-idling findings. Cole and Ray (1985), Ray and Cole (1985b,a) explored the effects of the direction of attention within the framework of the intake-rejection hypothesis (Lacey et al., 1963; Lacey, 1967; Lacey and Lacey, 1970). This hypothesis introduced the notion of sensory 'intake' tasks (i.e. externally directed attention) and non-sensory 'rejection' processes (i.e. internally directed attention), such as mental arithmetic, mental imagery and working memory tasks. The rejection aspect of the theory related to the proposal that in order for example, to facilitate mental imagery, one needs to inhibit or 'reject' incoming sensory information. Ray and Cole (1985b,a) found increased alpha power in rejection tasks such as mental imagery and arithmetic especially at parietal sites.

Similar to the findings of Ray and Cole (1985a), Klinger et al. (1973) observed that imagination was associated with increased alpha, Schupp et al. (1994) reported lower alpha power for perceptual tasks as opposed to mental imagery, an association has been observed between average alpha amplitude and mental rotation ability Williams et al. (1995), Klimesch et al. (1990) found that participants who did well in memory tests had higher average alpha frequencies than those who did poorly, indicating the possible importance of alpha mechanisms for memory systems.

Klimesch et al. have since hypothesised a wider role for alpha oscillatory networks of various cognitive processes that involve both attention and memory. The basic principle involved here is that activation of this network would lead to alpha desynchronisation (see Klimesch, 1997 for a review). More recently, Klimesch et al. (1999, 2000) have proposed that alpha synchronisation may index inhibitory processes serving to increase signal to noise ratios—the greater the task demands

within this network, the more inhibition needed, the greater the synchronisation. Klimesch's proposals are compatible with the notion of 'surround inhibition' wherein active cortical areas, indexed by alpha desynchronisation are surrounded by a 'doughnut' of alpha synchronisation or inhibition (Suffczynski et al., 2001). Thus, the surrounding inhibition, controlled by thalamo-cortical and reticular nucleus pacemaker cells, acts to increase the gain on the focally active area of alpha desynchronisation in a manner in keeping with Crick's spotlight of attention hypothesis (Crick, 1984). These findings suggest that alpha activity is not a simple index of cortical idling, but that it is a measure of active processing necessary for internally driven mental operations.

Thus there exists a lack of consensus in the literature regarding the functional significance (if any) of oscillations in the traditional alpha bandwidth of 8–12 Hz. The conventional view that alpha reflects a state of cortical idling (Adrian and Matthews, 1934; Pfurtscheller et al., 1996) has been modified to accommodate findings of increased alpha power during certain internal tasks, such that it is proposed that alpha indexes early inhibition of sensory input mechanisms (Ray and Cole, 1985b,a). More recently this idea has been broadened to propose alpha as a mechanism for increasing signal to noise ratios within the cortex by means of inhibition of unnecessary or conflicting processes to the task in hand (Klimesch et al., 1999, 2000).

In order to tease apart these competing theories experimentally, we employed tasks that manipulated both cognitive processing requirements (difficulty) and direction of attention (externally vs. internally directed attention). In our first experiment we tested the hypotheses that alpha indexes cortical idling by determining whether alpha power over sensory areas decreases not only during external as opposed to internal tasks, but also as a function of increasing task demands. We also tested the alternative hypothesis that alpha power reflects the inhibition of sensory input mechanisms necessary for internally directed attention, by testing whether alpha power was greater during internal as opposed to external tasks, and that during sensory-intake tasks (but not during internally

directed attention) alpha increases in line with increasing task demands over task-irrelevant areas. Finally, we tested the hypothesis that alpha is an index of a more generalised inhibition system serving to increase signal to noise ratios, by testing whether alpha power increases during internally directed attention and as task demands increase during sensory-intake tasks, and also that it increases with task demands during internally directed attention.

2. Experiment 1

2.1. Method

2.1.1. Subjects

Twelve participants (6 male and 6 female) were tested, ages ranged from 27 to 48 years (mean: 34.4). All participants reported normal hearing, haptic sensation, normal or corrected to normal vision and no known psychiatric or neurological problems. Participants gave written informed consent and were paid GB£15 for taking part. Ethics Committee approval was granted for this study.

