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EEG Differences between Eyes-Closed and Eyes-Open Resting Remain in Healthy Ageing

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Abstract

In young adults and children, the eyes-closed (EC) resting state is one of low EEG arousal, with the change to eyes-open (EO) primarily involving an increase in arousal. We used this arousal perspective to interpret EC/EO differences in healthy young and older adults. EEG was recorded from 20 young ($M_{age} = 20.4$ years) and 20 gender-matched older ($M_{age} = 68.2$ years) right-handed adults during two 3 min resting conditions; EC then EO. Older participants displayed less delta and theta, some reduction in alpha, and increased beta. Global activity in all bands reduced with opening the eyes, but did not differ with age, indicating that the energetics of EEG reactivity is maintained in healthy ageing. However, older adults had more focal changes than young adults, particularly in beta, suggesting the mobilisation of additional localised resources. This maintained reactivity, and heightened focal activity, may underlie preserved performance levels in healthy ageing.

Keywords: Normal ageing; Resting EEG; Eyes Open vs. Eyes Closed; Arousal/Activation; Clinical screening tool; EEG reactivity.

1. Introduction

1.1. EEG arousal and activation

The defining characteristic of electroencephalographic (EEG) alpha is that the dominant synchronisation reflected in eyes-closed (EC) conditions is desynchronised or blocked in eyes-open (EO) conditions (Adrian and Matthews, 1934; Berger, 1933; Chapman et al., 1962; Gale et al., 1971; Glass and Kwiatkowski, 1970; Jasper, 1936; Legewie et al., 1969; Smith, 1938; Volavka et al., 1967). This alpha desynchronisation probably reflects increased visual system activity mediated by the Reticular Activating System (Gale et al., 1971; Hardle et al., 1984; Volavka et al., 1967), or widespread cortical and thalamo-cortical interactions, aiding information processing (Fisch, 1999; Gevins et al., 1997; Klimesch, 1999) by activating the entire cortex (Başar and Schürmann, 1999).

In a series of studies with a particular focus on the link between arousal and alpha, we applied Pribram and McGuinness' (1975) distinction between *arousal* and *activation*, defining “arousal” as the current energetic level of the organism, and “activation” as the mobilisation of energy needed for performance. Skin conductance level (SCL) has a long history of use as an arousal measure in autonomic studies (e.g., in the context of the Orienting Reflex: Barry, 2004; Barry and Sokolov, 1993), and we initially developed our arousal/activation energetics concepts using this autonomic measure. In a series of studies we linked current arousal levels to physiological phasic response amplitudes, and task-related activation to behavioural performance measures (Vaez Mousavi et al., 2007a, 2007b, 2009). These links are shown schematically in Figure 1. From this perspective, current arousal level acts as an amplifier of physiological responses, while task-related activation reduces reaction time and errors, serving to enhance behavioural performance.

Fig. 1 about here

We first linked SCL to global EEG alpha power in a resting state study in children

(Barry et al., 2004a), where higher SCL was associated with lower levels of global alpha power across the scalp. We replicated this in children with AD/HD, and in age- and gender-matched controls (Barry et al., 2009c). We also manipulated arousal with caffeine, and found that EC resting global alpha power decreased and SCL increased with caffeine in young adults (Barry et al., 2005, 2008) and in children (Barry et al., 2009b), confirming the inverse alpha/arousal nexus. Subsequently, Barry et al. (2007) found that EO in young adults was associated with increased SCL and a global reduction in alpha power compared with EC, leading us to equate energetics differences associated with EC/EO with activation. Barry et al. (2009a) confirmed these EC/EO findings in children. The relation between these independent variables was explored by Barry et al. (2011) in young adults. Caffeine and opening of the eyes were found to have additive effects on both the arousal-defining SCL increase and the decrease in global alpha amplitude.

These eight separate EEG/SCL studies provide a solid base for our conceptualisation of global alpha as an inverse marker of arousal, as indicated on the vertical axis of Figure 1. An important measurement characteristic of alpha as the EEG marker of arousal derives from our concept of arousal-as-amplifier. This “amplifier” concept suggests that a pure arousal shift in cortical source activity will produce an amplified increase/decrease in band activity across the scalp – an EEG arousal change at any electrode will be proportional to the existing band level at that electrode. Alpha alone meets this criterion for an EEG arousal measure compatible with neuroanatomical models involving midbrain interactions with the thalamus and cortex (Robbins et al., 1998; Détári, 2000). In contrast, focal changes in band activity that depart from this global distribution reflect underlying activity in localised processing-specific brain regions. In the EC/EO studies mentioned above, reductions in the non-alpha bands were focal: delta in frontal and lateral regions, theta in posterior regions, and beta in posterior and right hemisphere regions. These focal changes illustrate the converse of our

arousal thesis: condition- or task-related energetics change (i.e., activation) may be accompanied by processing-specific focal EEG changes marking regional brain activity (e.g., delta and theta with visual processing: Grillon and Buchsbaum, 1986; alpha in posterior cortex in spatial vs. verbal processing: Gevins et al., 1997).

1.2. EEG arousal and activation in healthy ageing

This arousal/activation perspective provides a novel and theoretically-important framework for the present study. To provide a basis for EEG exploration in cognitive decline, we here examine EC/EO effects in the traditional delta, theta, alpha, and beta EEG band amplitudes in healthy ageing. Such data can be obtained easily from almost all participants, and may prove to be of clinical value. In previous work, mainly with EC conditions, delta power has been shown to decrease with increasing age (Babiloni et al., 2006; Breslau et al., 1989; Duffy et al., 1984; Gaál et al., 2010; Giaquinto and Nolfé, 1986; Polich, 1997; Sleimen-Malkoun et al., 2015; Vysata et al., 2012), as has theta power (Breslau et al., 1989; Cummins and Finnigan, 2007; Duffy et al., 1984; Polich, 1997; Sleimen-Malkoun et al., 2015; Vysata et al., 2012); more recently, similar findings have been reported in these bands during EO conditions (Vlahou et al., 2014; Wang et al., 2016). Alpha power has generally been shown to reduce with age (Babiloni et al., 2006; Breslau et al., 1989; Fan et al., 2014; Polich, 1997; Sleimen-Malkoun et al., 2015; Vysata et al., 2012), while results in resting beta power have been less consistent (*decrease*: Breslau et al., 1989; Vysata et al., 2012; vs. *increase*: Duffy et al., 1984; Fan et al., 2014; Giaquinto and Nolfé, 1986; Marciani et al., 1994; Wang et al., 2016). However, Pollock et al. (1990) found no correlations of band powers with age in a group of middle-aged and elderly healthy adults (56-76 years), but the restricted age range may have obscured results. Hence our investigation sought to compare participants from discrete age groups (i.e., young university students vs. independent-living retirees). In their review, Dustman et al. (1993) reported the main age findings as alpha

frequency slowing, and an increase in beta to about age 60, followed by a decrease. They viewed increased beta as a favourable sign regarding health and cognitive functioning, and the increase of diffuse slow waves (delta and theta) as related to cognitive problems. This latter interpretation is compatible with van der Hiele et al.'s (2008) report that increased EC theta predicted later reductions in global cognitive and executive performance. We therefore predicted that, in contrast to the young adults, the healthy older adults would show this pattern of reduced EEG band amplitudes in delta, theta, and alpha, and an increase in beta for both EC and EO resting conditions.

Age-related topographical EEG changes may have important implications in relation to the regional activation pattern(s) in older adult populations, helping to distinguish between global arousal changes and focal changes indicating different brain processes. Unfortunately, there are few detailed reports of topographic changes with healthy ageing; most early reports used few electrodes, and more recent studies have tended to group electrodes into broad regions (e.g., Gaál et al, 2010: anterior/posterior). However, there has been some indication that delta, theta, and alpha power become more temporal with age (Babiloni et al., 2006; Breslau et al., 1989), and that alpha power remains dominantly occipital and hemispherically balanced (Giaquinto and Nolf, 1986). Beta power increase with age was noted to be right-enhanced by Fan et al. (2014), although this study involved only 9 older subjects. It is therefore of some novelty to compare the absolute EEG band amplitude topographies of our samples, separately for each band and resting condition.

Reports of healthy ageing impacts on the EC/EO effects are also limited. EEG reactivity, or the EC to EO reduction, in alpha power is known to be diminished in dementia (van der Hiele et al., 2008), although Duffy et al. (1984) and Könönen and Partanen (1993) noted decreases with healthy ageing. Moreover, van der Hiele et al. (2008) found that, independent of diagnostic group (i.e., elderly controls, mild cognitive impairment,

Alzheimer's disease), decreased baseline alpha EC/EO reactivity predicted poorer global cognitive and executive function at follow-up. Unfortunately, none of these EC/EO reactivity studies included topographic analysis. In the context of these sparse reports, it is important to investigate EC/EO changes in the EEG of healthy young and older groups.