2.1.2. EEG recording

The participants were fitted with an electrode-cap containing 28 electrodes, arranged according to the international 10–20 system plus eight additional electrodes: FTC1, FTC2, TCP1, TCP2, CP1, CP2, PO1 and PO2. Four facial electrodes were employed to measure eye movements from which horizontal, vertical and radial electrooculographs (EOGs) were derived. These were positioned at the left (E5) and right (E6) outer canthi and approximately 2 cm above and below the left eye (E1 and E3, respectively).

EEG was recorded relative to the left ear and re-referenced off-line to linked ears. Data were digitised at 500 Hz with a bandpass of 0.1–200 Hz (24 dB/octave roll-off). All data were recorded and processed using a SynAmps amplifier and NEUROSCAN 4.1.1 software.

2.1.3. Procedure

This protocol employed matched externally and internally directed attentional tasks. Both sets of tasks comprised of 3 levels of gradually increasing

task demands. For each subject, all tasks were performed in each of the auditory, haptic and visual modalities. Order of modality was fully counter-balanced between subjects. Two sets of stimuli were employed for each modality: participants 1–6 used set 1; participants 7–12 used set 2. All recording sessions were conducted between 15:30 and 18:30 pm in an attempt to minimise time of day effects.

2.1.4. Externally directed tasks

For each level participants were presented with a sequence of 6 randomly ordered stimuli (see external stimuli for details), repeated 3 times, with a pause of 4 s between sequences. Stimulus durations were 0.5 s, with an SOA of 0.7 s. Level 1 required the participant simply to attend to the stimuli. Level 2 involved the answering of a simple question (e.g. ‘How many stimuli are there in each series?’). Level 3 involved the answering of a more demanding question (e.g. ‘How many different types of stimuli are there?’). Questions were asked prior to each presentation of the stimuli sequences, and responses were given post-stimulus presentation.

2.1.5. External stimuli

2.1.5.1. Acoustic. A sequence comprised of 3 different pure tones at approximate natural scalar frequencies, pseudo-randomly ordered within the sequence. Stimulus set 1: F#, F#, F#, G, D, D (F# = 370 Hz; G = 392 Hz; D = 293.7 Hz). Stimulus set 2: D, C#, E, E, E, E (C# = 277.2 Hz; E = 329.6 Hz). These tones were generated by Neuroscan STIM software and were presented binaurally using STIM foam insert headphones at 90 dB.

2.1.5.2. Haptic. A sequence comprised of 3 different grades/textures of sandpaper (grit size 40–1200 g). Each stimulus was applied in sequence, by the experimenter, simultaneously to the opposed left and right index fingers of the participant. Stimulus set 1: S, M, R, M, S, M (S = 1000 g; M = 180 g; R = 40 g). Stimulus set 2: S, S, R, M, M, S (S = 1200 g; M = 240 g; R = 60 g).

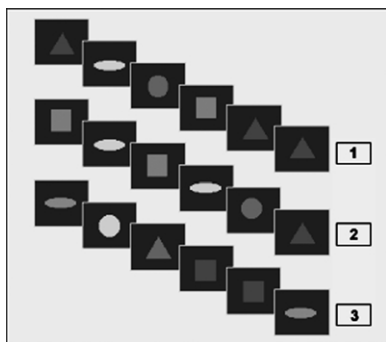


Fig. 1. Visual stimuli sets 1, 2 (experiments 1 and 2) and 3 (experiment 2).

2.1.5.3. Visual. A sequence comprised of 4 different stimuli: circles, squares, ellipses and triangles. Shapes were differentially coloured. Presentation was via a SVGA 15 inch computer monitor and Neuroscan STIM software (Fig. 1).

2.1.6. Internal tasks

For the internal tasks, the first step involved training participants to be able to imagine the previously presented sequences of stimuli. Training took the form of repeated presentation of the stimuli until the participant reported confidence in their ability to imagine the sequence.

As in the external tasks three levels were employed. Level 1 involved the participant imagining the randomly ordered sequence of 6 stimuli, 3 times (S's were instructed to try to replicate the timing and spacing of the original stimuli as well as the stimuli themselves). Level 2 involved the participant imagining the sequences again and answering a simple question regarding the stimuli. Level 3 involved the participant imagining the sequence once again and answering a more demanding question. Questions were the same as in the external tasks and were asked prior to each imagination of the stimuli sequences. Responses were given post-stimulus imagination. The questions play the dual role of increasing task demands and providing the behavioural evidence that the participants had successfully 'imagined' the stimuli.

2.1.7. Data preparation

Ocular artefact rejection was carried out using methods described previously (Croft and Barry, 2000). The EEG data were epoched from 1000 to 11 000 ms after sequence onset and spline-fit to 8192 points. A fast-Fourier transform of the data enabled extraction of the alpha component (α) from the raw EEG within a frequency range of 8–11.9 Hz.

In order to explore topographical (sagittality and laterality) effects, the scalp electrodes were divided into 6 surface areas: left anterior (FP1, F3, F7, FTC1); right anterior (FP2, F4, F8, FTC2); left central (C3, T3, CP1, TCP1); right central (C4, T4, CP2, TCP2); left posterior (T5, P3, PO1, O1); right posterior (T6, P4, PO2, O2).

2.1.8. Statistical analysis

Repeated measures polynomial contrasts were employed to test for differences in *attention* (external vs. internal); *increasing task demands* (levels 1–3); *sagittality* (anterior, central and posterior sites); *laterality* (left vs. right).

2.2. Results

Significant main effects for *attention* were observed in all modalities. Mean α -amplitudes were greater during internally as opposed to externally directed attention tasks (auditory ($F(1, 11) = 5.2$; $P < 0.05$); haptic ($F(1, 10) = 5.6$; $P < 0.05$); visual ($F(1, 10) = 15.7$; $P < 0.01$) see Table 1).

In the auditory and visual modalities, the increase in mean α -amplitudes from external to internally directed attention was greater at anterior and posterior than central sites (($F(1, 11) = 18.9$; $P < 0.001$) and ($F(1, 10) = 17.2$; $P < 0.01$) respectively, see Fig. 2).

Effects of increased task-demand were found in the haptic and visual modalities. Mean α -amplitudes were greater in level 3 as opposed to level 1 conditions (haptic ($F(1, 10) = 23.326$; $P < 0.001$); visual ($F(1, 11) = 5.76$; $P < 0.01$). A similar trend was noted in the auditory modality ($F(1, 11) = 5.185$; $P = 0.07$).

2.3. Discussion

With regard to attention, it was observed that mean α -amplitudes were greater during internally

Table 1
Means (top) and standard deviations (below) for attention and difficulty in μV

Acoustic				
	Difficulty			
Attention	Easy	Medium	Hard	Grand mean
External mean	0.947	1.066	1.086	1.033
S.D.	0.135	0.122	0.102	0.115
Internal mean	1.125	1.168	1.129	1.141
S.D.	0.122	0.115	0.129	0.119
Grand mean	1.036	1.113	1.108	
S.D.	0.122	0.115	0.112	
Haptic				
	Difficulty			
Attention	Easy	Medium	Hard	Grand mean
External mean	0.841	0.973	0.967	0.927
S.D.	0.109	0.122	0.112	0.112
Internal mean	0.987	1.046	1.105	1.046
S.D.	0.129	0.122	0.129	0.125
Grand mean	0.914	1.01	1.036	
S.D.	0.115	0.119	0.115	
Visual				
	Difficulty			
Attention	Easy	Medium	Hard	Grand mean
External mean	0.584	0.657	0.594	0.611
S.D.	0.076	0.086	0.063	0.073
Internal mean	0.957	1.076	1.105	1.046
S.D.	0.122	0.132	0.132	0.125
Grand mean	0.772	0.865	0.851	
S.D.	0.086	0.092	0.086	

directed attention than externally directed attention in all modalities. This effect was larger for the mean of anterior and posterior sites as opposed to

central sites in the auditory and visual modalities but was more widespread during haptic tasks. Additionally, it was found that α -amplitudes were greater with increased task demands, significantly so for haptic and visual modalities and at trend level for the auditory modality. This suggests that straightforward explanations of alpha reflecting cortical idling are not tenable as the idling hypothesis predicts that alpha power should decrease both during externally directed attention and as task complexity increases. An alternative explanation for the increases in alpha power is that it indexes the greater degree of inhibition necessary not only during internally as opposed to externally directed attention but also as task demands increase. Our results are thus more compatible with the proposals of Klimesch et al. (1999, 2000) than those of Cole and Ray (1985), Ray and Cole (1985b,a).