With a focus on topographic aspects that can inform us about arousal/activation interpretations of these effects, the major novelty of this contribution is its placement in a theoretical context that integrates electrophysiology and behaviour. Such clarification of normal EEG changes in healthy ageing may provide theoretically-supported benchmarks to assist our understanding of the basis for cognitive dysfunction in age-related mild cognitive impairment and dementia, and provide markers of wellness in our ageing populations.

2. Methods

2.1. Participants

Participants in the Young adult group were 20 university students (5 males, 15 females) from the School of Psychology who participated voluntarily as one means of satisfying a course requirement. Their mean age was 20.4 (range 18.8–25.6) years, and all were self-reported as being right handed. The Older group consisted of 20 sex- and handedness-matched adults living independently in a Wollongong retirement resort community, with mean age 68.2 (range 59.8–74.8) years. They were recruited via a flyer and received A\$40 in recompense for their voluntary participation. All subjects were screened for self-reported neurological disorders, head injury, learning disability and psychiatric conditions. They were required to abstain from caffeine and other psychoactive substances for at least 2.5 h prior to the testing session; older participants were required to report all current medication use and dosage. The older adults also completed a cognitive screening instrument, the Rowland Universal Dementia Assessment Scale (RUDAS; Storey et al., 2004), scoring a mean of 28.0 out of 30 (range 24–30), all above the cut-off for possible

cognitive impairment (22).

This study was carried out in accordance with the Declaration of Helsinki. The protocol was approved by the Joint University of Wollongong/South East Sydney and Illawarra Area Health Service Human Research Ethics Committee. Written informed consent was obtained from all participants prior to participation.

2.2. Physiological recording

EEG was continuously recorded from A2 and 19 scalp sites using an electrode cap with tin electrodes, referenced to A1. Vertical electro-oculogram (EOG) was recorded from tin electrodes placed above and below the left eye, and horizontal EOG was recorded from electrodes beyond the outer canthi. Care was taken to balance the impedances at A1 and A2, and all impedances were below 10 k Ω . Data were sampled continuously at 1000 Hz with a gain of 500, and recorded DC–30 Hz for offline analysis by a Neuroscan Synamps 2 system using Neuroscan Acquire software (Compumedics, Version 4.3.1).

2.3. Procedure

When participants arrived the experimental procedure was explained, they read an information sheet, signed the consent form, and completed a simple screening questionnaire. Older participants completed the RUDAS (Storey et al., 2004) in another session within 1 week of their EEG session. Participants were seated in an air-conditioned room, and fitted with the physiological measurement equipment. Prior to the experiment each participant completed a brief EOG calibration task that involved making a series of vertical and horizontal eye movements, and eye blinks. They then began a number of laboratory activities that began with resting EC followed by EO baseline periods of 3 min each. During the EO condition, participants were instructed to visually fixate on a small cross presented on a computer screen in front of them.

2.4. Data extraction

The continuous EEG was EOG corrected using the Revised Aligned-Artifact Average (RAAA) procedure of Croft and Barry (2000), and then digitally re-referenced to linked ears. The EEG data from each 3 min segment (EC, EO) were divided into 90 sequential 2 s epochs. These were baselined across their duration, and rejected if activity at any scalp site exceeded $\pm 100 \mu\text{V}$ at any time. Each accepted epoch was subjected to a Discrete Fourier Transform (DFT) with a 10% Hanning window. A correction (of 1.05) was applied to compensate for this window. At each electrode, absolute amplitudes in the delta (0.5–3.5 Hz), theta (4.0–7.5 Hz), alpha (8.0–13.0 Hz) and beta (13.5–24.0 Hz) bands were calculated, and averaged across epochs. Such amplitude measures are increasingly preferred over the traditional power measures, which often need logarithmic or other transformations to reduce their skew (e.g., Barry et al., 2011). This shift from power to amplitude has been implemented in studies from our lab for some years – such as EEG involvement in the Orienting Reflex (Barry et al., 2012), and EEG-ERP brain-dynamics (Barry, 2009; Barry et al., 2014; De Blasio et al., 2013), and is becoming more widespread in the literature (e.g., Mathewson et al., 2015; Breska and Deouell, 2017).

2.5. Statistical analyses

EEG data were averaged in 9 regions: left frontal (Fp1, F3, F7), midline frontal (Fz), right frontal (Fp2, F4, F8), left central (T7, C3), midline central (Cz), right central (T8, C4), left posterior (P7, P3, O1), midline posterior (Pz) and right posterior (P8, P4, O2) for each Group (Young, Older) and Condition (EO, EC). EEG amplitudes in these nine topographic regions were analysed separately for each band. Each analysis included a Sagittal factor and a Lateral factor (i.e., a four-way mixed MANOVA was used: Group $\times$ Condition $\times$ Sagittal $\times$ Lateral), with repeated measures on the last three factors. The Sagittal factor included planned contrasts that compared the frontal regions (F) with the posterior regions (P), and the central regions (C) with the mean of the frontal and posterior regions (F/P). The Lateral

factor included planned contrasts that compared activity in the left hemisphere (L) with the right (R), and the midline region (M) with the mean of the two hemispheres (L/R). These contrasts and their interactions allow precise identification of all possible topographic patterns over the nine regions, and provide a systematic analysis that optimises the MANOVA approach (O'Brien and Kaiser, 1985). As all contrasts were planned independently of the data, and there were no more of them than the degrees of freedom for effect, Bonferroni-type adjustments of α were not required (Tabachnick and Fidell, 2013). Unless otherwise stated, all F tests have (1, 38) degrees of freedom, and effects approaching significance ($.05 \leq p < .10$) are reported but not discussed.

From our perspective that global alpha is an inverse measure of arousal, and that the major effect of opening the eyes is to increase cortical arousal, the EC to EO change in alpha at each electrode should be correlated with its EC resting value. Topographic variation in the changes in other bands, previously interpreted as focal changes in brain activity associated with visual processing, should result in smaller correlations. To examine this we computed Pearson correlations of the within-group means across subjects at each site, using scatterplots with trend lines for illustration.

3. Results

3.1. Overall spectral distribution

The numbers of accepted epochs for the Young group ranged from 75 to 90 ($M = 86.2$, $SD = 4.8$) in EC, and 79 to 90 ($M = 88.3$, $SD = 3.4$) in EO; corresponding numbers in the Older group ranged from 84 to 90 ($M = 89.5$, $SD = 1.4$) for EC and 69 to 90 ($M = 87.8$, $SD = 5.6$) for EO. Because there were significantly more EC epochs in the Older than Young group (t -test for unequal variances: $t = -2.9$, two-tailed $p = .008$), the numbers of accepted Go and NoGo epochs were added as covariates in the MANOVAs described in section 2.5. The spectral distributions at Fz, Cz, Pz, and the mean across O1 and O2, are shown for each group

in Figure 2, with 95 % Confidence Intervals indicated by the error bars. Amplitudes as a function of frequency are shown for EC on the left and EO on the right. Band limits are indicated at Cz for EC activity. The mean weighted peak alpha frequency for each group and condition is shown on the O1/O2 spectra. Generally speaking, the young group shows more activity than the older group in delta, theta, and alpha; the reverse is apparent for beta. It can be seen that the age difference is significant in different bands at different electrodes, but this single-electrode perspective is relatively underpowered compared with the planned topographic analyses. The peak alpha frequency was higher for Young ($M = 9.68$, $SD = 0.64$ Hz) than Older ($M = 9.18$, $SD = 0.81$ Hz) participants ($F = 7.97$, $p = .008$, $\eta_p^2 = .17$), but did not differ with hemisphere or Condition; there were no interactions.

Fig. 2 about here

3.2. Delta

Figure 3 (top left) shows that across Group and Condition, delta was dominant in the midline ($M > L/R$: $F = 356.95$, $p < .001$) and right hemisphere ($L < R$: $F = 13.28$, $p < .001$), with a vertex maximum ($C > F/P \times M > L/R$: $F = 59.56$, $p < .001$; see Table 1 for the full statistics including effect size. To save space, statistics for the following contrasts are provided only in Table 1. In delta, the regression over covariates was significant for Condition and Group. The headmaps of the top row show that across Group delta activity was reduced in EO relative to EC conditions, more so in the posterior region, particularly hemispherically, less so centrally, and somewhat more so in the right hemisphere, particularly centrally (see top right headmap). Across Condition, the left column of Figure 3 shows that there was a significant global delta reduction in older compared to young adults, more so in the midline and posterior regions, and in the posterior hemispheres, and somewhat so in the right hemisphere and at the vertex (see bottom left headmap). The reduced delta in older than young adults was significantly greater for EC than EO in frontoparietal regions, as is apparent

in the bottom row of Figure 3; that is, the older (cf. young) adults showed substantial frontoparietal focal delta activity with opening of the eyes (see bottom right headmap).