3. Experiment 2

In order to clarify and replicate the findings from experiment 1, a number of modifications were made: (1) The levels of increasing task demands (for both internal and external conditions) were reduced from 3 to 2 in order to remove possible differences in subjective difficulty between questions two and three. (2) The questions constituting the new level 2 were standardised into the type 'are the 1st (2nd/3rd) and 4th (5th/6th) stimuli the same'? These first two refine-

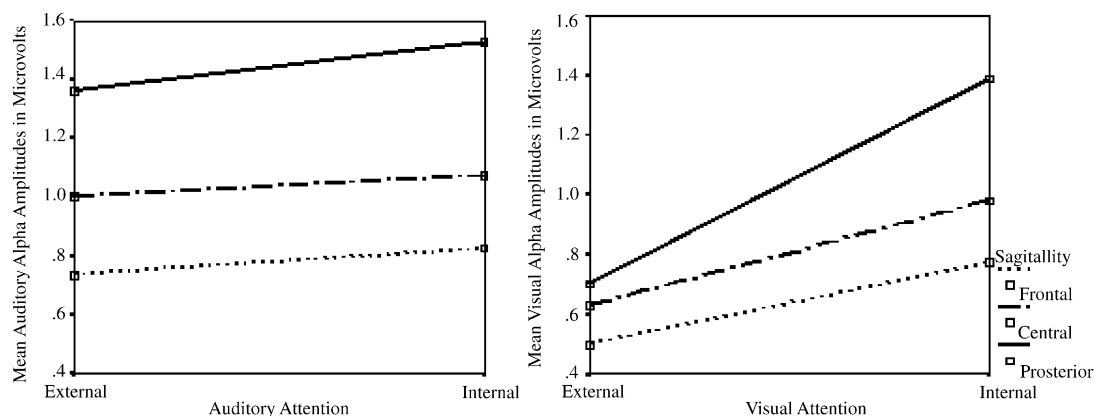


Fig. 2. Mean alpha amplitudes in μV for *attention*sagittality* contrast.

ments were introduced in order to make firmer inferences regarding the effect of task complexity upon alpha and so afforded a more robust test of the idling hypothesis. (3) A new set of acoustic, haptic and visual stimuli was included in order to maintain modality and stimulus balance (see procedure). This was necessary as an extra group of 6 participants were involved in the second experiment compared to the first, and (as before) each group were assigned a separate set of stimuli in order to control for the effects of stimulus alone. (4) In all conditions in all three modalities the participants were instructed to keep their eyes open at all times, and in order to facilitate the mental imagery, the participants fixated upon a plain black background. This was in order to control for the possibility in experiment 1 that some subjects may have closed their eyes during the visual imagination tasks, which may have affected alpha readings. (5) A more detailed topographical analysis was employed, which allowed observations to be made as to the whereabouts of the changes in alpha as recorded from the scalp. The hypotheses tested were as for experiment 1.

3.1. Method

3.1.1. Subjects

Eighteen participants (12 male and 6 female) were tested, ages ranged from 21 to 38 years (mean: 26.6). All participants reported normal hearing, haptic sensation, normal or corrected to normal vision and no known psychiatric or neurological problems. Ethics Committee approval was granted for this study.

3.1.2. EEG recording

The EEG and EOG recording details were as for experiment 1.

3.1.2.1. Procedure. The protocol used was the same as for the first experiment with modifications as described above. This resulted in the following configuration:

External task (level 1)—presentation of stimuli.
External task (level 2)—presentation of stimuli + question.

Training session—repeat of stimulus presentation until participant is able to successfully imagine them.

Internal task (level 1)—imagining of stimuli.

Internal task (level 2)—imagining of stimuli + question.

In order to keep the stimuli balanced between subjects a new stimulus set (stimulus set 3) was introduced for all three modalities. Auditory set 3: E, G, E, D, D, G (E=329.6 Hz; G=392 Hz; D=293.7 Hz). Haptic set 3: M, R, S, S, R, M (Grit size: S=1200 g; M=240 g; R=40 g). Visual set 3: see Fig. 1.

3.1.3. Statistical analysis

In order to obtain a more detailed picture of the topography of any EEG changes, electrode sites were examined individually rather than grouped into regions. Corresponding electrode amplitudes in different conditions (external vs. internal; task demand level 1 vs. task demand level 2) were compared using Wilcoxon *t*-tests. Topographical maps were drawn using the resulting *z*-values according to the method of spherical splines (Perrin et al., 1989). In order to compensate for Type I error due to the number of comparisons being calculated, a randomisation test procedure was employed (Burgess and Gruzelier, 1997, 1999). This resulted in a more conservative *z*-value of 2.7–2.9 at the 95-percentile level, compared to 1.96 uncorrected.