Table 1 and Fig. 3 about here

3.3. Theta

The mean headmap over Group and Condition (top left, Figure 4) shows that theta was dominant in the midline, particularly at the vertex, in the right hemisphere, and in the posterior region, more so hemispherically (also see Table 1). In theta, the regression over covariates was nonsignificant for both Condition and Group. The headmaps in Figure 4 (top row) show that across Group there was significantly less theta activity globally in EO than EC conditions, particularly in the posterior (more so on the right) and midline regions (particularly at the vertex), but less so centrally and in the left hemisphere (see top right headmap). Across Condition, the older adults had relatively less theta globally when compared to the young (left row, Figure 4), somewhat more so posteriorly, and significantly so in the midline (more so frontally) and right hemisphere (more so posteriorly). As apparent in the bottom row of Figure 4, the relative reduction in theta activity in older (cf. young) adults was somewhat less in EO compared with EC in the right hemisphere, and significantly more so in the posterior region, particularly on the right. That is, the older (cf. young) adults showed substantial parietal focal theta activity with opening of the eyes (see bottom right headmap).

Fig. 4 about here

3.4. Alpha

As shown in Figure 5 (top left), mean alpha across Group and Condition was strongly posterior (note the relative central reduction in Table 1), and midline dominant (particularly centrally) with a right hemisphere bias; the posterior dominance was enhanced in the right hemisphere and reduced in the midline (see Table 1). In alpha, the regression over covariates

was significant for Condition, but not Group. Across Group, the top row of Figure 5 shows significant alpha reductions in EO cf. EC. This decrease was larger posteriorly, somewhat more so in the hemispheres, and particularly so on the right, and in the midline and right hemispheric regions, but was reduced across the central region, particularly in the hemispheres (see top right headmap). The bottom left headmap of Figure 5 shows that, across Condition, the older adults had somewhat less alpha globally compared to the young adults; significant reductions were found in the right hemisphere and posterior region (particularly in the hemispheres), and in the posterior right region, but smaller reductions were seen centrally. Also apparent in the bottom row of Figure 5, the older (cf. young) reduction in alpha activity was somewhat reduced globally in EO compared with EC, and significantly so in posterior and posterior hemispheric regions; and less so in central and central hemispheric regions. The topography of this reactivity is similar to the EC alpha.

Fig. 5 about here

3.5. Beta

The top left headmap of Figure 6 shows that the mean beta, over Group and Condition, was centroparietal (note the dual underlining of effect and statistic in Table 1; see table notes), and midline with a right hemispheric bias. These effects interacted differently, with the central enhancement larger in the midline (vertex maximum) and the posterior dominance greater in the hemispheres (see Table 1). In beta, the regression over covariates was significant for Condition, but not Group. Across Group, the top right headmap of Figure 6 shows significant beta reductions in EO relative to EC conditions globally, but also particularly in the midline and posterior regions, and in the posterior hemispheres. Across Condition (left column headmaps), there was significantly more beta globally in older than young adults (again note the underlining in Table 1), somewhat more so in the left hemisphere and parietal left region, and significantly so frontocentrally and in the frontal

hemispheres, as seen in the bottom left headmap. As is apparent in the bottom row of Figure 6, the greater beta activity in older than young adults was significantly greater in EO compared with EC in the posterior region and reduced in the central region (see bottom right headmap). That is, the older (cf. young) adults showed significant parietal focal beta activity with opening of the eyes.

Fig. 6 about here

3.6. Alpha and arousal

Figure 7 shows scatterplots of the EC to EO reduction (i.e., reactivity) in mean EEG band amplitude at each electrode as a function of its EC value, with each point representing one electrode, in either the Young or Older group. A regression line through the origin tests the hypothesis that the reactivity is proportional to the EC amplitude at each electrode. Over both groups, correlations over electrodes ranged from $r(36) = -.41$ for beta to $r(36) = -.88$ for alpha; all were significant ($p < .01$; one-tailed). However, the correlations for delta, theta, and beta were significantly smaller than for alpha ($N = 38$, $Z \geq 1.86$, $p < .05$; one-tailed). Within alpha, although the correlation was somewhat smaller for the Older ($r(17) = -.83$) than the Young group ($r(17) = -.91$), these values did not differ significantly ($N = 19$, $Z = 0.99$, $p = .16$; one-tailed).

Fig. 7 about here

4. Discussion

Across groups, the topographies of the band *amplitudes* used here are broadly consistent with the *power* data in EC and EO resting conditions reported by Barry et al. (2007, 2009a). All bands are midline dominant, with a right hemisphere elevation. This right hemisphere elevation is associated with a lower level of cortical activation, particularly in alpha (Barry et al., 2007), and is expected from the left hemisphere dominance of the right-

handed participants. The Young data are similar to our previous results from a separate university sample comparable in age (Barry et al., 2007), recorded with a different system some 10 years earlier, showing more posterior distributions in the upper than lower bands.