3.2. Results

Results for the comparisons of EEG amplitudes between externally and internally directed attention conditions can be seen in Fig. 3. Those for level 1 vs. level 2 tasks can be seen in Fig. 4. Upper maps indicate *z*-values reflecting the difference between the two conditions. Lighter colours reflect increased amplitudes during internal or increased task demand conditions. Lower (smaller) maps show the randomisation values for the differences.

Attention. As can be seen from Fig. 3, significant differences between attentional conditions were found in all three sensory modalities in the alpha band. These significances reflected greater α -amplitudes during internally as opposed to exter-

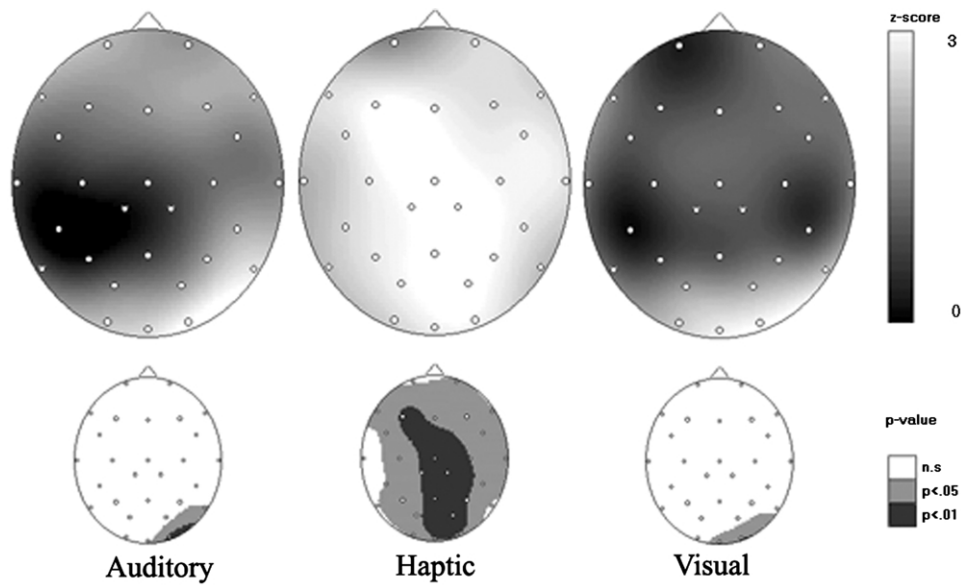


Fig. 3. EEG amplitudes in the alpha bandwidth measured during externally and internally directed attention. The z -values indicate the differences between the two conditions. The P values are the randomisation probabilities for those differences.

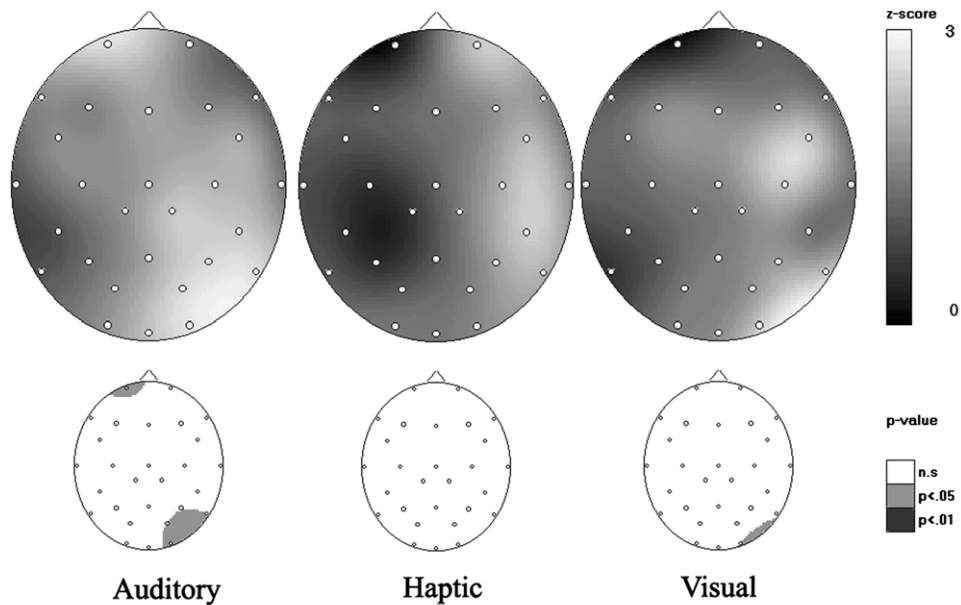


Fig. 4. EEG amplitudes in the alpha bandwidth measured during levels 1 and 2 of increased task demands. The z -values indicate the differences between the two conditions. The P values are the randomisation probabilities for those differences.