4.1. Main and topographic effects of age

In general, the Older group had smaller amplitudes than the Young group in resting delta and theta, somewhat so in alpha, with larger amplitudes in beta. These main findings are compatible with Duffy et al. (1984) and Polich (1997), with the frequency transition from marked slow wave reductions, through small alpha reductions, to the increase in beta activity. They contradict a report by Breslau et al. (1989) who found a reduction in all bands in resting (EC) and alert (EO, listening to a story) EEGs in their old (mean age 70) compared with a young (mean age 23) control group. Reduced beta in the elderly has been associated with cognitive impairment and reduced general health (Dustman et al., 1993), and the beta elevation here supports the independent living and functioning status of our Older adult group.

Topographically, the Older (cf. Young) group had reduced delta in the midline and posterior region, particularly in the posterior hemispheres. They also had reduced theta activity in the midline, particularly frontally, and in the right hemisphere, particularly posteriorly, generally confirming and extending the reduced resting-state EO theta previously reported in healthy cognitive ageing (Cummins and Finnigan, 2007). The significant reduction in alpha activity in the older group was prominent in the posterior region, particularly on the right. In contrast, the beta activity increase in the older group was significantly larger in frontocentral areas and the frontal hemispheres. These novel topographic findings confirm the value of full-cap data analysis in ageing studies.

Our finding of reduced alpha frequency in the Older group is also broadly consistent with the Dustman et al. (1993) review. Note that this is a relatively small effect (Giaquinto

and Nolfi, 1986; Polich, 1997), and thus may not be apparent with few epochs or poor frequency resolution, such as in many early studies.

4.2. Changes with EC/EO

Across groups, the EO (cf. EC) condition was associated with reduced EEG amplitude in each band, as similarly reported in young adults by Barry et al. (2007) and in children by Barry et al. (2009a) using power measures. The reductions were larger in the posterior region for each band. In delta and theta, the difference in topography of the reactive change compared with the EC baseline condition indicates a substantial contribution of focal activity reflecting regional visual processing. The posterior alpha reduction in EO compared to EC generally reflected the EC alpha topography, suggesting mainly an arousal change. The beta reduction was also notable in the midline region, and there was some frontal increase.

These reductions in EEG band activity from EC to EO conditions differed with age. In delta and theta, the reactivity was smaller in the Older than Young group; particularly in delta in non-central sites, and in theta in posterior sites. These slow wave reductions did not match the EC topography in either group. In alpha, reductions were similar to the EC topography, and somewhat smaller globally in the Older group, as in Könönen and Partanen (1993), and particularly so in posterior regions, echoing Duffy et al. (1984). The beta reactivity change was smaller in the Older group in the non-central sites, quite different from the EC topography. That is, the EEG reactivity associated with opening the eyes was smaller in our Older adult group, suggesting a general reduction of EEG reactivity with healthy ageing. There was also a significant shift from the arousal reactivity shown in beta by the Young group to more focal processing in the Older group, suggesting activation of differential processing.

4.3. Global alpha decrease marks arousal change

With opening the eyes, the decrease in alpha at each electrode was highly correlated

with the EC amplitude at that electrode. This indicates that the reactivity in alpha was global across the scalp, supporting the conceptualisation of the change in alpha as largely an arousal increase, perhaps reflecting the uncoupling of extensive thalamocortical interactions supporting visual processing (Gevins et al., 1997; Klimesch, 1999). This effect was significantly stronger for alpha than the other bands, confirming the unique alpha/arousal nexus in contrast to the more-focal changes in the other bands (Barry et al., 2007). Decreased localised delta and theta are generally associated with stimulus processing, and hence indicate increased activation in the EO condition associated with unstructured visual processing of the immediate environment in the absence of a given task. Studies from our laboratory have previously demonstrated this connection in children (Barry et al., 2009a) and young adults (Barry et al., 2007). The present study thus confirms the nature of this effect in young adults, and extends it to well-functioning older adults, suggesting that this interpretation of the effect of eyes-opening on alpha is of considerable generality across the lifespan. Interestingly, this link between the EC to EO change and the EC amplitude at each electrode was somewhat weaker in the Older than Young group, but not significantly so. This may suggest that the alpha/arousal nexus reduces somewhat with increasing age, a possibility worth exploring in future studies. We have also recently reported age-related changes in task related processing, as indexed by ERPs, in this sample of participants (Barry et al., 2016). The role of arousal/activational differences in such performance changes with normal ageing is of interest, and future investigations may therefore benefit by assessing if the relationships between the ongoing EEG and ERP outcomes (e.g., *EEG phase effects*: Barry et al., 2004b, 2014; *EEG amplitude effects*: De Blasio et al., 2013) remain stable across the lifespan. Such aspects of event-related EEG dynamics (for reviews see Palva and Palva, 2007, 2011) may offer alternative insights into the EEG of ageing than can be explored here.