nally directed attention. In the auditory modality these differences were observed at O2, OZ, T6 and at trend level at O1. In the haptic modality, the significant differences were more widespread at FP2, F3, F4, C3, C4, P3, P4, O1, O2, F7, T4, Fz, Cz, Pz, Oz, FTC1, FTC2, TCP1, TCP2, CP1 and CP2 and at trend level at F8. In the visual modality, the observed differences were very similar to those in the auditory modality, being significant at O2 and Oz, and at trend level at O1 and T6.

Increasing task demands. As can be seen from Fig. 4, significant differences were found in both the auditory and visual modalities in the alpha band. These significances reflected greater α -amplitudes during level 3 as opposed to level 1 tasks. In the auditory modality these differences were observed at FP1, P4, O2, T6, PO2 and at trend at TCP2. In the visual modality, the observed differences were significant at O2 and T6, and at trend level at C4 and FTC2.

3.3. Discussion

In line with results from experiment 1, greater mean α -amplitudes were observed in internally as opposed to externally directed attention at various electrode sites, in all modalities. In other words, further evidence was found in the EEG for increased alpha during imagination as opposed to sensory-intake tasks. This was particularly evident at sites near visual cortical areas, e.g. Oz and O2. It should of course be noted that these findings are mainly over scalp sites that reflect activity in and around the parieto-occipital and calcarine sulci where traditional alpha activity is thought to be generated (Hari et al., 1997; Salenius et al., 1995).

As far as increased task demands were concerned, mean α -amplitudes were greater for level 2 as opposed to level 1 tasks in the auditory and visual modalities, at sites similar to those for attention. These effects in the haptic modality were not found to be significant. However, there is the possibility of a type II error. If the effects were more subtle and distributed they would therefore be more likely to show-up when electrodes were grouped into scalp regions (as in experiment 1) than with direct electrode *t*-test comparisons, par-

ticularly, with the conservative probability adjustments used in this analysis. Indeed, a polynomial contrast of level 1 vs. level 2 tasks, using electrodes grouped as in experiment 1, revealed effects at trend level, wherein mean alpha amplitude was greater during increased task demands ($F(1, 16) = 2.688$; $P = 0.121$).

4. General discussion

These results suggest that straightforward explanations of alpha reflecting cortical idling are implausible. For instance, alpha levels were greater in line with the increased task demands associated with answering questions pertaining to the stimuli, the opposite to what would be expected from the idling hypothesis (Pfurtscheller et al., 1996). The lack of an interaction between attention and task demands in experiment 1 reveals that alpha power was greater with increased task demands, not only during sensory-intake tasks (externally directed attention) but also during internally directed attention. The more parsimonious explanation for this is that the sensory inhibition hypothesis built around the intake-rejection model by Ray and Cole (1985a) is too specific and that alpha synchronisation reflects a more generalised inhibition of non-task relevant areas, such as the hypothesis proposed by Klimesch et al. (1999, 2000). In this context, our findings suggest that in situations or tasks where attentional demands require inhibition of non-task relevant areas or processes, one would expect to find increased alpha activity.

There is one other interpretation of our findings that may prove a fruitful avenue of investigation. Although not directly related to the theories being tested in this paper, von Stein et al. have proposed that alpha oscillations may be considered an index of top-down processing in general (von Stein et al., 2000). This is based on findings showing increased synchronisation between distant cortical areas in alpha during expectancy and goal-oriented conditions and also long range (polysynaptic), fronto-parietal coherences in alpha during working memory and mental imagery tasks (von Stein et al., 2000). It is tempting to speculate that

von Stein's and Klimesch's ideas are compatible, with active inhibition being but one aspect of the role for alpha in the mechanisms of top-down processing, however, more work is needed to investigate the role of functional connectivity during tasks that elicit increased alpha power.

In summary, the findings observed in these two experiments show clear differences in the measures of mean alpha amplitude between internally and externally directed attention, and between tasks of different complexity. This supports the growing body of evidence that suggests that the notion of alpha reflecting cortical idling is no longer tenable. The parsimonious explanation of our findings suggests that increased alpha power may index the active inhibition of non-task relevant cortical areas. However, the exact nature of the alpha responses reported here remains unclear and is the object of further investigation.

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