4.4. Older adults maintain arousal and activation

Volf and Gluhik (2011) have speculated that age-related changes in “background” or resting EEG activity provide the context for compensatory mechanisms in ageing “which may be somehow related to both mobilization of larger resources ensuring cognitive activity and reorganization of cortical networks in the areas prone to age-related physiological changes” (p. 566). Interestingly, Deiber et al. (2013) have similarly linked such EEG topographic shifts in different bands during *active* cognitive tasks to the possible engagement of circuits at different frequencies during attention. Also, reduced task-related beta has been linked to poorer task performance (Gola et al., 2012), and Gola et al. (2013) related such beta reductions to difficulty in activation and deficits in sustained attention. Here, the focal posterior reduction and frontal-right increase in beta activity with the EC to EO transition can be interpreted as indicating focal processing changes additional to those shown by the Young group. That is, the general age differences interpreted in light of the arousal/activation thesis suggest that the older adults generally maintain reactivity to environmental change, with the addition of further processing resources, even in resting conditions. This may contribute to healthy/high functioning older individuals being able to match task performance (including everyday general functioning) of young persons. However, here we examined only resting conditions, so this novel hypothesis must remain tentative.

4.5. Limitations

Although matched on size and sex by the Young group, the Older group size was small and not balanced on sex, being a convenience sample from the retirement community. It has long been established that sex differences in EEG profiles occur throughout the lifespan (Langrová et al., 2012; Wada et al., 1994), and exploring such differences in ageing could be instructive. Larger groups, balanced and matched on sex, would also improve the generalisability of the findings. Further, while the present older participants were screened to avoid the problems of mild cognitive impairment, the inclusion in future studies of a wider

range of neuropsychological assessment instruments for both the older and young participants, and/or the incorporation of these and other populations with pathological ageing, would refine the information available.

In addition, motivational aspects could differ between the young student volunteers and the older volunteer group. Although such differences would be expected to impact task performance rather than resting EEG measures, future studies should attempt to estimate motivation levels and utilise these for better control.

4.6. Conclusion

This study provides useful information in relation to establishing the EEG profile of healthy ageing, and how it is affected by the simple manipulation of opening the eyes. This resting state study generated a wealth of new information in regard to the amplitude and topography of the traditional EEG bands, and their changes from young adults to healthy older volunteers. We suggest that healthy older adults, compared with young adults, maintain reactivity of their energetics system(s) and harness additional focal brain activity, even in resting conditions, and that this may provide the basis for their maintenance of perceptual and cognitive performance in later years (Barry et al., 2016). As these data do not require a task, they can be recorded with little difficulty from populations with mild cognitive impairment and dementia, and may provide valuable insight into the arousal, activation, and task-specific brain contribution to pathological ageing. Indeed, it is likely that many clinics already have these data at hand, and due to the ease of analysis we encourage their exploration in this context. Replication and elaboration of the present findings in older samples, including both healthy and cognitively-impaired participants, could eventually provide a simple clinical screening tool useful in clarifying the onset of mild cognitive impairment, and help early detection of the dementias that plague old age.

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Figure 1. *Arousal* and *activation* are separable aspects of the energetics dimension. Arousal is the energy level of a particular state, such as shown here for a baseline and task. The change in arousal level due to an increase in processing demands is the activation due to that task or increased processing state. These energetics levels can be measured directly by SCL or (inversely) by alpha band activity. Activation may or may not be accompanied by focal changes in EEG bands marking the utilisation of processing-specific brain regions.

Figure 2. Eyes closed (left) and eyes open (right) EEG spectra at the midline sites and the O1/O2 mean for the young and older adult groups. The assessed EEG bands are indicated at Cz for eyes closed, and the vertical lines in the O1/O2 plots indicate the mean peak alpha frequencies for the young (black) and older (grey) adult groups. Error bars indicate 95% Confidence Intervals.

Figure 3. Topographic effects of EC vs. EO for the Young and Older groups in the Delta band. These are available in colour online.

Figure 4. Topographic headmaps for each condition and group in the Theta band. These are available in colour online.

Figure 5. Effects of condition and group on the topography of Alpha amplitude. These are available in colour online.

Figure 6. Topographic effects of condition and group in the Beta band. These are available in colour online.

Figure 7. Scatter plots of the eyes-open (EO) minus eyes-closed (EC) change in mean amplitude (i.e., reactivity) plotted as a function of EC mean amplitude for each electrode for each group, separately for each band. Each point represents one electrode. The linear trend lines are fitted across the groups for each assessed band, with the coefficient of determination, R^2 , shown. Separate correlations for Young and Older groups, r_y and r_o , are also indicated.

Table 1. Topographical, Condition, and Group effects in each assessed EEG band.

Effect	DELTA			THETA			ALPHA			BETA		
	<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2
Topography												
Sagittal												
F < P				17.57	<.001	.32	86.52	<.001	.69	16.07	<.001	.30
C < F/P							11.24	.002	.23	<u>6.19</u>	<u>.017</u>	<u>.14</u>
Lateral												
L < R	13.28	<.001	.26	8.70	.005	.19	15.87	<.001	.29	4.36	.044	.10
M > L/R	356.95	<.001	.90	258.09	<.001	.87	147.58	<.001	.80	49.99	<.001	.57
Sagittal × Lateral												
F < P × L < R							7.25	.010	.16			
F < P × M < L/R				36.41	<.001	.49	4.95	.032	.12	4.37	.043	.10
C > F/P × M > L/R	59.56	<.001	.61	50.49	<.001	.57	6.94	.012	.15	20.27	<.001	.35
Condition												
Regression [†]	13.14	.001	.26				9.55	.004	.21	8.69	.006	.19
EC > EO [†]	5.45	.025	.13	55.65	<.001	.60	142.25	<.001	.79	29.21	<.001	.44
Condition × Topography												
EC > EO × F < P	7.06	.011	.16	43.68	<.001	.53	63.45	<.001	.63	69.79	<.001	.65
EC > EO × C < F/P	6.14	.018	.14	8.93	.005	.19	38.66	<.001	.50			
EC > EO × L < R	3.70	.062	.09	7.94	.008	.17	9.88	.003	.21			
EC > EO × M > L/R				28.94	<.001	.43	42.31	<.001	.53	98.11	<.001	.72
EC > EO × F < P × L < R				10.26	.003	.21	6.19	.017	.14			
EC > EO × F < P × M < L/R	5.20	.028	.12				3.57	.066	.09	31.21	<.001	.45
EC > EO × C > F/P × L < R	4.03	.052	.10									
EC > EO × C > F/P × M > L/R				6.19	.017	.14	23.99	<.001	.39			
Group												
Regression [†]	14.18	.001	.28									
Young > Older [†]	31.23	<.001	.46	9.35	.004	.20	3.69	.062	.09	<u>4.41</u>	<u>.043</u>	<u>.10</u>
Group × Topography												
Young > Older × F < P	7.24	.011	.16	3.80	.059	.09	19.72	<.001	.34	14.16	.001	.27
Young > Older × C < F/P							4.91	.033	.11	11.65	.002	.23
Young > Older × L < R	2.89	.097	.07	5.08	.030	.12	7.56	.009	.17	3.00	.092	.07
Young > Older × M > L/R	10.52	.002	.22	7.42	.010	.16						
Young > Older × F < P × L < R				7.32	.010	.16	5.76	.021	.13	2.99	.092	.07
Young > Older × F < P × M < L/R	6.71	.013	.15	10.72	.002	.22	6.70	.014	.15	6.37	.016	.14
Young > Older × C > F/P × M > L/R	3.32	.076	.08									
Group × Condition												
Young > Older × EC > EO [†]							3.21	.081	.08			
Group × Condition × Topography												
Young > Older × EC > EO × F < P				9.06	.005	.19	11.86	.001	.24	6.10	.018	.14
Young > Older × EC > EO × C < F/P	7.45	.010	.16				4.74	.036	.11	5.62	.023	.13
Young > Older × EC > EO × L < R				4.09	.050	.10						
Young > Older × EC > EO × F < P × L < R				4.92	.033	.11						
Young > Older × EC > EO × F < P × M < L/R							9.43	.004	.20			
Young > Older × EC > EO × C < F/P × M < L/R							7.06	.011	.16			

Note: Underlined statistical results indicate a reversal of the corresponding underlined effect or interaction. The reversal of any pair of directional indicators within a single effect is statistically equivalent; e.g., F < P × M < L/R ≡ F > P × M > L/R. Significant effects are indicated with bold *p* values. EC = Eyes Closed; EO = Eyes Open; F = Frontal; C = Central; P = Parietal; L = Left; M = Midline; R = Right. [†]Denotes tests with (1, 37) degrees of freedom due to covariate.